

Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions

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Summary

Aquatic animals use a variety of strategies to reduce the energetic cost of locomotion. Efficient locomotion is particularly important for breath-holding divers because high levels of exercise may quickly deplete oxygen reserves, leading to the termination of a dive. We investigated the swimming behavior of eight adult Weddell seals, which are proficient divers, in McMurdo Sound, Antarctica. A newly developed data logger was attached to free-ranging females at their own breeding sites to record swimming speed, depth, two-dimensional accelerations (stroke frequency and body angle) and temperature. All seals conducted multiple deep dives (the mean dive depth range for each animal was 223.3±66.5–297.9±164.7 m). Prolonged gliding while descending was observed with thinner females ($N=5$ seals). But the fatter females ($N=3$ seals) exhibited only swim-

and-glide swimming, characterized by intermittent stroking and fluctuating swim speed, throughout their descent and ascent. The body angles of four of the seals were restricted to less than 30° by the location of breathing holes in the ice and the slope of local bathymetric features. Of these four, the three fatter seals adopted the stroke-and-glide method while the other thinner seal descended with prolonged periods of gliding. Prolonged gliding seems to be a more efficient method for locomotion because the surface time between dives of gliding seals was significantly less than that of stroking animals, despite their same stroke frequencies.

Key words: acceleration data logger, body angle, stroke frequency, prolonged glide, stroke-and-glide, Weddell seal, *Leptonychotes weddellii*.

Introduction

Foraging aquatic mammals must divide their time between two important resources: oxygen located at the water surface and prey items located at depth (Dunstone and O'Connor, 1979). Air-breathing animals foraging below the water surface perform a dive cycle comprising three activities: time spent at the water's surface, time spent foraging at depth, and time spent travelling between the two (Wilson and Wilson, 1988; Houston and Carbone, 1992; Carbone and Houston, 1996). Kramer (1988) suggested that natural selection would favor animals that maximize the proportion of time spent in the foraging area. Other theoretical studies assumed that a diver should maximize the proportion of time spent in the foraging area to the entire dive cycle (Kramer, 1988; Wilson and Wilson, 1988; Houston and Carbone, 1992; Carbone and Houston, 1996; Mori, 1998; Thompson and Fedak, 2001). We focused on total traveling time (descent plus ascent) and the time spent on the water's surface as potential decision variables.

Oxygen stores are depleted through metabolic processes in the locomotory muscles. Therefore, efficient locomotion is important for air-breathing divers (Skrovan et al., 1999). When submerged, they must balance the energetic demands of movement with the conservation of a limited oxygen store (Castellini et al., 1985; Skrovan et al., 1999). High levels of exercise will presumably lead to the termination of a dive as oxygen reserves are quickly depleted (Skrovan et al., 1999). Aquatic animals use a variety of strategies to reduce the cost of locomotion. For example, burst-and-glide swimming in fishes promotes energy conservation (Weihs, 1974; Fish et al., 1991). Williams et al. (2000) demonstrated that prolonged gliding in Weddell seals affected their recovery oxygen consumption at the sea surface between dives. They monitored a seal's flipper movements using a backward-looking video system, mounted on the seal's back, and a tail-mounted accelerometer. However, these observations were of seals translocated to an isolated hole drilled through sea ice over

deep water and away from any existing breeding colonies (Davis et al., 1999).

Using acceleration data loggers, Yoda et al. (2001) developed a new technique for monitoring the behavior of free-ranging penguins. They showed that an acceleration profile could be used for detecting fine-scale movements (lying, standing, walking, tobogganing, diving, resting at the water surface and porpoising). Similarly, Tanaka et al. (2001) described the tail movements and body angle of chum salmon *Oncorhynchus keta*. We monitored the flipper movements and body angle of free-ranging Weddell seals *Leptonychotes weddellii* at their own breeding sites using small data loggers that can record swimming speed, depth, two-dimensional (2-D) accelerations (flipper movements and body angle) and temperature. Acceleration data were used to define different swimming strategies and their pattern of use. Changes in swimming behaviors are discussed with respect to optimal stroking patterns according to individual and geographic conditions.

Materials and methods

Field experiments

Experiments were conducted using lactating Weddell seal *Leptonychotes weddellii* (Lesson) females with live pups from November 10 to December 12, 2000, at Big Razorback Island (77.68°S, 166.50°E) and Turks Head (77.67°S, 166.78°E) in the region of McMurdo Sound, Ross Island, Antarctica (Fig. 1A). Both breeding sites are covered by fast ice during the breeding season. Tidal cracks or holes drilled through the sea ice facilitated the use of a depth gauge (type-8, Tsurumi Seiki Co., Ltd, Tsurumi, Japan) to measure the bathymetry of each study site. Weddell seals use naturally occurring cracks to enter the water from the surface of the sea ice. At Big Razorback Island, these cracks are oriented close and parallel to the coastline of the island. As such, to reach deep water, seals must swim at a relatively shallow angle (approx. 30°) and follow the slope of the island (Fig. 1B). In contrast, the primary crack at Turks Head is perpendicular to the coastline and over deep water. Additionally, the underwater slope is much steeper than at Big Razorback Island and seals along this crack may dive vertically to reach deeper depths (Fig. 1C). The females were anesthetized using the inhalant Sevoflurane (Kusagaya and Sato, 2001), and a quick-setting epoxy resin (Evercoat Ten-Set; Fibre Grass-Evercoat, Cincinnati, USA) was used to attach acceleration data loggers to their dorsal pelage. The data loggers were attached to four seals at Big Razorback Island and to four seals at Turks Head, and were retrieved the following day. The remaining adhesive fell off with the pelage at molt.

Index of fatness

The proportion of positively buoyant tissues, such as blubber, to other tissues, such as bone and muscle, influences a seal's body composition and overall buoyancy. Crocker et al. (1997) and Beck et al. (2000) suspected that these factors

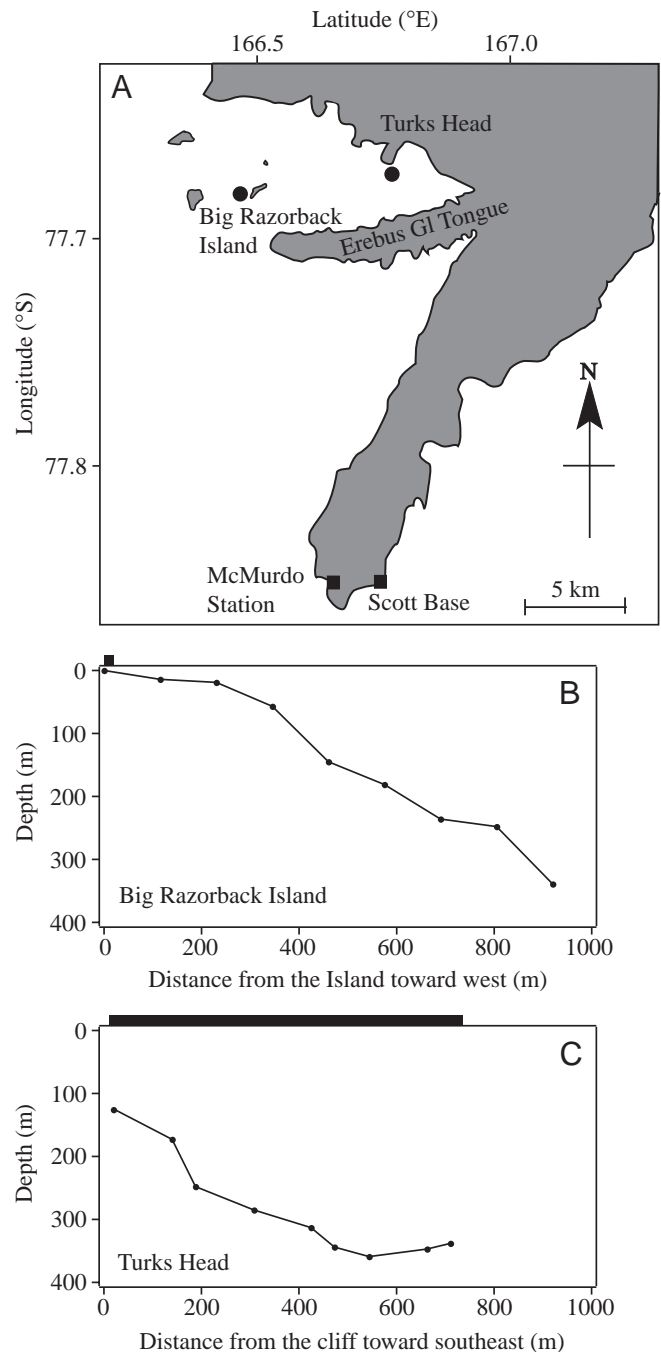


Fig. 1. (A) Study sites (closed circles) near McMurdo Station, Antarctica. Land and the ice tongue are represented by gray color. The sea (white) was covered by fast ice during the study period. (B) The bathymetry of Big Razorback Island and (C) Turks Head. The location of ice holes and tidal cracks are shown by black horizontal bars (B,C).

could affect the diving behaviors of northern elephant seals *Mirounga angustirostris* and grey seals *Halichoerus grypus*. Suspecting that buoyancy may similarly affect diving Weddell seals, we employed Stirling's 'index of fatness' (calculated as axillary girth/standard length) (Stirling, 1971) to quantify the body condition of each instrumented female. Using data

Table 1. Study sites, morphological information and summary diving statistics for study animals

Seal	Index of fatness	Fatness category ^a	Number of deep ^b dives	Primary descent swimming behavior ^c	Dive depth (m)	Dive duration (min)	Descent+ Ascent time (min)	Bottom time (min)	Post-surface time (min)	Body angle in descent ^d and ascent (degrees)
Big Razorback Island										
Sarah	0.87	Fatter	7	Stroke-and-glide	297.9±164.7 (403.8)	19.1±11.3 (26.7)	12.0±6.6	7.1±5.0	7.7±3.5	26.6±2.5 (29.2)
Mumin	0.87	Fatter	12	Stroke-and-glide	232.9±80.4 (290.3)	16.7±6.4 (22.1)	9.9±3.3	6.8±3.5	7.1±4.6	27.4±1.4 (29.5)
Emmalian	0.78	Fatter	23	Stroke-and-glide	248.6±111.2 (405.8)	18.1±5.7 (25.2)	10.4±3.9	7.7±4.2	6.3±3.0	24.7±4.2 (30.1)
Jumbo	0.75	Thinner	29	Prolonged glide	247.7±42.0 (293.3)	18.2±4.3 (29.4)	9.9±3.7	8.3±4.0	3.8±1.5	25.3±6.1 (40.5)
Turks Head										
Windy	0.72	Thinner	29	Prolonged glide	243.8±139.9 (398.8)	13.2±9.4 (25.3)	6.1±3.3	7.0±6.3	2.5±2.5	44.8±10.1 (66.5)
Andrea	0.69	Thinner	7	Prolonged glide	223.3±66.5 (328.5)	12.8±4.1 (16.6)	8.8±4.2	4.0±3.1	2.3±1.6	28.4±12.1 (53.8)
Mina	0.74	Thinner	30	Prolonged glide	271.8±82.3 (364.0)	13.8±4.7 (20.2)	6.5±2.2	7.3±3.0	2.5±1.2	46.0±10.8 (66.4)
Hiroko	0.71	Thinner	42	Prolonged glide	237.1±96.1 (391.5)	15.6±7.5 (27.2)	8.4±3.9	7.2±4.6	4.1±2.7	No data
<i>P</i> value ^e					0.10	<0.01	<0.0001	0.49	<0.0001	<0.0001

Values are means ± s.d.; maximum values are given in parentheses.

^aThe population mean of 0.78 (Sato et al., 2002a) was used as the category boundary.

^bDives deeper than 50 m were used for analysis.

^cSee text for definitions.

^dAbsolute angle in descent was used for calculation.

^eKruskal–Wallis test was used.

Dive depth, the maximum depth of the dive; dive duration, the time elapsed between the start and end of the dive; bottom time, the duration from the first ascent to last descent in each dive.

reported by Fujise et al. (1985) on the external measurements and organ masses of five Weddell seals collected at Syowa Station, we calculated the linear regression:

$$P_B = -22.5 + 67.4I_F, \quad (1)$$

where P_B is percentage, by mass, of total blubber in body composition (%) and I_F is index of fatness. The regression was significant ($r^2=0.959$, $N=5$, $F=70.790$, $P<0.01$), indicating that Stirling’s index of fatness was a good estimate of body composition. The mean I_F of lactating females in McMurdo Sound, in 2000, was 0.78 ± 0.7 , range 0.68–0.92 (Sato et al., 2002a). Using this average as a boundary, three (‘Sarah’, ‘Mumin’ and ‘Emmalian’) of the seals in the present study were categorized as fatter seals, and the others (‘Jumbo’, ‘Windy’, ‘Andrea’, ‘Mina’ and ‘Hiroko’) were categorized as thinner seals (Table 1).

Multi-sensor data logger

A multi-sensor data logger (UWE1000-PD2GT: 22 mm diameter, 124 mm length; 80 g in air; Little Leonardo Corp., Tokyo, Japan) was used to record swimming speed and depth at 1 s intervals, 2-D accelerations (for determining flipper movement and body angle) at 1/16 s intervals, and temperature at 30 s intervals. The cross-sectional area of the instrument was less than 0.2% of the maximal cross-sectional area of an adult Weddell seal and, therefore, we felt that any influence on swimming behavior would be minimal (Wilson et al., 1986). The logger uses a two-axis acceleration sensor (Model ADXL210, Analog Devices, Inc., Norwood, USA). The sensor can measure both dynamic acceleration (such as propulsive

Table 2. Summary of methodological data

Seal	Swimming speed (m s ⁻¹) calibration line	Correlation coefficient	Adjustment angle, mean ± s.d. (degrees)
Sarah	0.06+0.07 R(i)	0.961	13.3±0.7
Mumin	0.12+0.07 R(i)	0.951	2.2±0.1
Emmalian	0.14+0.07 R(i)	0.944	3.3±0.5
Jumbo	0.09+0.07 R(i)	0.969	13.2±0.9
Windy	0.09+0.11 R(i)	0.970	9.1±1.5
Andrea	0.01+0.08 R(i)	0.979	10.3±2.9
Mina	0.07+0.06 R(i)	0.972	6.8±1.0
Hiroko	No data		No data

See text for an explanation. R(i), number of propeller rotations per second.

activities) and static acceleration (such as gravity), allowing it to be used as a tilt sensor. The measuring range of the accelerometer is ± 49 m s⁻² with a resolution of 0.02 m s⁻². However, the sensitivity of the sensor can be affected by thermal changes. The temperature was therefore simultaneously recorded to allow for *post-hoc* data corrections. This was unnecessary, however, as the ambient saltwater temperature remained constant at -1.8°C for the duration of the experiment.

Swimming speed was calculated using the rotation (revs s⁻¹) of an external propeller. However, the flow of water across the propeller may also vary with the location of the instrument or the girth of the seal. Therefore, the rotation value was converted to actual swimming speed (m s⁻¹) using a calibration

line that was estimated for each animal. The calibration line was created from a linear regression of revs s^{-1} against a second independent method of calculating swimming speed. Information on the body angle (from an acceleration sensor along the longitudinal axis of the seal) and vertical speed (as determined from the depth recorder) provided us with an independent estimate of the actual swimming speed. For example, an animal with a vertical speed of 1.3 m s^{-1} and a body angle of 60° would have a true swimming speed of 1.5 m s^{-1} (i.e. $1.3 \text{ m s}^{-1}/\sin 60$). This second method is only reliable for steeper body angles, however, and as such it was

not used as the primary method of determining swimming speed. Calibration lines were obtained from each animal with correlation coefficients higher than 0.944 (Table 2). The propeller of one seal did not rotate well and was not used (Table 2). Rotation values of revs s^{-1} were not converted to swimming speed when they were lower than the stall revs s^{-1} of the logger, determined experimentally to be 0.3 m s^{-1} .

The maximum range of the depth sensor was 1000 m, with a resolution of 0.24 m. The beginning or end of a dive was considered to be the moment when depth was greater than, or less than, 2 m, respectively. Dive duration was defined as the time elapsed between the start and end of the dive. Dive depth was defined as the maximum depth of the dive. Bottom time, which was assumed to be the time spent in the foraging area, was defined as the duration from the first ascent to last descent in each dive. According to Kooyman (1968), dive duration is positively related to the number of breaths after the dive rather than the number of breaths before the dive. Therefore, post-surface time was used in analyses of dive recovery time. In these analyses, we only used dives with a maximum depth greater than 50 m. The measuring range of the temperature sensor was -22°C to 50°C , with a resolution of 0.018°C and an accuracy of 0.1°C .

Acceleration data analysis

A preliminary experiment was conducted on a captive male (body mass 76 kg) Larga seal *Phoca largha* in the Minamichita Beachland Aquarium on June 19, 1998. Equipped with a PD2GT logger, the seal was released in an outdoor pool and its behavior was monitored using a video camera (DCR-TRV9, Sony). The resulting acceleration profiles were compared to the visual record, confirming that side-to-side flipper movements could be detected as fluctuations in acceleration along the transverse axis (hereafter referred to as swaying acceleration). Additionally, fluctuations in acceleration along the longitudinal axis (surging acceleration) and the estimated body angle of the seal were consistent (Sato and Naito, 2002).

We attached PD2GT loggers to free-ranging adult female Weddell seals to record their flipper stroke frequencies and body angle. Swaying acceleration often contained low frequency variations that were assumed to be the result of various turning and rolling movements. These variations were separated using a 0.1 Hz highpass filter (IFDL Version 3.1; WaveMetrics, Inc., USA). The remaining peaks and troughs with absolute amplitudes greater than 0.5 m s^{-2} were considered to be strokes and used in analyses. Peak–trough duration or trough–peak duration corresponds to a single flipper stroke (i.e. left-to-right or right-to-left). Flipper stroke frequencies (Hz) during descending and ascending were calculated from the total number of strokes divided by the duration of each phase (ascending and descending) for each dive deeper than 50 m.

The acceleration sensor along the longitudinal body axis of the body measured the surging accelerations,

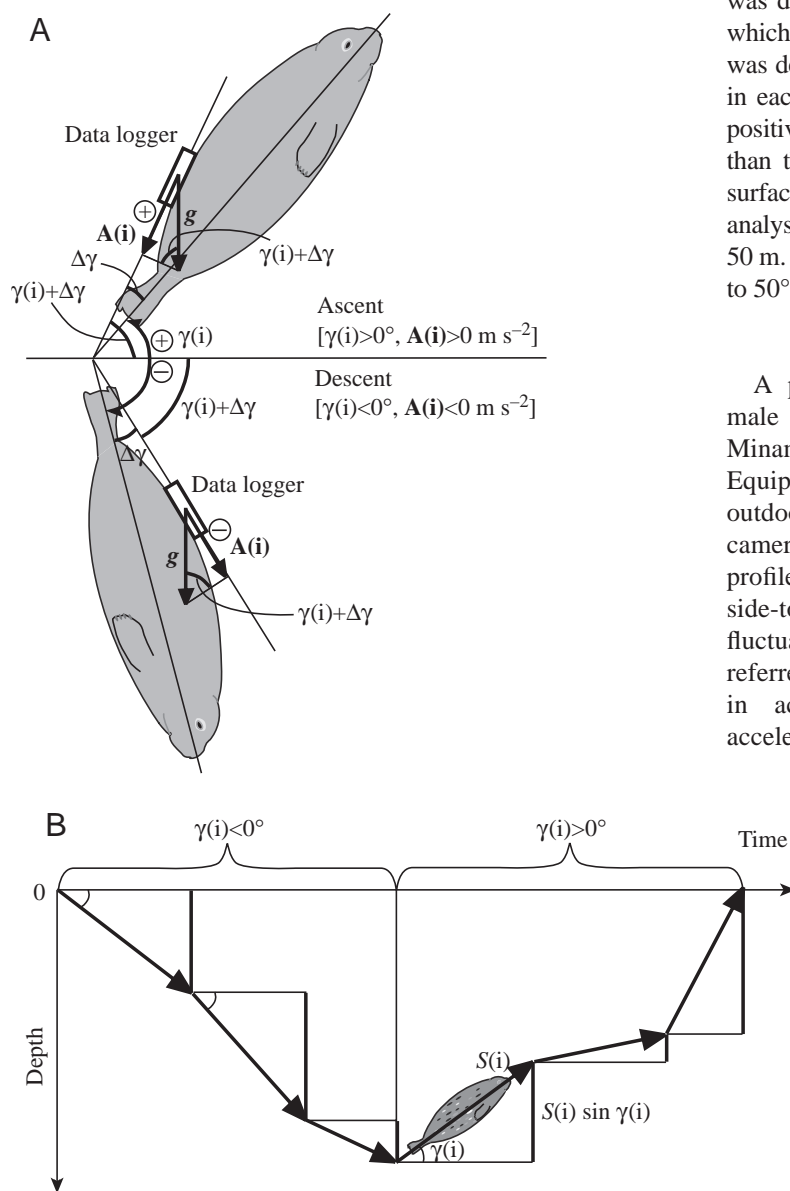


Fig. 2. (A) Schematic diagram showing the direction of surging acceleration $\mathbf{A}(i)$, recorded by a PD2GT logger placed on a seal, and gravity g ($=9.8 \text{ m s}^{-2}$). The angle of the logger is composed of the body angle of a seal $\gamma(i)$ and the adjustment angle $\Delta\gamma$. Descending body angles are represented as negative values. (B) A schematic of a dive profile calculated from swimming speed $S(i)$ and body angle $\gamma(i)$.

which are affected by both the forward movements of the animal and gravity (Yoda et al., 2001; Tanaka et al., 2001). High frequency variations in the surging acceleration record are believed to be caused by flipper movements. These were filtered out using a 0.1 Hz lowpass filter (IFDL Version 3.1; WaveMetrics, Inc., USA). As described by Tanaka et al. (2001), when the animal is still or moving at a constant speed, the gravity vector will change in response to the body angle. Together, these vectors were used to calculate the body angle. Fig. 2A shows the direction of the surging acceleration recorded by a PD2GT logger attached on the back of a seal. A descending seal would have surging accelerations and body angles represented as negative values. Body angles and surging accelerations of ascending seals are positive.

The data logger was attached to the seal's back at the point of maximum girth. But length from the nose to the logger varied from 43% to 63% of the standard length (from the nose to the end of the tail). This distance was decided according to the degree of fatness of each seal, with 'fatter' seals having a relatively longer distance. It was impossible to align the PD2GT logger exactly parallel to the longitudinal axis of a seal. Therefore, it was necessary to calculate this difference as an adjustment angle $\Delta\gamma$ (Fig. 2A). The relationships between surging acceleration $\mathbf{A}(i)$ (m s^{-2}), the acceleration of gravity \mathbf{g} ($=9.8 \text{ m s}^{-2}$), body angle $\gamma(i)$ (degrees) and the adjustment angle $\Delta\gamma$ (degrees) can be expressed by:

$$\frac{\mathbf{A}(i)}{\mathbf{g}} = \sin[\gamma(i) + \Delta\gamma]. \quad (2)$$

$\sin[\gamma(i)]$ may then be expressed using:

$$\sin\gamma(i) = \sin \left\{ \text{asin} \left(\frac{\mathbf{A}(i)}{\mathbf{g}} \right) - \Delta\gamma \right\}. \quad (3)$$

As shown in Fig. 2B, the cumulative value of depth change in a dive (calculated from the swimming speed and body angle), must be zero:

$$\sum_{i=0}^N S(i) \sin[\gamma(i)] = 0, \quad (4)$$

where $S(i)$ is the swimming speed (m s^{-1}). The number of propeller rotations per second $R(i)$, is linearly correlated with the swimming speed:

$$S(i) \propto R(i). \quad (5)$$

Therefore, Equations 3, 4 and 5 give:

$$\sum_{i=0}^N R(i) \sin \left\{ \text{asin} \left(\frac{\mathbf{A}(i)}{\mathbf{g}} \right) - \Delta\gamma \right\} = 0. \quad (6)$$

The adjustment angle $\Delta\gamma$ for a specific dive can therefore be determined through iterative procedures using Equation 6.

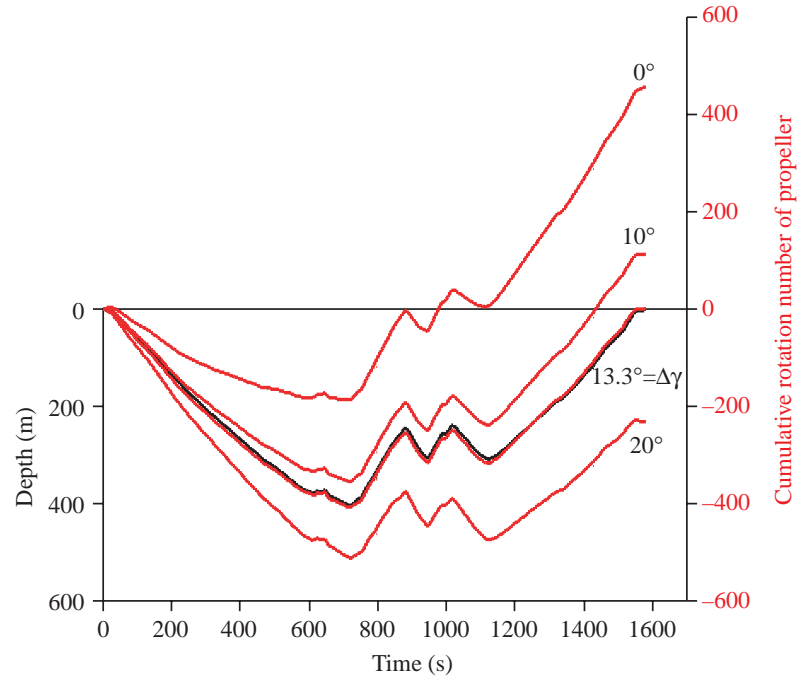


Fig. 3. The comparison between a measured dive profile (black line) and calculated dive profiles (red line) using several adjustment angles $\Delta\gamma$. An adjustment angle of 13.3° is appropriate for this dive.

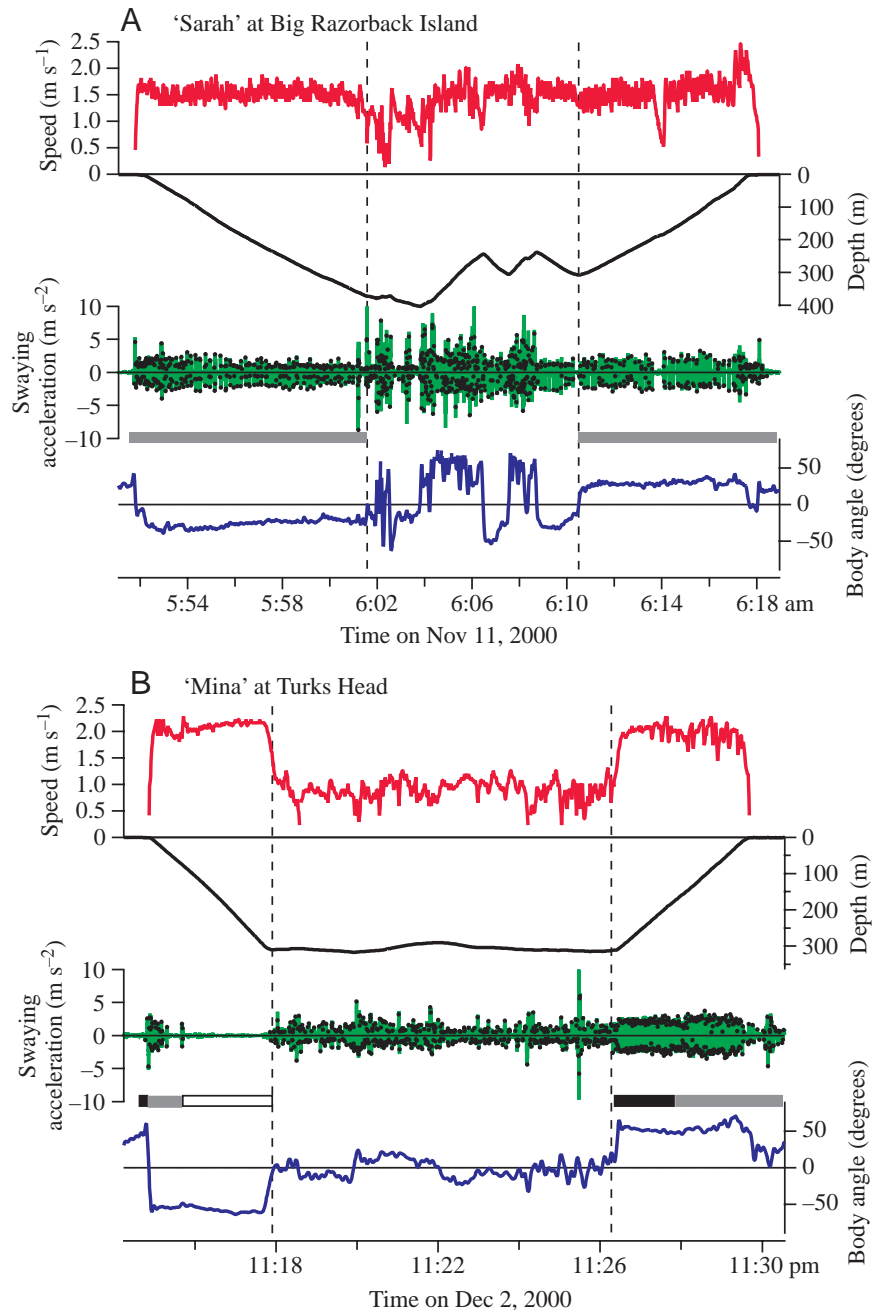
Table 3. A matrix of Spearman rank correlation coefficients among parameters

	Number of dives	Swim speed ($N=84$ dives)	Body angle ($N=137$ dives) ^a	Stroke frequency ($N=179$ dives)
Descent				
Descent time	179	-0.04	-0.584***	-0.081
Swim speed	84		0.591***	-0.668***
Body angle	137 ^a			-0.484***
Ascent				
Ascent time	179	-0.007	-0.347***	-0.354***
Swim speed	84		0.216	0.669***
Body angle	137			0.576***

^aBody angle is negative when descending. The absolute value was used for statistical test.
*** $P < 0.0001$.

Fig. 3 shows the results of one dive calculated using several values for $\Delta\gamma$. This procedure was repeated on five dives for each animal, the mean of which was used as the adjustment angle for the given seal. The mean adjustment angle varied between seals; however, reliable values could be obtained for each seal with small standard deviations (s.d.) (Table 2).

The results are presented as means \pm s.d. Statistical analysis followed Zar (1984). We used StatView (version 5.0) for statistical tests and considered results statistically significant if $P < 0.01$.



Results

Each of the instrumented Weddell seals conducted multiple deep dives. The mean of the maximum depths of dives for each animal ranged from 223.3 ± 66.5 m to 297.9 ± 164.7 m (Table 1); however, there was no significant difference in dive depth between individuals (Kruskal–Wallis test, $P=0.10$; Table 1). Dive duration, travel time (descent time plus ascent time), post-surface time and body angle were significantly different between individuals (Kruskal–Wallis test, $P<0.01$; Table 1), but there was no significant difference in bottom time (Kruskal–Wallis test, $P=0.49$; Table 1). The swimming speed did not significantly affect the descent or ascent time of a dive (Table 3). However, body angle was significantly correlated with descent and ascent times (Table 3), as steeper angles are

Fig. 4. Typical dives at (A) Big Razorback Island, with a gradual slope, and (B) Turks Head, with a steep slope. The x -axis is time, swimming speed is in red, and dive depth is in black; the black dots over the green lines represent strokes recorded as swaying acceleration, and the vertical dashed lines delineate the separation of the dive into three phases: descent, bottom and ascent. Swimming behavior is categorized as continuous stroking (black horizontal bar), stroke-and-glide swimming (grey horizontal bar) and prolonged gliding (open horizontal bar). Blue lines represent the body angle calculated from surging acceleration.

related to shorter travel time. While descending, steeper body angles were related to an increase in swimming speed (Table 3). Additionally, steeper body angles were associated with a reduction in the stroke frequency (Table 3), indicating that Weddell seals choose to glide while descending at steep angles. This explains the counterintuitive result of a negative relationship between stroke frequency and swimming speed while descending (Table 3). By contrast, despite a lack of significant correlation between body angle and swimming speed while ascending (Table 3), steeper body angles were associated with an increase in the stroke frequency (Table 3) and there is a positive relationship between stroke frequency and swimming speed (Table 3).

Comparisons of diving behaviors at both sites revealed that seals at Big Razorback Island (hindered from diving vertically to reach deeper water by the island's more gradual slope) conducted dives with a longer dive duration, a longer travel time, a longer post-surface time (except for Jumbo), and shallower body angles than seals instrumented at Turks Head (where there was

a steeper bathymetric slope) (Fig. 1, Table 1). The data presented in Fig. 4 describe a typical dive at each site. The bottom times of both seals were similar (8.9 min and 8.3 min), but Sarah from Big Razorback Island had a longer travel time (descent time plus ascent time = 16.9 min) than Mina (6.4 min) from Turks Head. Additionally, Sarah's mean descent and ascent body angles were $\pm 30^\circ$, compared to Mina's steeper angles of $\pm 50^\circ$ (Fig. 4).

From the swaying acceleration data, 'Sarah' adopted a stroke-and-glide method throughout her dive (i.e. both descending and ascending) (Figs 4A, 5A). In contrast, Mina's flipper movements were only substantial during the beginning of her descent, gliding from about halfway through her descent until reaching the bottom (Fig. 4B). After continuous stroking

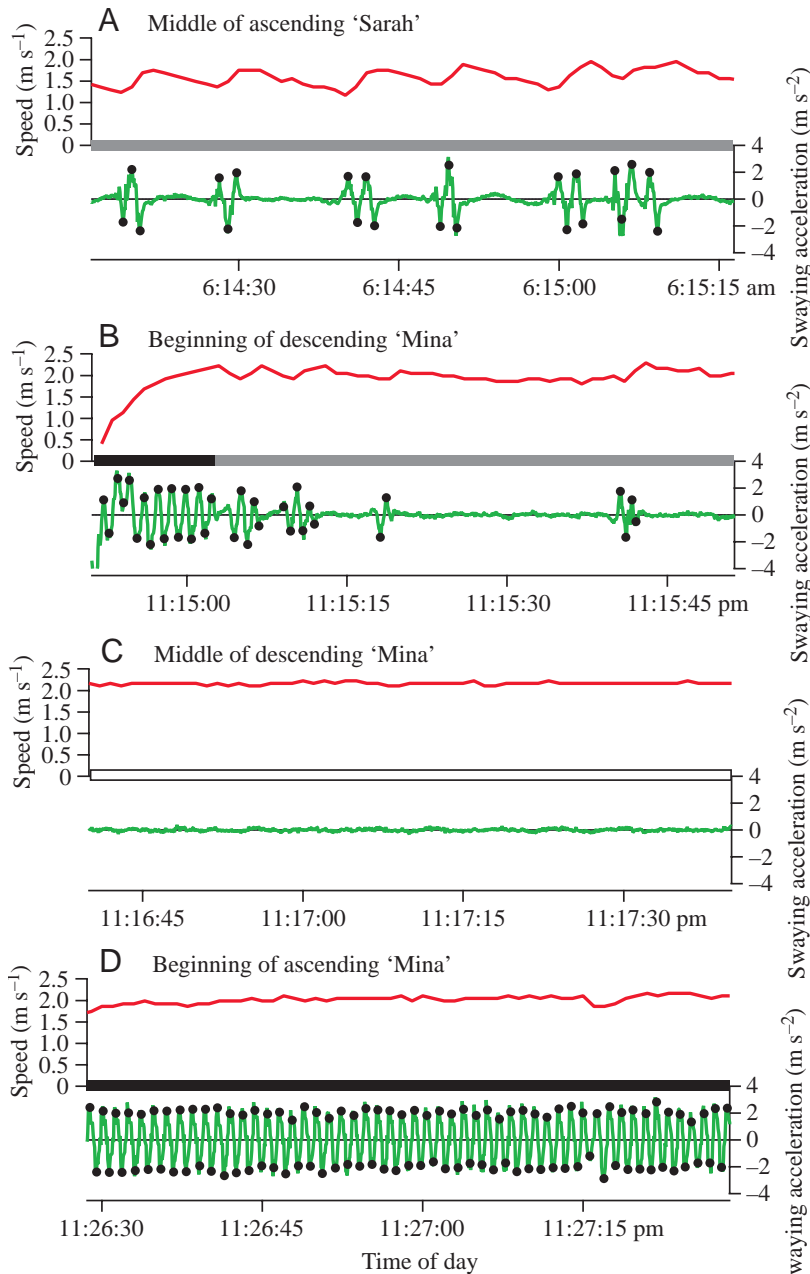


Fig. 5. Typical profiles of swimming speed (red lines), swaying acceleration (green lines), and flipper strokes (black dots) that correspond with stroke-and-glide swimming (grey horizontal bar), prolonged gliding (open horizontal bar) and continuous stroking (black horizontal bar).

ratio (i.e. ascent/descent) < 1 were characterized as stroke-and-glide swimmers, while those with a mean stroke frequency ratio > 1 were characterized as prolonged gliders. Interestingly, the five thinner seals were categorized as prolonged gliders, while the three fatter seals were categorized as stroke-and-glide swimmers (Table 1, Fig. 6). Comparing swimming methods among four seals at Big Razorback Island, where the gradual slope prevents seals from vertical dives, only Jumbo, a thinner seal, was characterized as a prolonged glider. All seals at Turks Head, where seals can dive vertically, adopted a prolonged glide method independent of their body angles.

Table 4 compares the results between stroke-and-glide swimmers and prolonged gliders. During a descent, the stroke frequency of stroke-and-glide swimmers (0.68 ± 0.16 Hz) was greater than that of prolonged gliders (0.30 ± 0.21 Hz), yet prolonged gliders had a faster swimming speed (1.7 ± 0.3 m s⁻¹ versus 1.3 ± 0.2 m s⁻¹). In comparison, the stroke frequency of prolonged gliders during the ascent phase (0.99 ± 0.28 Hz) was greater than that of stroke-and-glide swimmers (0.40 ± 0.20 Hz), and prolonged gliders had a slightly faster swimming speed (1.6 ± 0.3 m s⁻¹ versus 1.5 ± 0.3 m s⁻¹). There was no significant difference in total stroke frequency (descent and ascent) between stroke-and-glide swimmers (0.54 ± 0.23 Hz) and prolonged gliders (0.65 ± 0.43 Hz). The ratio of the post-surface time to dive duration in stroke-and-glide swimmers (0.44 ± 0.25) was significantly larger than that for prolonged gliders (0.29 ± 0.42).

at the beginning of her ascent the remainder was characterized by a stroke-and-glide pattern similar to Sarah's (Fig. 4B). This stroke-and-glide behavior is defined by intermittent strokes and corresponding fluctuations in swimming speed (Fig. 5A,B). Swimming speed either increased or remained constant while stroking continuously (Fig. 5B,D); interestingly, gliding seals also managed to keep their swimming speed constant (Fig. 5C).

There was a significant negative relationship between the mean stroke frequencies during descent and ascent (Spearman rank correlation = -0.427 , $N=179$ dives of eight seals, $P < 0.0001$; Fig. 6), indicating that seals who descended using lower frequency strokes, ascended with higher frequency strokes, and *vice versa*. Seals with a mean stroke frequency

Discussion

Prolonged gliding as a diving behavior of Weddell seals was described by Williams et al. (2000). While some of the seals in our study exhibited prolonged gliding behavior, others did not. Some seals utilized a stroke-and-glide method throughout both the descending and ascending phases of a dive, and swimming behavior (i.e. stroking or gliding) seems to be related to the seal's index of fatness (Table 1). The three fatter Weddell seals in our study were the only ones to adopt a stroke-and-glide swimming method during the descent and ascent (Fig. 6); their stroke frequency during descent was significantly greater than while ascending (Table 4). However, despite this extra effort, swimming speed was actually lower

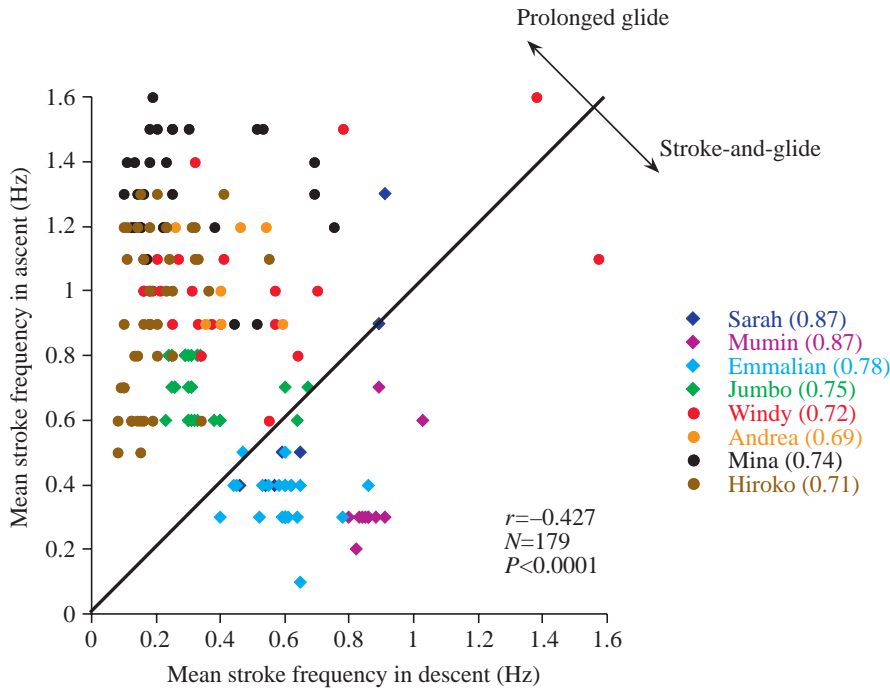


Fig. 6. The relationships between the mean stroke frequencies during descent and ascent. The thick diagonal line, representing identical stroke frequencies in descent and ascent, divides seals into prolonged gliders or stroke-and-glide swimmers. The numbers in parentheses indicate the given seals' fatness index. Note that stroke-and-glide swimmers are the 'fatter' seals. r , Spearman rank correlation.

during the descent phase of a dive (Table 4). In contrast, there was no difference in the ascent or descent swimming speed of prolonged gliders, who primarily stroked while ascending (Table 4). This suggests that fatter seals may be stroke-and-glide swimmers because they must actively work against their overall positive buoyant force (*versus* thinner prolonged-gliders who were negatively buoyant). Likewise, stroke-and-glide swimmers expended less energy than prolonged gliders (measured as stroke frequency) when ascending, as they were assisted by their net positive buoyancy, though apparently not enough to allow them to glide. Supporting the conclusion of Williams et al. (2000), the ratio of post-surface time to dive duration was greater in stroke-and-glide swimmers than in prolonged gliders, despite their same stroke frequencies (Table 4), suggesting that prolonged gliding (which requires less recovery time) is a more efficient method of locomotion. This is further emphasized by Jumbo, the only thinner seal at Big Razorback Island who was also the only prolonged glider at Big Razorback Island. Her post-surface time was much shorter than those of the other three seals at this location, even though each of the four seals had similar dive depths and durations, and the same body angles (Table 1).

For thinner, negatively buoyant seals, body angle should also be important. While descending, steeper body angles would bring the vector of forward motion closer to that of the force of gravity, making it easier to descend. Among the prolonged gliders at Turks Head, the more stout seals, Windy

and Mina, had much steeper body angles (Table 1), presumably enabling them to glide, and this would also decrease the time necessary to reach the bottom. Andrea was the thinnest and also had the most shallow body angle (Table 1), which enabled her to reach further for exploration. Jumbo, despite being a prolonged glider, had a relatively shallow body angle (Table 1); however, she was diving at Big Razorback Island and was restricted from steeper angles by the shape of the slope at that colony (Fig. 1B). Similarly, as each of the three fatter seals were at Big Razorback Island, it is perhaps not surprising that they were all stroke-and-glide swimmers, considering their inability to descend at steep angles. Unfortunately, the two fatter seals instrumented at Turks Head (with $I_F = 0.83$ and 0.81) did not dive deeper than 50 m (Sato et al., 2002a), therefore we could not fully test this hypothesis. Overall, a wide variety of factors including topography, seal morphology and perhaps prey distribution could affect their body angles.

Davis et al. (2001) identified three modes of swimming (prolonged gliding, stroke-and-glide and continuous stroking), based on the interval between strokes. We chose to categorize diving behavior based also on relative swimming speeds because we found transitions between these categories to be gradual. While continuously stroking, swimming speed was constant (Fig. 5D) or accelerated (Fig. 5B), indicating that thrust was equal to or exceeded the drag and any external forces such as gravity or buoyancy. This can be expressed more formally as:

$$\mathbf{T} \geq \mathbf{D}_T + mg \sin \gamma(i) - \mathbf{B} \sin \gamma(i), \quad (7)$$

where \mathbf{T} is thrust force ($\text{m kg}^{-1} \text{s}^{-2}$), \mathbf{D}_T is drag of a stroking seal (m kg s^{-2}), m is the mass of seal (kg), g is the gravity acceleration ($= 9.8 \text{ m s}^{-2}$), $\gamma(i)$ is the seal's body angle (degrees), and \mathbf{B} is the buoyancy (m kg s^{-2}). When descending, $\gamma(i) < 0$ and gravity g contributes to thrust \mathbf{T} ; however, drag \mathbf{D}_T and buoyancy \mathbf{B} act against forward motion. The reverse is then true when ascending ($\gamma(i) > 0$). While stroking-and-gliding, swimming speed fluctuated with each flipper stroke (Fig. 5A,B), accelerating while stroking and decelerating while gliding. This indicates that seals move through the water using both thrust and inertial forces. As such it is not appropriate to define a swimming behavior using only the stroke interval. For example, depending on the stroke frequency interval chosen for a swimming behavior category, a long gliding phase of a stroke-and-glide swimming seal could be mistakenly characterized as prolonged gliding. By also using the relative swimming speed, one would appropriately categorize the behavior as stroke-and-glide. Prolonged gliding is

Table 4. Comparison between stroke-and-glide swimmer (N=3) seals and prolonged glider (N=5) seals

	Stroke-and-glide throughout descent and ascent		Prolonged gliding descent and stroking ascent	
Swim speed in descent (m s^{-1})	1.3±0.2 (1.4)		1.7±0.3 (1.7)) NS
Swim speed in ascent (m s^{-1})	1.5±0.3 (1.5)		1.6±0.3 (1.7)	
Stroke frequency in descent (Hz)	0.68±0.16 (0.62)		0.30±0.21 (0.25)) ***
Stroke frequency in ascent (Hz)	0.40±0.20 (0.36)		0.99±0.28 (0.98)	
Stroke frequency in descent and ascent (Hz)	0.54±0.23 (0.48)	— NS —	0.65±0.43 (0.59)	
Post-surface duration/dive duration	0.44±0.25 (0.36)	— *** —	0.29±0.42 (0.22)	

Values are means ± S.D., median values are given in parentheses.
 Mann-Whitney test was used to test between stroke-and-glide swimmer and prolonged glider.
 Wilcoxon paired-sample test was used to test between descent and ascent.
 * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$. NS, not significant.

characterized as no flipper movement and a constant swimming speed (Fig. 5C), which occurs when the net effect of gravity and buoyancy parallel to the body angle is equal to the drag of the gliding seal D_G :

$$D_G = B \sin \gamma(i) - mg \sin \gamma(i). \quad (8)$$

As such, prolonged gliding of Weddell seals might also be expressed as 'gravity gliding'.

Gravity gliding among diving animals has been reported previously for the Weddell seal, northern elephant seal *Mirounga angustirostris*, bottle nose dolphin *Tursiops truncatus* and the blue whale *Balaenoptera musculus* (Skrovan et al., 1999; Williams et al., 2000), while the corollary, buoyant gliding, has been reported in right whales, a northern elephant seal, penguins and some flying birds (Nowacek et al., 2001; Davis et al., 2001; Sato et al., 2002b; Ross, 1976; Tome and Wrubleski, 1988; Stephenson et al., 1989; Lovvorn, 1994; Watanuki et al., 2003). Buoyant gliding in penguins is accomplished by changing the volume of gas-filled cavities using water pressure. This creates a dynamic buoyancy component that varies with depth and may actually accelerate the swimming speed of some ascending penguins (Sato et al., 2002b). The swimming speed of gravity-gliding Weddell seals did not change with respect to depth (Fig. 4B) because body tissues such as blubber, bone and muscle are less compressible than air. However, in both cases, external net forces such as gravity and buoyancy, are equal to or larger than the drag of gliding animals, enabling them to glide for long periods with a constant or increasing speed.

Finally, a surprising result is that despite the extra effort necessary for seals to reach deep depths at Big Razorback Island (due to the shallow body angles required by bathymetry) *versus* Turks Head, the maximum depth and bottom time of seals at the two colonies were not statistically different

(Table 1). Theoretical studies by Thompson and Fedak (2001) and Mori et al. (2002) predicted a positive correlation between patch quality and patch residence time. If true, differences in prey density (higher at Big Razorback Island) may explain this result. Using digital still cameras mounted on the back of diving adult Weddell seals, a concurrent study calculated a higher index for prey distribution at Big Razorback Island than at Turks Head (Watanabe et al., in press). Further quantitative investigation is needed to verify this as a proximate cause.

List of symbols

- A(i)** surging acceleration (m s^{-2})
- B** buoyant force (m kg s^{-2})
- D_G** drag force of a gliding seal (m kg s^{-2})
- D_T** drag force of a stroking seal (m kg s^{-2})
- g** gravitational acceleration ($=9.8 \text{ m s}^{-1}$)
- i** = 0, 1, 2, 3... N (s)
- I_F** index of fatness
- m** mass of seal (kg)
- P_B** percentage of total blubber (%)
- $R(i)$** number of propeller rotations per second (revs s^{-1})
- $S(i)$** swimming speed (m s^{-1})
- T** thrust force ($\text{m kg}^{-1} \text{ s}^{-2}$)
- $\gamma(i)$** body angle of a seal (degrees)
- $\Delta\gamma$** adjustment angle (degrees)

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