

DIURNAL AND SEASONAL VARIATIONS IN THE DURATION AND DEPTH OF THE LONGEST DIVES IN SOUTHERN ELEPHANT SEALS (*MIROUNGA LEONINA*): POSSIBLE PHYSIOLOGICAL AND BEHAVIOURAL CONSTRAINTS

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Summary

This study seeks to understand how the physiological constraints of diving may change on a daily and seasonal basis. Dive data were obtained from southern elephant seals (*Mirounga leonina*) from South Georgia using satellite relay data loggers. We analysed the longest (95th percentile) dive durations as proxies for physiological dive limits. A strong, significant relationship existed between the duration of these dives and the time of day and week of year in which they were performed. The depth of the deepest dives also showed a significant, but far less consistent, relationship with local time of day and season. Changes in the duration of the longest dives occurred irrespective of their depth. Dives were longest in the morning (04:00–12:00 h) and shortest in the evening (16:00–00:00 h). The size of the fluctuation varied among animals from 4.0 to 20.0 min. The daily pattern in dive depth was phase-shifted in relation to the diurnal rhythm in dive duration. Dives were deeper at midday and

shallower around midnight. Greater daily changes in duration occurred in seals feeding in the open ocean than in those foraging on the continental shelf. The seasonal peak in the duration of the longest dives coincided with austral midwinter. The size of the increase in dive duration from autumn/spring to winter ranged from 11.5 to 30.0 min. Changes in depth of the longest dives were not consistently associated with particular times of year. The substantial diurnal and seasonal fluctuations in maximum dive duration may be a result of changes in the physiological capacity to remain submerged, in addition to temporal changes in the ecological constraints on dive behaviour. We speculate about the role of melatonin as a hormonal mediator of diving capability.

Key words: phocid, marine mammal, southern elephant seal, *Mirounga leonina*, metabolism, foraging, melatonin, aerobic dive limit, diving.

Introduction

Southern elephant seals (*Mirounga leonina*) are prodigious divers. They spend 90% of their time while at sea diving to average depths of 300–600 m (Slip et al., 1994) and are able to reach depths in excess of 1500 m (McConnell and Fedak, 1996). The mean dive duration of southern elephant seals is 25.2 min for females and 24.1 min for males (Boyd and Croxall, 1996); however, the longest recorded dive lasted 2 h (Hindell et al., 1992).

Both physiological and ecological constraints influence dive duration. Seals exploiting food sources at depth are forced to return to the surface to breathe and are entirely dependent upon internal oxygen reserves whilst submerged. From calculations based on mass-specific oxygen stores of 79 ml O₂ kg⁻¹ body mass (Kooyman, 1989) and estimates of diving metabolic rate, the theoretical aerobic dive limit (ADL) of southern elephant seals is 27.5–30.2 min in females and 42.0–51.4 min in males (Hindell et al., 1992). This is the estimated dive duration after which a net increase in lactate production is expected to occur as a result of the exhaustion of

oxygen stores and a shift to anaerobic respiration in some tissues (Kooyman et al., 1983). The key word here is 'estimated'. There is very little information on how metabolic rate varies in seals diving at sea. Most dives performed by southern elephant seals are within their predicted ADL and show considerable variability in both depth and duration. This behavioural variability in dive duration may reflect the availability and distribution of prey and immediate foraging success (McConnell et al., 1992; Jonker and Bester, 1994).

Elephant seals frequently perform dives approaching and even in excess of their estimated ADL. Because these dives are rarely followed by extended surface intervals or short aerobic processing dives to eliminate lactate, elephant seals appear to rely on aerobic pathways of metabolism while submerged (Hindell et al., 1992; Fedak and Thompson, 1993). The disparity between theoretical predictions and empirical evidence of the maximum diving ability of these animals may be a result of plasticity in the physiological determinants of diving duration.

Some seasonal changes in dive behaviour suggest that southern elephant seals undergo changes in their capacity to remain submerged throughout the year. Female southern elephant seals exhibit an increased ability to exceed or extend their ADL in winter compared with summer (Hindell et al., 1992). The estimated ADL of southern elephant seals was exceeded in 44% of dives performed by post-moult females and in 7% of those performed by post-breeding females. Since oxygen storage and utilisation ultimately limit dive duration, the observed seasonal changes in dive duration may result from temporal variability in these physiological constraints.

Diurnal and seasonal adjustments in the dive behaviour patterns of southern elephant seals have been observed in a variety of circumstances and locations (Hindell et al., 1992; Jonker and Bester, 1994; Slip et al., 1994). Dives performed around noon are significantly longer (23–40 min) than those performed around midnight (15–20 min) and are deeper during the day by 30–300 m (Jonker and Bester, 1994). Female southern elephant seals perform dives with a greater amount of 'bottom time' during winter (post-moult) compared with summer (post-breeding) (Jonker and Bester, 1994).

To investigate temporal variability in physiological capacity, it was necessary to account for behavioural variability in dive duration. Here, we take a new approach and examine the diurnal and seasonal variability in the duration of the longest dives and the depth of the deepest dives of adult southern elephant seals from South Georgia tracked during their post-moult migration (McConnell and Fedak, 1996). The strategy used in this paper attempts to separate behavioural choice from the physiological limitations on dive duration. It is based both upon observations that southern elephant seals occasionally perform extremely long dives, which are in excess of their expected capabilities, and on the assumption that these dives approach their maximum breath-hold capacity. This study examines the upper edge (actually the 95th percentile within time bins) of dive duration distributions as a proxy for physiological dive limits.

It is necessary to account for the confounding effects of concomitant changes in dive depth that may be associated with location and foraging success. Changes in dive duration are influenced by variations in dive depth, since there is a minimum length of time that a seal must take to complete a dive of specified depth (e.g. DeLong and Stewart, 1991; Jonker and Bester, 1994). Although the relationship between the two is complex, there is often a significant positive correlation between the depth and duration of a dive (DeLong and Stewart, 1991; Hindell et al., 1992). Consequently, many of the ecological factors that control dive depth may also influence dive duration, even in the case of the longest dives. In this study, therefore, we attempt to control for the confounding effects of dive depth. We also review the wide variety of potential causes of diurnal and seasonal variability in dive duration and discuss the extent to which each may be responsible for the temporal patterns in maximum duration and depth reported in this paper.

Materials and methods

Information on the dive behaviour of southern elephant seals was obtained using Argos satellite relay data loggers (SRDLs) deployed on 12 animals at South Georgia between 1990 and 1994 (as described by McConnell and Fedak, 1996). The process by which dive data were collected and processed by the SRDLs is detailed by McConnell et al. (McConnell et al., 1992). The SRDL consists of sensors, a computer and a transmitter. The computer compiles information from sensors detecting pressure, wet/dry conditions and swimming distance to create compressed records of individual dive depth, dive duration, surface interval and swimming speed (Fedak et al., 1996). When the antenna of the SRDL is at the surface of the water, the transmitter relays the information to a satellite, which estimates the location of the animal. Dive information exploration and analysis were performed using the MAMVIS visualization system (Fedak et al., 1996) and SAS (SAS Institute Inc., USA).

All seals were captured on land at the end of their annual moult in March and were tracked over part or all of the at-sea phase of their post-moult migration before they returned to breed in October. In this study, we consider only the nine seal-deployments that lasted over 100 days. These involved five adult females, two adult males and one sub-adult male (Table 1). One of the eight seals (1547a) tracked from March 1992 was captured again in March 1993 and tracked for a second period. This second track is referred to as seal 1547b and, for convenience, the two deployments are referred to as separate 'seals' in this paper.

For each seal, the dive durations were binned into local time of day (00:00–23:00 h) and also week of the year (0–51). Within each time bin, the 95th percentile individual dive duration was selected and termed $DURATION_{\text{HOUR}}$ and $DURATION_{\text{WEEK}}$ respectively. The depths of these selected dives are referred to as $DEPTH^*_{\text{HOUR}}$ and $DEPTH^*_{\text{WEEK}}$ respectively. In addition, the 95th percentile individual dive depths, irrespective of dive duration, within each time bin were selected and termed $DEPTH_{\text{HOUR}}$ and $DEPTH_{\text{WEEK}}$ respectively. Bins with fewer than 20 dives were excluded from the analysis.

Since both time of day and week of the year are circular statistics, they were transformed to the cosine and sine of local time of day h [$\cos(h/23) \times 360$ and $\sin(h/23) \times 360$, respectively] and cosine and sine of week of the year w [$\cos(w/51) \times 360$ and $\sin(w/51) \times 360$, respectively] (Fisher, 1993).

$DURATION_{\text{HOUR}}$ and $DEPTH_{\text{HOUR}}$ were regressed against local time (models 1a and 2a). $DURATION_{\text{WEEK}}$ and $DEPTH_{\text{WEEK}}$ were regressed against week of the year (models 1b and 2b). In models 3a and b, $DEPTH^*_{\text{HOUR}}$ and $DEPTH^*_{\text{WEEK}}$ were added as explanatory variables to models 1a and 2a to control for the potential confounding effects of dive depth on temporal changes in $DURATION_{\text{HOUR}}$ and $DURATION_{\text{WEEK}}$. These latter models were compared with the simpler models (1a and b) by carrying out a t -test on the null hypothesis (H_0) that the coefficient of $DEPTH^*_{\text{HOUR}}$, or of $DEPTH^*_{\text{WEEK}}$, was equal to zero.

The regression models are summarised as:

$$DURATION_{\text{HOUR}} = B_0 + B_1 \cos h + B_2 \sin h, \quad (\text{model 1a})$$

$$DURATION_{\text{WEEK}} = B_0 + B_1 \cos w + B_2 \sin w, \quad (\text{model 1b})$$

$$DEPTH_{\text{HOUR}} = B_0 + B_1 \cos h + B_2 \sin h, \quad (\text{model 2a})$$

$$DEPTH_{\text{WEEK}} = B_0 + B_1 \cos w + B_2 \sin w, \quad (\text{model 2b})$$

$$DURATION_{\text{HOUR}} = B_0 + B_1 \cos h + B_2 \sin h + B_3 DEPTH * HOUR, \quad (\text{model 3a})$$

$$DURATION_{\text{WEEK}} = B_0 + B_1 \cos w + B_2 \sin w + B_3 DEPTH * WEEK, \quad (\text{model 3b})$$

where B_0 , B_1 , B_2 and B_3 are coefficients.

The regression lines and 95% confidence limits produced from the regression models were used to establish whether peaks or troughs occurred in $DURATION_{\text{HOUR}}$, $DURATION_{\text{WEEK}}$, $DEPTH_{\text{HOUR}}$ and $DEPTH_{\text{WEEK}}$ in each animal using the method indicated in Fig. 1. The following criteria were used to define a peak: the lowest value of the y variable (depth or duration) was 90% or less of the maximum value of that variable, and the value of the upper 95% confidence limit was lower than the highest value of the lower 95% confidence limit at two points on the regression line. A complementary method was used to determine troughs. A significant increase was said to occur if the lower 95% confidence limit was higher on the right-hand side of the graph than the upper 95% confidence limit on the left-hand side of the graph. The timing and value of maxima and minima (irrespective of whether they qualified as peaks or troughs) were obtained by visual inspection of the significant (F -test, $P < 0.05$) regression model lines.

Results

Movements

Detailed descriptions of the movements of the seals used in this study have been presented elsewhere (McConnell and Fedak, 1996). The nine deployments ('seals') considered in this analysis are divided into three groups according to their

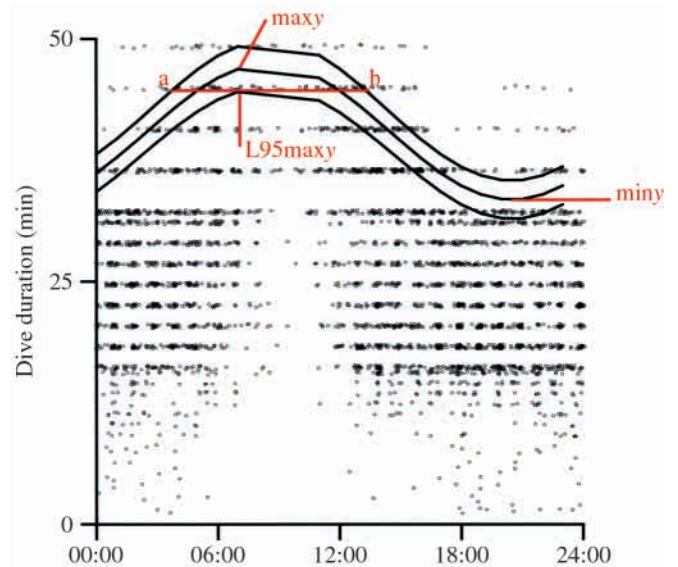


Fig. 1. Illustration of the method used to identify temporal peaks and troughs. This example shows the dive duration data ($N=3582$) against local time of day for seal 2842. Values predicted from the regression of $DURATION_{\text{HOUR}}$ (see Materials and methods) against local time of day (model 1a), with upper and lower 95% confidence limits (L95) for the expected mean value, are shown. Two criteria were necessary to define a peak: (i) $miny \leq 0.9maxy$; (ii) a line drawn at the L95maxy level must cross the upper 95% confidence limits at two points (here a and b). A complementary method was used to determine troughs.

destination (Fig. 2; Table 1). First, in both years, female 1547a/b travelled to the west coast of the Antarctic Peninsula (AP) and foraged on the continental shelf and at the shelf margin. Second, the three males (1545, 2844 and 2848) remained relatively close to South Georgia (SG) throughout the tracking period. The sub-adult male (1545) moved further afield and into deeper water than the other two males, travelling in three loops from its starting point. The two adult males foraged primarily in the shallower water close to South Georgia (particularly in mid-winter), but occasionally over

Table 1. Details of southern elephant seals fitted with satellite relay data loggers at South Georgia (for further details, see McConnell and Fedak, 1996)

Seal	Sex	Mass (kg)	Start of track	End of track	Duration of track (days)	Destination*
1547a	F	370	07 Mar 1992	23 Oct 1992	230	AP
1547b	F	—	02 Mar 1993	08 Jul 1993	128	AP
1545	M	178	06 Mar 1992	12 Sep 1992	190	SG
2844	M	—	24 Mar 1992	27 Aug 1992	156	SG
2848	M	—	29 Mar 1992	08 Sep 1992	163	SG
2840	F	331	09 Mar 1992	14 Nov 1992	250	OO
2841	F	300	10 Mar 1992	17 Nov 1992	252	OO
2842	F	343	11 Mar 1992	12 Dec 1992	276	OO
2843	F	284	11 Mar 1992	23 Jul 1992	134	OO

Note that 3 seals were not weighed.

*The three destination groups are Antarctic Peninsula (AP), close to South Georgia (SG) and the distant open ocean (OO) to the east. Further details are given in the Results section.

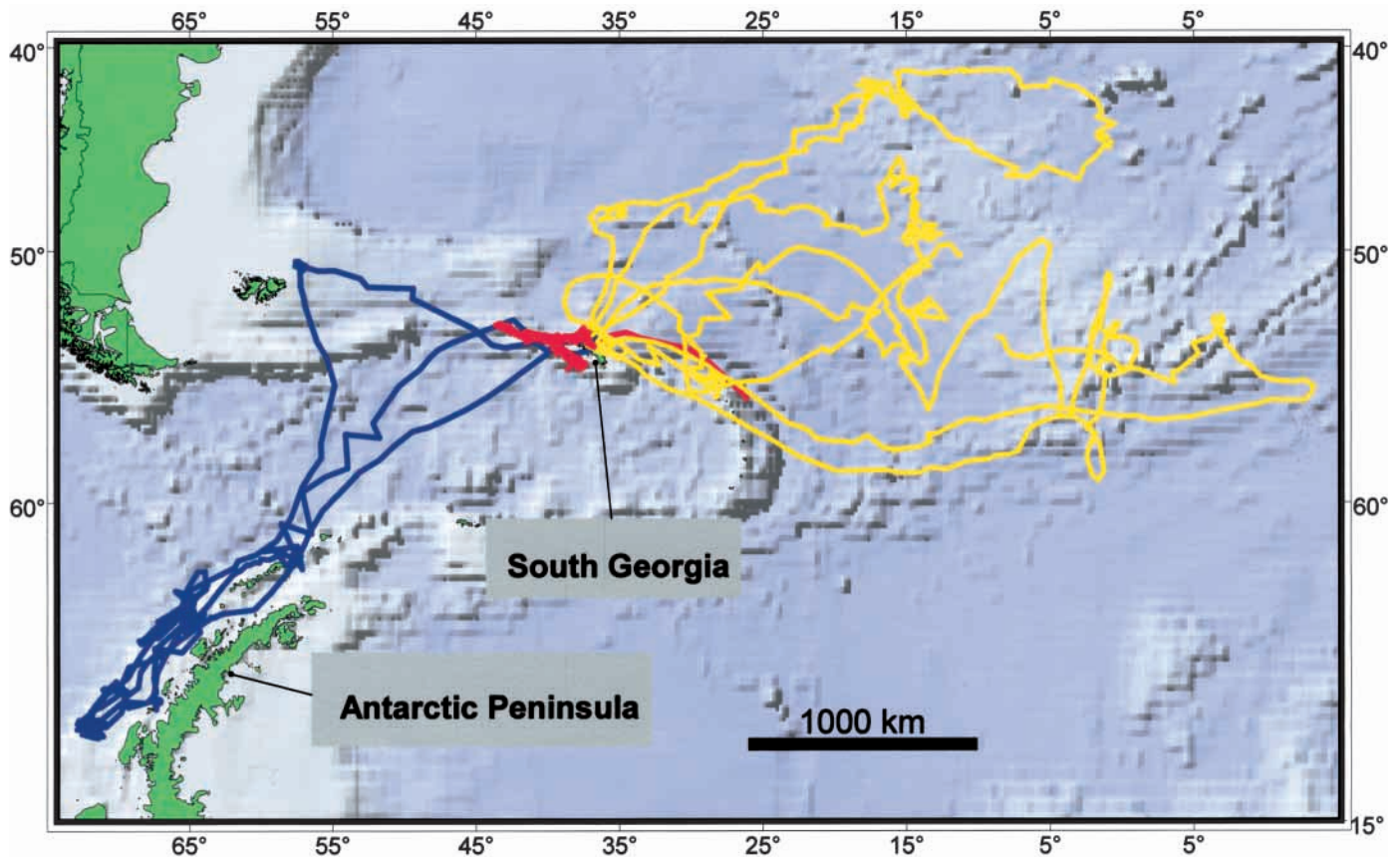


Fig. 2. Tracks of nine southern elephant seals from South Georgia (data from McConnell and Fedak, 1996). The tracks are divided into those that went south-west to the Antarctic Peninsula (blue), those that went east into the open ocean (yellow) and those that remained close to South Georgia (red).

deeper water along the shelf break. Third, four of the females (2840, 2841, 2842 and 2843) travelled east to forage in the open ocean (OO in Table 1) over the abyssal plain, in water that was much deeper than their maximum dive depths.

Diurnal changes in dive behaviour

In total, 31 674 dive records were collected. The frequency distributions of, and relationship between, maximum dive depths and dive durations are shown in Fig. 3. The mean dive duration was 22.2 min, with a maximum of 98.3 min. The mean maximum depth was 363 m with a maximum of 1653 m.

Regression model 1a: DURATION_{HOUR}

In eight seals (all except 2844), the relationships between *DURATION_{HOUR}* and time of day were highly significant (*F*-test, $P \leq 0.002$), and the strengths of the relationships (r^2) were between 0.49 and 0.95 (Fig. 4; Table 2). No diurnal cycle was seen in seal 2844.

Peaks and troughs were identified at the maxima and minima in all the eight seals with significant regressions. The peaks in *DURATION_{HOUR}* occurred in the morning between 04:00 and 12:00 h (mean 08:20 h) and the troughs occurred between 16:00 and 00:00 h (mean 19:30 h). The amplitude of the change in *DURATION_{HOUR}* ranged from 4.0 to 20.0 min and was more pronounced in the females that foraged in the deep ocean (OO)

(mean 15.6 min, range 13.0–20.0 min) than in those that foraged at or close to the continental shelf (AP and SG) (mean 5.7 min, range 4.0–7.5 min).

Regression model 2a: DEPTH_{HOUR}

Only three seals (2848, 2840 and 2841) showed significant relationships between *DEPTH_{HOUR}* and local time (*F*-test, $P \leq 0.002$), and the strength of the relationships (r^2) was between 0.52 and 0.76 (Fig. 5; Table 2).

Peaks and troughs were identified at the maxima and minima in all the three seals with significant regressions. The peaks in *DEPTH_{HOUR}* occurred around mid-day between 11:30 and 12:30 h (mean 12:00 h). All three minima occurred at 00:00 h. The mean amplitude of the change in *DURATION_{HOUR}* was 173 m and ranged from 130 and 150 in males 2480 and 2481 to 240 m in male 2848.

Regression model 3a

The inclusion of *DEPTH*_{HOUR}* in regression model 3a only made a significant improvement in the prediction of *DURATION_{HOUR}* in seal 1545 (*t*-test, $P = 0.022$), increasing r^2 from 0.54 to 0.66.

Seasonal changes in dive behaviour

Not all weeks of the year were represented in the seasonal

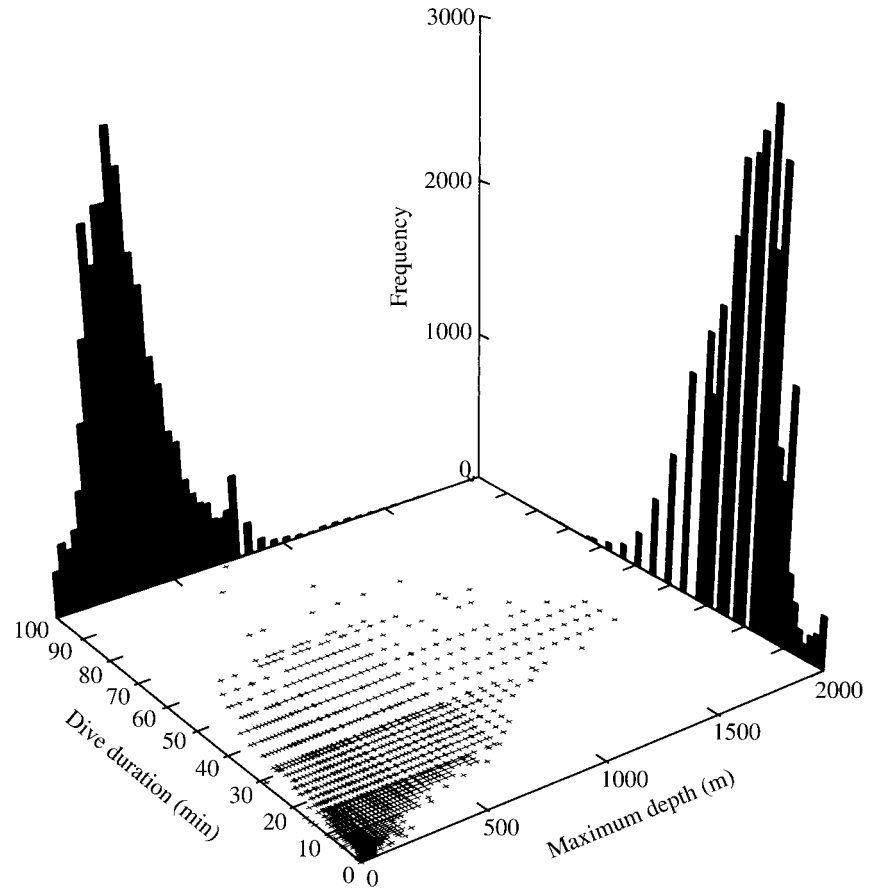


Fig. 3. The frequency distributions of, and relationship between, maximum dive depths and dive durations from 31 674 dive records.

Table 2. Results of the regressions of $DURATION_{\text{HOUR}}$ and $DEPTH_{\text{HOUR}}$ against local time of the day

Seal	Model													
	1a: $DURATION_{\text{HOUR}}$							2a: $DEPTH_{\text{HOUR}}$						
	P^*	Maximum (min)	Time of maximum (local time, h)	Minimum (min)	Time of minimum (local time, h)	Maximum minus minimum (min)	P_{\ddagger}^*	P^*	Maximum (m)	Time of maximum (local time, h)	Minimum (m)	Time of minimum (local time, h)	Maximum minus minimum (m)	
1547a	0.002	31.0	07:30	27.0	20:00	4.0	0.135	0.300	–	–	–	–	–	
1547b	0.002	37.5	04:00	30.0	16:00	7.5	0.787	0.089	–	–	–	–	–	
1545	0.001	27.5	06:30	23.0	18:30	4.5	0.022	0.066	–	–	–	–	–	
2844	0.443	–	–	–	–	–	0.287	0.502	–	–	–	–	–	
2848	0.001	47.0	09:00	38.0	21:30	9.0	0.944	0.002	720	12:30	480	00:00	240	
2840	0.001	47.0	11:00	31.0	21:30	16.0	0.687	0.001	820	11:30	690	00:00	130	
2841	0.001	50.0	12:00	30.0	00:00	20.0	0.411	0.001	700	12:00	550	00:00	150	
2842	0.001	47.0	07:00	33.5	20:30	13.5	0.762	0.103	–	–	–	–	–	
2843	0.001	42.0	07:00	29.0	20:30	13.0	0.949	0.462	–	–	–	–	–	
Mean		41.0	08:20	30.1	19:30	10.9			746	12:00	573	00:00	173	

Maxima, minima and their times were obtained visually from the significant regressions shown in Figs 4 and 5.

*Probability that H_0 is true, derived from an F -test of the regression model. Probabilities <0.05 are in bold type, and probabilities less than 0.001 are truncated at 0.001.

‡Probability that H_0 (the true coefficient of $DEPTH^*_{\text{HOUR}}$ in regression model 3a=0) is true, derived from a t -test. Probabilities <0.05 are in bold type, and probabilities <0.001 are truncated at 0.001.

data. Most of the satellite tracks started around week 10 (March). Seal track durations varied from 128 to 276 days, resulting in the tracks terminating between weeks 28 and 49. Note that the longer seal tracks have greater power to detect seasonal trends.

Regression model 1b: $DURATION_{\text{WEEK}}$

In all nine seals, the relationships between $DURATION_{\text{WEEK}}$ and date using model 1b were highly significant (F -test, $P \leq 0.001$), and the strengths of the

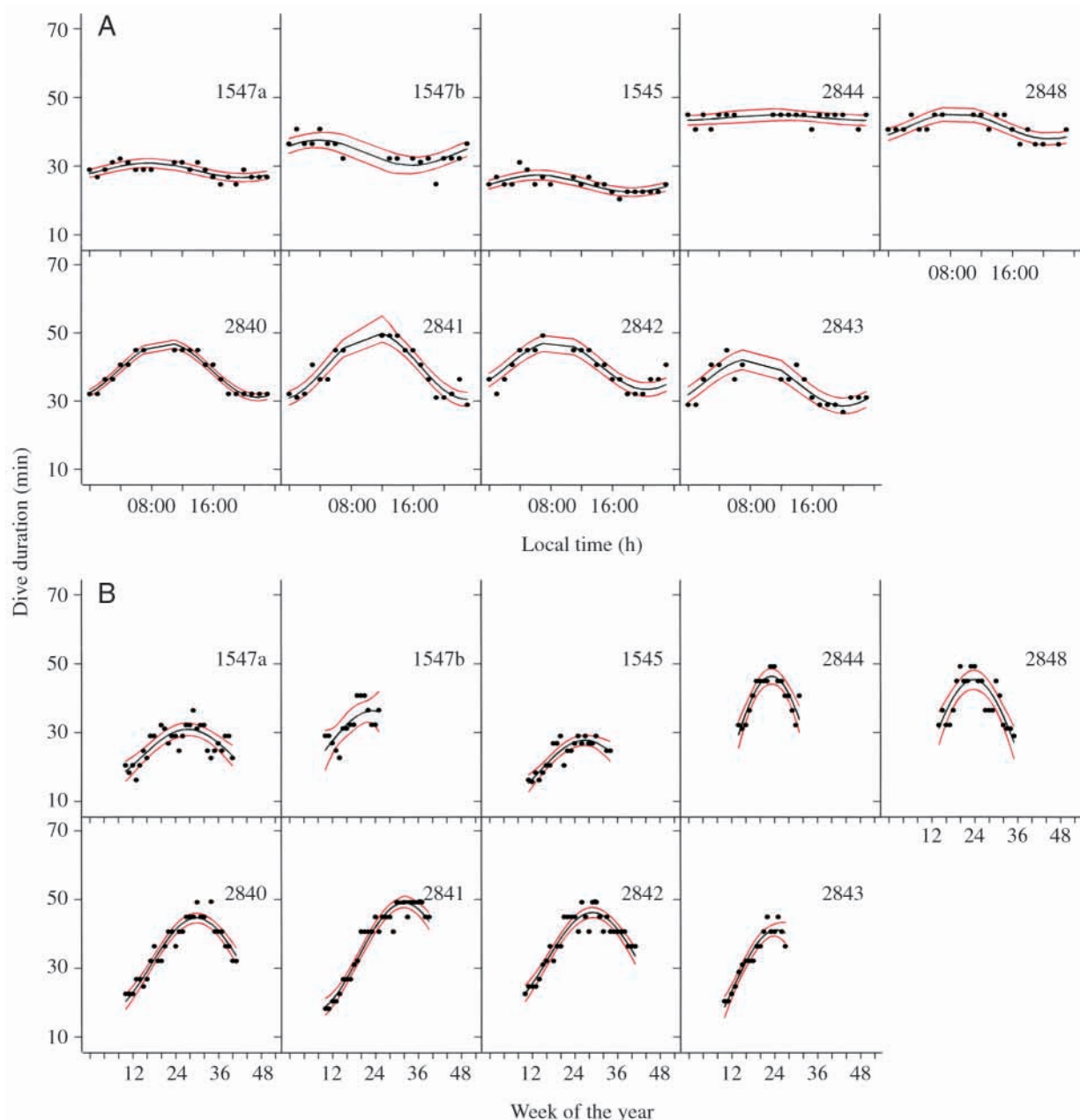


Fig. 4. Plots and regressions of $DURATION_{\text{HOUR}}$ against time of day (A) and $DURATION_{\text{WEEK}}$ (see Materials and methods) against week of the year (B). Regression models 1a and b were used respectively (see text). The upper and lower 95% confidence limits for the expected mean values are also shown in red.

relationships (r^2) were between 0.51 and 0.95 (mean 0.78) (Fig. 4; Table 3).

Peaks were identified at the maxima of all except two seals (1547b and 2843). The average peak in $DURATION_{\text{WEEK}}$ occurred at week 27.4. The maxima in the two seals without peaks (1547b and 2843) occurred at a similar date (week 23 and 24 respectively), coincided approximately with the end of their tracking period and showed signs of a downturn. We therefore include these maxima as peaks and revise the mean peak date to week 26.6 (4 July).

No troughs were identified at any minima. All but one

minimum coincided approximately with the start of tracking in March. The exception, seal 2848, had a slightly lower value at week 35 (1 September). The mean maximum and minimum values of $DURATION_{\text{WEEK}}$ were 40.9 and 21.9 min, respectively, resulting in a mean change of 19.0 min. The changes were greater (≥ 21.5 min) in the open-ocean (OO) females (2840, 2841, 2842 and 2843).

Regression model 2b: $DEPTH_{\text{WEEK}}$

In eight seals (all except 2843), the relationships between $DEPTH_{\text{WEEK}}$ and week of the year were significant (F -test,

Table 3. Results of regressions of $DURATION_{WEEK}$ and $DEPTH_{WEEK}$ against week of the year

Seal	Model												
	1b: $DURATION_{WEEK}$						3b	2b: $DEPTH_{WEEK}$					
	P^*	Maximum (min)	Time of maximum (week)	Minimum (min)	Time of minimum (week)	Maximum minus minimum (min)	$P_{‡}^*$	P^*	Maximum (m)	Time of maximum (week)	Minimum (m)	Time of minimum (week)	Maximum minus minimum (m)
1547a	0.001	31.0	28	19.0§	10	12.0§	0.314	0.001	700	25	350§	10	350§
1547b	0.001	36.5§	23	25.0§	10	11.5§	0.279	0.001	730§	10	460	19	270§
1545	0.001	27.5	27	16.0§	11	11.5§	0.018	0.023	590§	33	360§	12	230§
2844	0.001	46.5	23	29.0§	14	16.5§	0.562	0.003	1120	22	300§	30	820§
2848	0.001	45.5	23	27.0§	35	18.5§	0.082	0.003	690§	20	300§	35	390§
2840	0.001	45.0	30	20.5§	10	25.5§	0.900	0.001	840§	39	610§	13	230§
2841	0.001	49.0	32	19.0§	10	30.0§	0.247	0.001	740§	33	530§	10	210§
2842	0.001	46.5	29	23.0§	10	23.5§	0.936	0.007	800§	39	650§	12	150§
2843	0.001	41.0§	24	19.0§	10	22.0§	0.207	0.206	–	–	–	–	–
Mean		40.9	26.6	21.9	13.3	19.0			776	27.6	445	17.6	331

Maxima, minima and their dates were obtained visually from the significant regressions shown in Figs 4 and 5.

*Probability that H_0 is true, derived from an F -test of the regression model. Probabilities <0.05 are in bold type, and probabilities less than 0.001 are truncated at 0.001.

‡Probability that H_0 (the true coefficient of $DEPTH_{WEEK}$ in regression model 3b=0) is true, derived from a t -test. Probabilities <0.05 are in bold type, and probabilities <0.001 are truncated at 0.001.

§No daily peak at the maximum value or trough at the minimum value was found using the method illustrated in Fig. 1.

$P \leq 0.023$), and the strength of these significant relationships (r^2) was between 0.29 and 0.79 (Fig. 5; Table 3). No seasonal cycle was seen in seal 2843.

Peaks were identified at the maxima of only two seals (1547a and 2844) at weeks 22 and 25 (2 and 23 June) respectively. A trough was identified at a minimum only in seal 1547b and it occurred at week 19 (12 May).

The relationship between $DEPTH_{WEEK}$ and week of the year varied considerably between seals. However, there was a common trend in three deep-ocean (OO) females (2840, 2841 and 2842) of increasing $DEPTH_{WEEK}$ with week of the year, the maxima being at the end of the tracking period at around weeks 33–39 (18 August to 29 September). A similar, though less strong, trend was seen in the sub-adult male seal (1545). This trend, however, was reversed in seal 2848. The trend of a strong seasonal peak in $DEPTH_{WEEK}$ in week 25 (23 June) in seal 1547a was reversed when the same animal (1547b) was tracked the following year, primarily because of deeper dives during travel to the Antarctic Peninsula and, once there, foraging on shallower parts of the shelf bed.

The size of the change in $DEPTH_{WEEK}$ with week of the year also varied considerably between seals. The largest change was of 820 m in seal 2844. Changes in the other seals varied between 150 and 390 m.

Regression model 3b

The inclusion of $DEPTH_{WEEK}$ in regression model 3b made a significant improvement in the prediction of $DURATION_{WEEK}$ only in seal 1545 (t -test, $P=0.018$), increasing r^2 from 0.78 to 0.84. This was the same animal for which there was a significant improvement in the predictive power of the regression using model 3a (see above).

Discussion

Southern elephant seals show marked temporal variability in their longest dives ($DURATION_{HOUR}$ and $DURATION_{WEEK}$). The relationships between $DURATION_{HOUR}$ and $DURATION_{WEEK}$ and both local time and week of the year, respectively, are strong and highly significant. The diurnal and seasonal relationships with the deepest dives ($DEPTH_{HOUR}$ and $DEPTH_{WEEK}$) are substantially weaker than the temporal relationships with $DURATION_{HOUR}$ and $DURATION_{WEEK}$. Trends in $DURATION_{HOUR}$ and $DURATION_{WEEK}$ are not paralleled by changes in $DEPTH_{HOUR}$ and $DEPTH_{WEEK}$.

It is important to consider the effect of overall variability in duration and depth on the distribution of the longest and deepest dives. Fig. 3 shows that the range of variability is large and that animals are very flexible in their choices of both duration and depth. Factors that influence the overall distribution of durations and depths will influence the chances of observing dives that approach the maxima. Maximum durations seem more certain to be constrained by physiological limits than are maximum depths, which are likely to be more affected by changes in oceanographic features and prey distribution.

Possible ecological influences on $DURATION_{HOUR}$ and $DURATION_{WEEK}$ and $DEPTH_{HOUR}$ and $DEPTH_{WEEK}$ include water depth and the vertical distribution of prey (e.g. Croxall et al., 1985; Mattlin et al., 1998). These factors may act as the immediate determinants of dive behaviour. However, factors that influence the physiological constraints on maximum breath-hold capacity, by changing both the rate of utilisation and the size of the usable oxygen stores, may also have an important impact on the durations of the longest dives. Metabolic rate is influenced by variation in activity levels

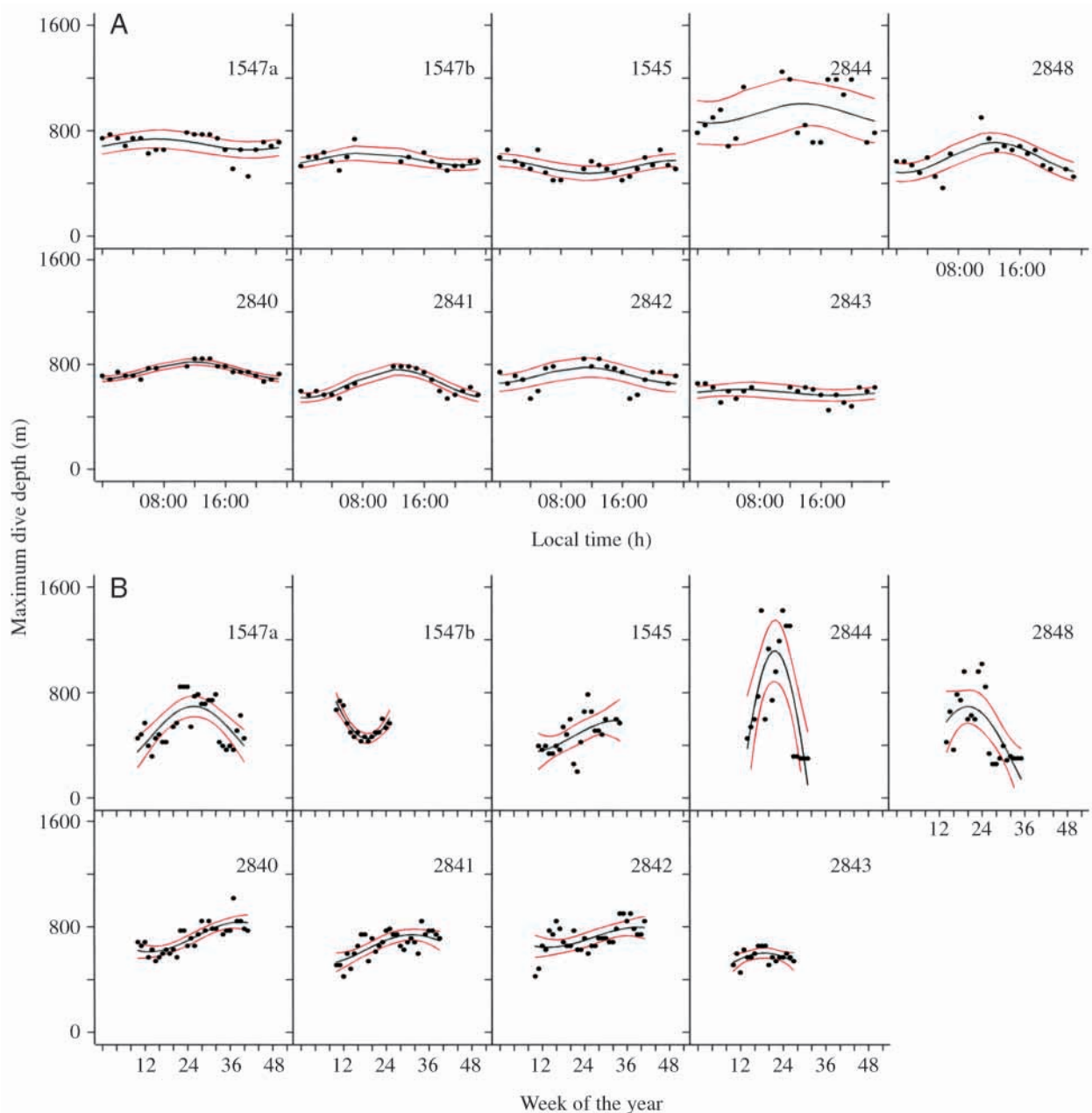


Fig. 5. Plots and regressions of $DEPTH_{\text{HOUR}}$ against time of day (A) and $DEPTH_{\text{WEEK}}$ (see Materials and methods) against week of the year (B). Regression models 2a and b were used respectively (see text). The upper and lower 95% confidence limits for the expected mean values are also shown in red.

(Davis et al., 1985), prey ingestion (Gallivan and Ronald, 1981), body temperature (T_b), the effect of buoyancy on the effort required to reach and maintain depth (Lovvorn and Jones, 1991; Lovvorn et al., 1991; Crocker et al., 1997; Fedak et al., 1994; Minamikawa et al., 1997; Webb et al., 1998) and reproductive condition (Prentice et al., 1989). Some of these factors change on a daily basis, whereas others vary over a longer time scale. Changes in the size of usable oxygen stores may occur gradually in response to body mass fluctuations, aerobic conditioning (Saunders and Fedde, 1991) and reproductive condition (Longo, 1983; Del Valle et al., 1993)

and may contribute to seasonal variation in $DURATION_{\text{WEEK}}$. Southern elephant seals may also exhibit endogenous circadian and circannual rhythms in oxygen storage and rates of utilisation of oxygen stores. It is possible that these rhythms are controlled by hormones such as melatonin, which mediates daily and seasonal responses to environmental variables, including photoperiod and temperature (Reiter, 1993).

All the above factors are likely to interact in complex ways, jointly influencing the maximum diving capability. The resulting balance determines the depths and durations chosen. In the following discussion, we consider the variation in

extreme dive performance in more detail and consider how these intrinsic and extrinsic factors might interact to influence the choice of durations and depths and dive behaviour limits.

Diurnal patterns in maximum dive duration and depth

The duration of the longest dives ($DURATION_{\text{HOUR}}$) was greatest in the morning, between 04:00 and 12:00 h and shortest in the evening, between 16:00 and 00:00 h. This trend was exhibited even in the absence of significant diurnal changes in the depth of the deepest dives ($DEPTH_{\text{HOUR}}$). The peaks and troughs in $DEPTH_{\text{HOUR}}$ did not occur at the same time as the changes in $DURATION_{\text{HOUR}}$. It appears that different factors influenced these two aspects of dive behaviour.

Dive duration

$DURATION_{\text{HOUR}}$ is likely to be influenced by both behavioural requirements and physiological constraints. A change in the diving activity patterns of southern elephant seals, associated with daily changes in prey distribution, may contribute to the diurnal variation in $DURATION_{\text{HOUR}}$ in the present study. For example, squid (a major prey item) begin to descend in the water column in the early morning, and both northern (*Mirounga angustirostris*) and southern elephant seals often engage in drift dives at this time of day (Slip et al., 1994; Crocker et al., 1997), the proposed function of which is rest and/or metabolic processing.

The diurnal pattern in $DURATION_{\text{HOUR}}$ may also relate to changes in energy assimilation throughout the day. Daily variability in prey distribution and availability may affect changes in the rate of digestion of southern elephant seals. In resting harp seals *Phoca groenlandica*, specific dynamic action increases metabolic rate to 1.67 times control levels (Gallivan and Ronald, 1981), and this contribution to metabolic rate would increase the rate at which oxygen stores are depleted.

Daily patterns in swimming velocity, reflecting changes in foraging behaviour, could contribute to the diurnal changes observed in $DURATION_{\text{HOUR}}$. Metabolic rate increases curvilinearly with swimming speed in seals (Williams and Kooyman, 1985; Davis et al., 1985; Feldkamp, 1987; Hind and Gurney, 1997). The shorter dives around midnight in this study may be a result of a raised metabolic rate during nocturnal bouts of intensive foraging, whilst the morning peak in $DURATION_{\text{HOUR}}$ could be a consequence of slower swimming speeds associated with a reduction in the active pursuit of prey at this time of day.

Daily fluctuations in T_b may contribute to diurnal changes in metabolic rate and thereby influence $DURATION_{\text{HOUR}}$. Many mammals and birds show a marked circadian fluctuation in T_b , which reaches a minimum in the middle of the night-time period (Saarela and Reiter, 1994; Cagnacci et al., 1997). Similar endogenous rhythmic oscillations in the core temperature of southern elephant seals could influence metabolic rate and contribute to the diel pattern in $DURATION_{\text{HOUR}}$. Inactivity on land in northern elephant seals is associated with a reduction of 2–3 °C in T_b (McGinnis and

Southworth, 1971). Lowered T_b may result in a reduction in metabolic rate (Butler and Jones, 1997). A reduction in core temperature caused by cold food items in the stomach may also augment the controlled downregulation of metabolic rate. The rate of cooling can be rapid, even in large seals (Hill et al., 1987).

Seasonal patterns in dive depth and duration

The peak in $DURATION_{\text{WEEK}}$ was consistently associated with austral midwinter. The relationship between $DEPTH_{\text{WEEK}}$ and time of year was relatively weak, and changes in $DEPTH_{\text{WEEK}}$ were not consistently associated with particular times of year. Although seasonal changes in $DEPTH_{\text{WEEK}}$ were often concurrent with those in $DURATION_{\text{WEEK}}$, variability in $DURATION_{\text{WEEK}}$ was not simply a direct consequence of dive depth (Table 3). We now consider possible explanations for these seasonal changes.

Dive depth

In those seals that fed epi-benthically on the continental shelf, variation in seafloor topography between foraging locations may account for the large variations in the seasonal pattern of $DEPTH_{\text{WEEK}}$. The effect of seafloor topography on dive behaviour is apparent in the dive record of female 1547a, which fed in the shallow waters off the coast of the Antarctic Peninsula (McConnell and Fedak, 1996). The seasonal pattern in $DEPTH_{\text{WEEK}}$ closely mirrored the changing depth of the water in which this animal foraged throughout the year. As the animal moved over the continental shelf, dive depth was relatively shallow. The peak in $DEPTH_{\text{WEEK}}$ occurred at a time when this animal was foraging in a localised deep area, north of Adelaide Island off the Antarctic Peninsula. $DEPTH_{\text{WEEK}}$ decreased again as the seal fed in shallower water on the seaward edge of the continental shelf. A similar effect of water depth on $DEPTH_{\text{WEEK}}$ is also seen in the males, which remained on the continental shelf close to South Georgia for the majority of the tracking period. The four females that foraged in the open ocean were unlikely to be influenced by changes in water depth during the tracking period because they foraged at mid-water depths. The depths of their dives were constrained by seafloor topography only for the limited time they were close to South Georgia.

Annual changes in the vertical distribution of prey may influence the dive depth of southern elephant seals, as has been suggested for other species. The strong diel component found in dive depth in Weddell seals *Leptonychotes weddelli* (Testa, 1994) and crabeater seals *Lobodon carcinophagus* (Nordøy et al., 1995) during autumn and spring is absent during the winter. An increase in mean dive depth in winter occurs in New Zealand fur seals *Arctocephalus forsteri* (Mattlin et al., 1998). These seasonal changes in dive behaviour may reflect the absence of diel vertical migrations of their prey in response to the lack of daylight experienced in the Antarctic in midwinter (Testa, 1994; Nordøy et al., 1995). Alternatively, they could reflect a change from feeding on pelagic, vertically migrating prey during the summer to foraging primarily on benthic

animals in autumn and winter (Testa, 1994; Mattlin et al., 1998).

Seasonal shifts in the vertical location of the temperature discontinuities between water masses may also change the depth distribution of prey species. Many mid-water squid also show considerable ontogenetic depth changes (Clarke, 1996; Rodhouse and Nigmatullin, 1996). As a consequence of the annual life cycle of many squid species, particular stages are present only at specific times of year (Rodhouse and Nigmatullin, 1996). Such annual changes in prey depth may help to account for the seasonal trend in $DEPTH_{WEEK}$ of the four females that foraged at mid-water depths in the open ocean.

Dive duration

$DURATION_{WEEK}$ is likely to be determined by the interactions between behavioural needs and physiological constraints. Increases in dive duration from summer to winter have been observed in subantarctic fur seals (*Arctocephalus tropicalis*; Georges et al., 2000) by a factor of 1.4, in New Zealand fur seals (Mattlin et al., 1998) by a factor of 2.1 and in Steller sea lions (*Eumetopias jubatus*; Merrick and Loughlin, 1997) by a factor of 1.5. Mattlin et al. (Mattlin et al., 1998) also express this increase as 6.9% of dive durations greater than ADL in summer compared with 31.3% in winter. In these studies, there were also seasonal increases in dive depth, and it was inferred that the underlying causes were likely to be ecological, or related to the requirements of feeding pups, rather than physiological.

The migratory movements of southern elephant seals may contribute to the seasonal trend in $DURATION_{WEEK}$ in this study. Rapid transit phases to and from the foraging grounds occur at specific times of the year, before and after the moult in autumn and the breeding season in spring (McConnell and Fedak, 1996). Dives at these times may involve more exercise and, thus, be associated with shorter durations.

Changes in prey type throughout the year may cause seasonal differences in dive duration. The diet of male southern elephant seals from Macquarie Island differs between summer and winter (Green and Burton, 1993). A greater variety of squid taxa are taken in winter in comparison with summer. This may result in seasonal variability in $DURATION_{WEEK}$ as a result of different foraging strategies employed in response to changes in abundance, location, calorific value and ease of capture of prey.

Buoyancy may have an important influence on oxygen expenditure during dives and could contribute to the marked seasonality in $DURATION_{WEEK}$. In shallow-diving animals that have large air spaces, such as diving ducks, work against buoyancy accounts for 36–38% of the mechanical work done during the power stroke, and buoyancy is therefore a significant factor in the locomotor costs of diving (Lovvorn et al., 1991). But even in deep-diving seals, buoyancy is likely to be important in influencing metabolic costs. Buoyancy may vary dramatically on a seasonal basis in elephant seals as a result of cyclical changes in body fat associated with protracted

fasting and rapid re-feeding. Southern elephant seals undergo prolonged periods of fasting when they come ashore to moult and to breed, in the autumn and spring, respectively. The animals have a low body fat content when they return to sea to forage. Body fat content increases as a function of time at sea. It is possible that these changes in body composition may affect dive behaviour (Webb et al., 1998; Beck et al., 2000) as well as influencing swimming speeds. Seals that are positively or negatively buoyant may require greater effort to reach and maintain position in the water column than neutrally buoyant conspecifics (Fedak et al., 1994). If buoyancy does change as a result of body composition, it can be predicted that southern elephant seals will be negatively buoyant when they return to sea after moulting and breeding and positively buoyant prior to coming ashore. The period during which the animals are neutrally buoyant (possibly around midwinter) is the time when they can maintain their position in mid-water with least metabolic cost, and this would enable them to perform their longest dives. As buoyancy increases further, the effort required to maintain position may increase and compromise maximum diving ability, thereby reducing $DURATION_{WEEK}$ once more. However, Beck et al. (Beck et al., 2000) found that dives of Canadian grey seals were longest during the mid-winter, pre-breeding period when seals were most buoyant, suggesting that something other than buoyancy was involved in producing the pattern of dive duration.

Reproductive condition in females may influence metabolic rate. Fecundity is high in adult females (Hindell, 1991; SCAR, 1991). Animals begin gestation around the annual moult in March and give birth in late September and October. It seems paradoxical that pregnant female elephant seals exceed the dive durations of non-pregnant animals, whilst subject to the additional oxygen requirements of the foetus (Le Boeuf, 1994). However, the metabolic rate of pregnant and pseudo-pregnant harp seal cows is dramatically lower than that predicted from allometric scaling equations (Renouf and Gales, 1994; Hedd et al., 1997). Pregnant women show evidence of a reduction in basal metabolic rate during the first 24 weeks of gestation (Prentice et al., 1989). Metabolic rate rises again near term. The energy-sparing adaptations operate most notably in women who are thin, suggesting that the metabolic suppression occurs in response to initial energy status (Prentice et al., 1989). It is possible that similar mechanisms operate in female southern elephant seals. Low body fat levels at implantation may result in a reduction in basal metabolic rate, which may allow them to perform longer dives through the autumn and winter.

An increase in erythrocyte mass and blood volume associated with pregnancy (Longo, 1983; Del Valle et al., 1993) may equip females with a greater breath-hold capacity in the winter months. The progressive reduction in dive duration in spring may relate to a reduction in the amount of available oxygen in the later stages of gestation, as the oxygen demands of the foetus outweigh the increase in oxygen storage capacity. But males too, showed a clear midwinter increase in $DURATION_{WEEK}$.

It is possible that the increase in $DURATION_{WEEK}$ in winter occurs in females despite their reproductive condition and that both males and females experience seasonal fluctuations in their basal metabolic rate. Captive female grey seals *Halichoerus grypus* (Boily, 1996; Boily and Lavigne, 1997), harbour seals *Phoca vitulina* (Rosen and Renouf, 1995) and harp seals (Renouf and Gales, 1994) show a marked underlying seasonal variability in metabolic rate. Harp seals exhibit an increase in total body fat from October to February despite a reduction in food intake over the same period (Lager et al., 1994). The standard metabolic rate and T_b of male and female harp seals of all ages is higher in spring and summer than in autumn and winter (Renouf and Gales, 1994). A similar endogenous circannual rhythm in the metabolic rate of southern elephant seals could contribute to the seasonal pattern in $DURATION_{WEEK}$.

The usable oxygen stores of southern elephant seals may show significant plasticity throughout the year and alter the ability of the animals to remain submerged. Little is known about the size of the usable oxygen stores of southern elephant seals. The oxygen stores of phocid seals are contained in the blood and muscle, and blood volume is proportional to lean body mass (Le Boeuf, 1994). As the animals gain lean mass whilst foraging at sea, they may experience a concomitant increase in blood volume and muscle mass, which could drive an increase in breath-hold capacity.

In southern elephant seals, increased dive duration in the winter months may be the result of improved oxygen delivery to the tissues caused by environmentally induced alterations in the oxygen affinity of haemoglobin and myoglobin, or increases in the oxygen storage capacity of the muscles. This has been documented in fish, birds and other mammals (Saunders and Klemm, 1994; Postnikova et al., 1999; Riera et al., 1993). Prolonged training results in increases in haemoglobin and myoglobin concentration (Saunders and Fedde, 1991) and changes in the metabolic properties of skeletal muscle. In the muskrat *Ondatra zibethicus*, increases from summer to winter in blood volume, blood oxygen-carrying capacity and skeletal muscle myoglobin content result in an increase in the usable oxygen stores from 25.2 to 35.7 ml O₂ STPD kg⁻¹ (MacArthur, 1990). This is thought to relate to aerobic conditioning of the animals as they increase diving activity beneath the ice. It has previously been postulated that the increase in dive duration in northern elephant seals with time at sea is a result of aerobic conditioning (DeLong and Stewart, 1991).

Periods of inactivity in mammals and birds lead to muscular atrophy (Saunders and Fedde, 1991). The protracted breeding and moulting fasts of southern elephant seals are associated with a reduction in muscle mass (Boyd et al., 1993). As a result, breath-hold capacity may be minimal on departure from South Georgia. An increase in aerobic conditioning with time at sea may contribute to the midwinter peak in $DURATION_{WEEK}$. The reduction in $DURATION_{WEEK}$ in spring may be a result of ecological or physiological factors that counteract the effects of high levels of physical fitness.

Possible involvement of melatonin

In the previous discussion, we have considered physiological and environmental factors that are likely to influence diving performance. We now consider the effects of melatonin, a hormone associated with diurnal and seasonal changes in many animals. The timing of the diurnal and seasonal maxima in $DURATION_{WEEK}$ is consistent with expected daily and annual peaks in melatonin levels in southern elephant seals (see Griffiths et al., 1979). The synthesis of melatonin is inhibited by light and is instrumental in the synchronisation of the body's endogenous rhythm with that of the external light/dark cycle (Reiter, 1981). Southern elephant seals sampled on land show diurnal rhythmicity in melatonin levels in response to photoperiod and exhibit pronounced seasonal fluctuations in melatonin levels as a consequence of the extreme light regime in the circumpolar regions (Griffiths et al., 1979). There are no such measurements on seals diving in tanks or at sea. Melatonin mediates physiological and behavioural responses to photoperiod (e.g. Rust and Meyer, 1969; Saarela and Reiter, 1994; Reiter, 1995; Cagnacci et al., 1997; Malpoux et al., 1997) in many species and may be responsible for environmentally induced changes in oxygen storage capacity or metabolic rate. Although there is no direct evidence of the involvement of melatonin in diving, it is possible that the pineal gland of pinnipeds, which is large in both relative and absolute terms (Cuello and Tramezzani, 1969; Tedman, 1977; Little and Bryden, 1990; Stokkan et al., 1995), relates to their diving habit. Nothing is known about how the brief periodic exposures to light at the sea surface experienced by diving elephant seals influence hormonal responses to light or how the seals regulate melatonin levels.

Melatonin mediates the circadian rhythms in T_b of rats and humans either by reducing the T_b set-point in the hypothalamus (Cagnacci et al., 1997) or by reducing sensitivity to T_b fluctuations, such that the animal tolerates a greater range of T_b values and does not defend itself against a drop in core T_b . It is possible that melatonin performs the same function in seals. Melatonin has numerous inhibitory effects on cell function because of its ability to prevent Ca²⁺ fluxes (Vanacek, 1998), and it may, therefore, be able to reduce the rate of many metabolic processes. It may contribute to the controlled downregulation of metabolism in diving seals. The hormone is also a major component of the body's direct and indirect antioxidative defence mechanism (Reiter, 1995; Reiter, 1996). Many of the tissues of southern elephant seals may be flooded by high concentrations of free radicals at the termination of each dive. It is possible that melatonin provides the tissues of southern elephant seals with extremely effective protection against reperfusion injury with the termination of the diving bradycardia. Melatonin therefore seems likely to be an important hormone in mammalian divers.

Concluding remarks

It is to be expected that factors such as prey distribution patterns, buoyancy changes and foraging success will vary dramatically among individuals and feeding locations and,

therefore, result in marked variability in dive duration. In contrast, we have documented a considerable degree of consistency in the timing of diurnal and seasonal increases in maximum dive duration, across individuals, sex and geographical range. This pattern is all the more remarkable given that it is not explained by changes in the depths of the longest dives. Also, throughout the Discussion, we have noted similar patterns of longer dives at midwinter and in the early morning in a number of other seal species.

Since physiological factors constrain the upper limit of dive duration, the consistent trends in $DURATION_{\text{HOUR}}$ and $DURATION_{\text{WEEK}}$ in the context of diverse ecological conditions suggest the existence of predictable temporal variation in the physiological determinants of diving ability. We speculate that daily and seasonal changes in metabolic rate, oxygen storage capacity and/or the ability to tolerate or reduce the production of free radicals are largely responsible for this temporal variability.

It is likely that daily and seasonal changes in the factors that dictate the physiological capacity to remain submerged are hormonally controlled. Melatonin levels are closely linked to ambient light levels and day length. This hormone is implicated as the internal mediator of many physiological processes and behavioural patterns showing distinct circadian and seasonal rhythms (Pevet, 2000). It is possible that melatonin is also involved in the hormonal regulation of temporal changes in oxygen storage and/or metabolic rate in diving seals. In addition, melatonin may play an important role in protecting tissues from the damaging effects of free radicals during intermittent ischaemia and reperfusion. These speculations are reinforced by the large size of the pineal gland in phocid seals, which suggests that it is functionally significant in these animals.

Although estimated ADLs give an indication of the maximum breath-hold durations of diving mammals, they are unable to predict temporal plasticity in the ability to remain submerged unless they take account of temporal variation in both oxygen storage and utilisation.

Experimental investigations of temporal variability of oxygen stores, metabolic regulation and the role of melatonin in diving animals are useful avenues for further research. In particular, melatonin concentrations from seals under naturalistic diving regimes with documentation of dive duration and metabolic rate would be very valuable.

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