

HEART RATES OF NORTHERN ELEPHANT SEALS DIVING AT SEA AND RESTING ON THE BEACH

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Summary

Heart rates of northern elephant seals diving at sea and during apnoea on land were monitored to test whether a cardiac response to submergence is an important factor in their ability to make repetitive, long-duration dives. Seven juvenile northern elephant seals were captured at Año Nuevo, CA, instrumented and translocated to release sites around Monterey Bay. Heart rate and dive depth were recorded using custom-designed data loggers and analogue tape monitors during the seals' return to Año Nuevo. Heart rates during apnoea and eupnoea were recorded from four of the seals after they hauled out on the beach. Diving patterns were very similar to those of naturally migrating juveniles. The heart rate response to apnoea at sea and on land was a prompt bradycardia, but only at sea was there an anticipatory tachycardia before breathing commenced. Heart rate at sea declined by 64% from the surface rate of 107 ± 3 beats min^{-1} (mean \pm S.D.), while heart rate on land

declined by 31% from the eupnoeic rate of 65 ± 8 beats min^{-1} . Diving heart rate was inversely related to dive duration in a non-linear fashion best described by a continuous, curvilinear model, while heart rate during apnoea on land was independent of the duration of apnoea. Occasionally, instantaneous heart rate fell as low as 3 beats min^{-1} during diving. Although bradycardia occurs in response to apnoea both at sea and on land, only at sea is heart rate apparently regulated to minimise eupnoeic time and to ration oxygen stores to ensure adequate supplies for the heart and brain not only as the dive progresses normally but also when a dive is abnormally extended.

Key words: diving, apnoea, heart rate, bradycardia, elephant seal, *Mirounga angustirostris*, data logger, translocation.

Introduction

The breath-holding ability of elephant seals (genus *Mirounga*) appears to be unequalled in the class Mammalia. While at sea during their biannual foraging migrations, northern elephant seals (*Mirounga angustirostris*) perform long-duration dives interrupted by only brief surface intervals (Le Boeuf *et al.* 1988; Stewart and DeLong, 1993). This pattern is repeated almost continuously for 2–8 months, and 80–95% of time at sea is spent submerged (Le Boeuf, 1994; Stewart and DeLong, 1995). Dive durations of adult females average at least 20 min, but surface intervals last only approximately 2 min, rarely exceeding 5 min even after dives as long as 119 min. Elephant seals adopt this pattern on their first trip to sea when mean dive durations are approximately 10 min, and by the time they are 2 years old the dive durations approach those of adults (Le Boeuf, 1994). Dives frequently exceed the calculated aerobic dive limit (ADL; Kooyman *et al.* 1983), which is the time limit imposed by oxygen stores and the estimated rate of oxygen consumption, yet there is no sign of a large increase in anaerobic metabolism and the extended

surface time needed to clear anaerobic end-products. During long dives, elephant seals may reduce their heart rate and peripheral blood flow considerably, which may result in a reduction in overall metabolic rate. A reduction in metabolic demand for oxygen may be the reason why elephant seals can repeatedly make long-duration dives with only short surface intervals (Le Boeuf *et al.* 1988). Therefore, the purpose of this study was to describe the heart rate response to diving in northern elephant seals.

Elephant seals also engage in long-duration breath-holds when hauled out on the beach, and their pattern of apnoea and eupnoea when sleeping is similar to the pattern imposed by diving at sea (Bartholomew, 1954; Hubbard, 1968; Blackwell and Le Boeuf, 1993). In juvenile and adult seals, the mean apnoea duration on land varies from 7 to 10 min, but can extend to at least 25 min. Castellini *et al.* (1994a) suggested that the cardiovascular response to diving and to apnoea on land may be similar and governed by the same control mechanisms. Therefore, this study was also designed to compare the heart

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rate response to diving with the heart rate response to apnoea on land in the same individuals.

A method that facilitates short-term studies of elephant seal diving has recently been demonstrated (Le Boeuf, 1994; G. W. Oliver, P. A. Morris, P. H. Thurson and B. J. Le Boeuf, in preparation). Juvenile (<3 years old) northern elephant seals haul out on the beach at the Año Nuevo rookery in central California twice a year, in the spring and autumn, for approximately a month each time. Juvenile seals that are captured just after hauling out and then translocated to a release site up to 100 km away return to Año Nuevo, usually within 1 week. If the seals cross deep water on their return path, then their diving pattern is very similar to the pattern adopted by seals migrating naturally. Therefore, in order to monitor the heart rate response to voluntary diving in northern elephant seals, we used this translocation method on seven juvenile seals instrumented with heart rate and time/depth recorders. Heart rate on the beach was also monitored in four of the same seals. We show that the heart rate response to apnoea at sea and on land was a prompt bradycardia and, although important differences between the two patterns existed, there is no doubt that heart rate reduction is an important part of an oxygen- and energy-conservation strategy both at sea and on land.

Materials and methods

Seals and translocation paradigm

We recorded heart rate and dive depth from seven juvenile northern elephant seals at different times between May 1991 and June 1993 (Table 1). Seals were captured less than 2 weeks after they had hauled out at Año Nuevo State Reserve, California. We immobilised the seals with an intramuscular injection of a mixture of Tiletamine HCl and Zolazepam HCl at an approximate dose of 1 mg kg⁻¹ (Telazol, Aveco Co., Fort Dodge, IA, USA) and transported them by truck to the Long Marine Laboratory, Santa Cruz, CA, USA. At the laboratory, seals were weighed and immobilised again to attach instruments and heart rate electrodes. Immobilisation was maintained throughout the attachment procedure by intravenous injections of 0.5 mg kg⁻¹ ketamine (Ketaset, Aveco Co.) and 0.025 mg kg⁻¹ Diazepam (Elkins-Sinn Inc., Cherry Hill, NJ, USA) at 15–30 min intervals. The seals were marked by placing numbered tags in the interdigital webbing of their rear flippers. Recording instruments (see *Instrumentation*) and a VHF radio were attached using hose-clamps glued to the fur in the mid-dorsal region (Le Boeuf *et al.* 1988). Three of the seals were instrumented with digital heart rate–time/depth recorders (HR-TDR), and four seals received analogue electrocardiogram (ECG) recorders (Holter monitors) paired with microprocessor-controlled time/depth recorders (TDR) (Table 1). The ECG signals were obtained by a modification of the method described by Fedak *et al.* (1988). Two skin-surface electrodes were attached to each seal, one on the ventral midline and one on the dorsal midline at the level of the heart. Seals instrumented with Holter monitors had a third electrode placed on the dorsal midline 15 cm posterior to the instrument attachment site.

On the day after capture, and at least 12 h after instrumentation, the seals were transported either by truck to the opposite side of Monterey Bay or by ship to offshore release sites. Seals were released on the beach at Hopkins Marine Station, Pacific Grove, CA, or at sea off a research vessel (Table 1; Fig. 1). Año Nuevo State Reserve was monitored daily with a hand-held VHF telemetry receiver (Telonics Inc., Mesa, AZ, USA) to locate the seals on their return. Returning seals instrumented with HR-TDRs were immobilised and the instruments were removed. In order to record heart rate on land from the four seals instrumented with Holter monitors, the instruments were not removed until 12–18 h after they had returned to the beach. Seals GG571 and GH929 were observed on the beach for 3.5 and 4 h, respectively. During this observation time, they were apparently sleeping or resting quietly. An observer approximately 5 m downwind of the seal noted the time of every breath and the duration of each apnoeic and eupnoeic period. Apnoea was defined as an expiratory pause of at least 1 min that was ended by an inspiration (Blackwell and Le Boeuf, 1993).

Instrumentation

HR-TDRs were used to record heart rate and dive depth from three seals. HR-TDRs consisted of a microprocessor with 64 kbytes of memory, an analogue-to-digital converter, and the electronic circuitry for a pressure transducer and an electrocardiogram (ECG) R-wave detector. The pressure transducer circuit had a resolution of 4.0 m of sea water over a range of 0–1000 m and was calibrated with a pressure gauge comparator and a National Institute of Standards and Technology (NIST)-traceable precision gauge. The ECG R-wave detector circuit was similar to that described by Shimizu (1978). A refractory period of 400 ms was selected to prevent triggering of the peak detector by high-amplitude T-waves, which limited the maximum heart rate recorded to 150 beats min⁻¹. This was a reasonable limit because the maximum instantaneous heart rate recorded with either HR-TDRs or Holter monitors (which had no maximum heart rate limit) was 133 beats min⁻¹. The amplified ECG and the detector circuit trigger output were displayed on an oscilloscope during the instrumentation procedure to verify that the R-wave detector was functioning properly. HR-TDRs were enclosed in cylindrical aluminium housings (22.0 cm long × 3.5 cm in diameter) sealed with O-rings. A water/pressure-proof bulkhead connector assembly (Underwater Systems Inc., Stanton, CA, USA) was used for electrical connection to the ECG leads. A VHF radio transmitter (6.0 cm long × 2.5 cm in diameter, Advanced Telemetry Systems, Inc., Isanti, MN, USA) was attached with hose-clamps to each HR-TDR housing. The HR-TDR was programmed to count the number of heart beats and every 10 s to store the count, clear the counter and store the current depth. Data were downloaded to a notebook computer and analysed using a custom-designed software program (written in the awk language) after recovery of each HR-TDR.

Heart rate was recorded from four other seals using analogue Holter monitors (model 90205, Space Labs Inc., Redmond, WA, USA). The Holter monitors recorded the ECG signal onto magnetic tape with a capacity of 48 h. Holter monitors were enclosed in aluminium housings (3.5 cm high \times 11.0 cm long \times 8.5 cm wide) and were connected to the ECG electrodes by water/pressure-proof bulkhead connector assemblies. A VHF radio transmitter and a microprocessor-controlled TDR (model Mk 3, Wildlife Computers, Redmond, WA, USA) were attached to the Holter monitor housing with hose-clamps. The TDR was programmed to record depth every 5 s, with a resolution of 2.0 m over the range 0–450 m and a resolution of 6.0 m over the range 450–1500 m. TDR data were downloaded to a notebook computer and were analysed using a custom-designed awk language program. The Holter monitor tapes were scanned and digitised using an FT2000A Medical Workstation computer system (Space Labs, Inc.). The FT2000A was also used to identify each R-wave and to record the duration of the R–R intervals. Accurate R-wave identification by the FT2000A was verified visually for each heart beat.

Analysis and statistics

The data collected at sea were analysed for the period from 1 h after release to 1 h before return to Año Nuevo. A dive was defined as submersion to a depth greater than 6.0 m. The depth of the dive was the maximum depth reached during the dive. The mean heart rate for each individual dive, surface interval (SI), beach apnoea and beach eupnoea was calculated by adding the total number of beats and dividing by the duration of each period. A dive cycle was defined as a dive and the subsequent SI and was analysed only if the ECG signal appeared to be reasonably noise-free throughout the cycle. Similarly, a beach apnoea cycle was defined as an apnoea and subsequent eupnoea, and was analysed only if the ECG was noise-free and the cycle was followed by another apnoea. Therefore, heart rate on the beach was analysed only during periods of quiet wakefulness or sleep. Comparison of the ECG recordings and the visual observation of respiration on the beach of seals GG571 and GH929 showed that entrance into both apnoea and eupnoea was accompanied by clear changes in heart rate. These changes confirmed the results of Castellini *et al.* (1994a,b) for elephant seals over 3 months old during land apnoea and eupnoea; therefore, these heart rate patterns were used to mark the timing of the apnoea cycles when visual observation was not possible.

Student's paired *t*-tests were used to compare heart rates during diving and during apnoea on land as well as heart rates during apnoea and eupnoea. Significance was accepted at the level of $P < 0.05$, except when it was necessary to use the sequential Bonferroni method to minimise Type-I errors (Rice, 1989). Relationships were examined using least-squares linear regression. Average relationships that take into account variability between subjects were determined using repeated-measures multiple linear regression with each seal being assigned a unique index variable. The relationship between

dive duration and mean dive heart rate was also examined using the curve-fitting procedure of the Marquardt–Levenberg algorithm to find the best continuous curvilinear model. The hypothesis of a threshold shift in this relationship was tested using an iterative least-squares linear regression technique to find the best continuous, two-segment regression model (Nickerson *et al.* 1989). The residual sum of squares (RSS) and means square error (MSE) values for each of the different models were compared using one-way repeated-measures analysis of variance (ANOVA) with Student–Newman–Keuls pairwise multiple comparisons.

Results

Behaviour

Seals released on the beach initially displayed short, shallow dives that increased in depth and duration with time as they followed the bottom contour to the continental shelf break (the 140 m bathocline, Fig. 1) and the Monterey submarine canyon. Once deep water was reached, long-duration, deep dives predominated. The seals released at sea immediately began making long-duration, deep dives. As seals approached the shore, their dives became progressively shorter and shallower until they hauled out on the beach at Año Nuevo. An example of such a progression is seen in Fig. 2A (top panel), an excerpt from the dive record of seal GH929. Seals spent 0.6–3.8 days at sea before returning to Año Nuevo (Table 1). There were no significant differences between groups for any of the dive behaviour or heart rate variables, whether the seals were grouped by sex, release type or instrument type. Therefore, we pooled the at-sea data for all seven seals.

When all dives were included, the mean dive depth for individual seals varied from 43 ± 37 m to 388 ± 149 m, the mean dive duration ranged from 5.6 ± 1.7 min to 22.7 ± 2.7 min (Table 2). The maximum duration observed was 31.3 min. Dives were almost always followed by short surface intervals, with a grand mean of 1.4 ± 0.4 min (mean \pm S.D.), so that the seals spent between 86 and 94 % of their time at sea submerged (Table 2). SI duration was positively related to the duration of the preceding dive for all seven seals (Fig. 3). Dive duration was not correlated with body mass or age, but appeared to be more closely related to where the seals were released or the proportion of time they spent in deep (>140 m) water. Therefore, the dives of each seal were divided into 'on the shelf' and 'off the shelf' groups (Table 2). We assumed that the initial or terminal group of dives shallower than 140 m were on the continental shelf and that dives deeper than 140 m were off the continental shelf. Dives on the shelf were shorter and were followed by shorter surface intervals than those in deeper water (Table 2).

Heart rate at sea

Heart rate at the surface, between dives, was high and stable, with means for individual seals for all dives ranging from 103 to 112 beats min^{-1} (Table 2), with slight oscillations presumably due to respiratory sinus arrhythmia. Upon

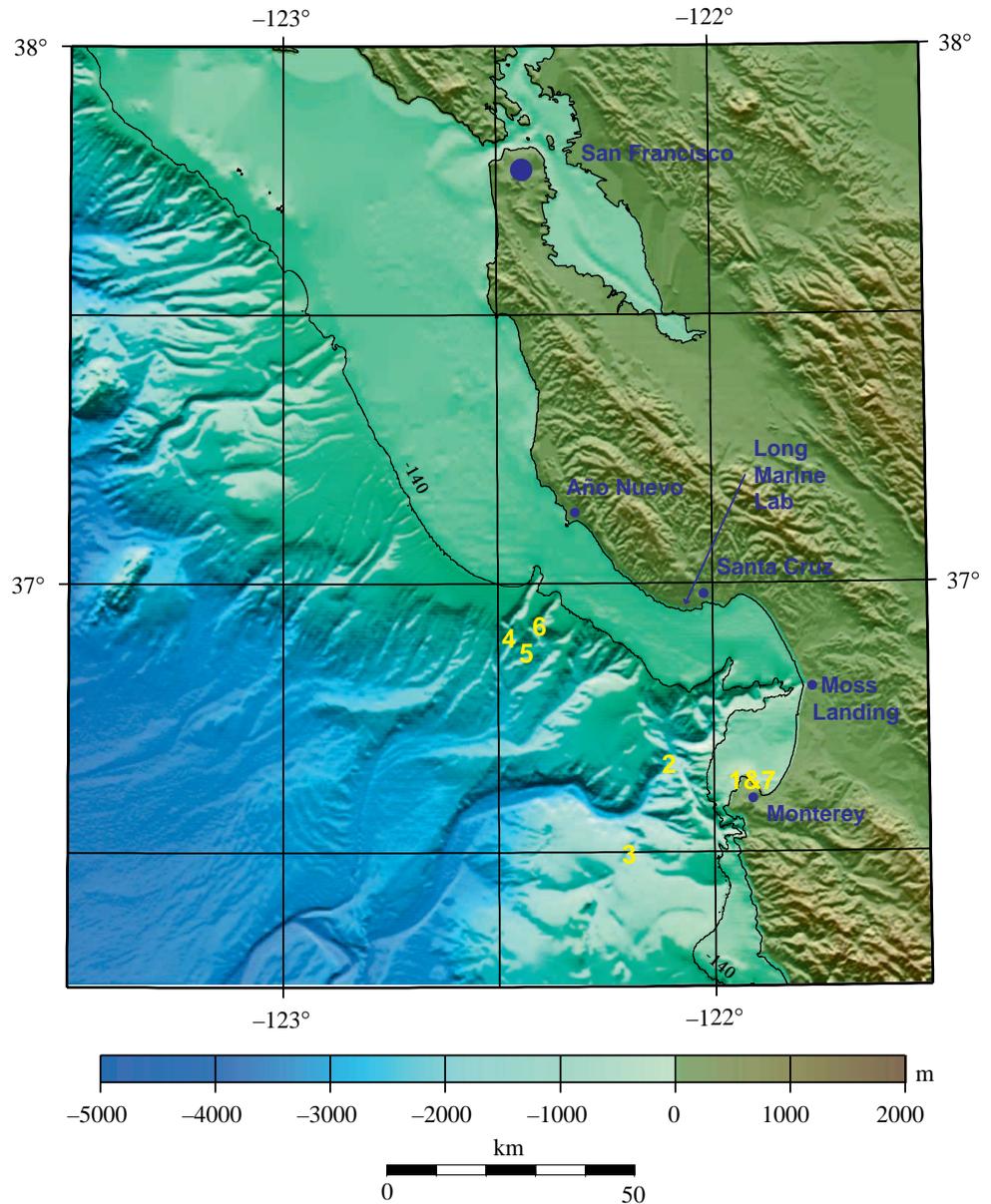


Fig. 1. Contour map of Monterey Bay. Colour scale shows depth (–m) or elevation with respect to sea level (0 m). Numbers denote seal release sites as follows: (1) seal GH817; (2) seal GH890; (3) seal GH911; (4) seal GJ711; (5) seal GH929; (6) seal GJ325; (7) seal GG571.

submergence, heart rate immediately decreased by 50–80% from the SI value. In two seals (GJ325 and GJ711), the first interbeat interval was often the longest seen in the dive. The pattern in most seals, however, was an initial dramatic fall in heart rate followed by a gradual decrease throughout the descent phase (Fig. 2B). In flat-bottom dives, heart rate levelled off between 20 and 50 beats min^{-1} (Fig. 2B, right). During the dive, heart rate was arrhythmic with oscillations of 10–20 beats min^{-1} being common. Heart rate began to rise gradually upon ascent, but this anticipatory tachycardia was most pronounced in the last 15 s of ascent so that, just before surfacing, heart rates had nearly returned to the pre-dive value. Mean dive heart rate was significantly lower than both the SI mean heart rate and the mean heart rate for the complete dive cycle (Table 2). Mean dive heart rate and mean dive cycle heart rate were both significantly higher in dives performed on the shelf than off the shelf (Table 2). Occasionally, heart rate

during a dive reached exceptionally low values. Such profound bradycardia was associated with a sudden change in dive behaviour, such as a reversal during ascent (Fig. 4A,B), and the longest interbeat interval observed was 26 s (instantaneous heart rate 2.3 beats min^{-1}).

Variability in the heart rate response over the course of many dives is seen in Fig. 2A. The mean diving heart rate was significantly negatively related to dive duration for all seven seals ($r^2=0.33\text{--}0.75$). For five of the seals, this relationship was clearly not linear. Data including all dives from three of these seals are illustrated in Fig. 5. The best and most parsimonious continuous curvilinear model found to describe the heart rate–dive duration relationship was a second-order polynomial. A two-segment linear regression threshold model was also fitted to these data. Three of the seals had a significantly negative first segment, while all five had a significantly negative second segment of steeper slope. The threshold between the phase with

Table 1. Summary of the translocated northern elephant seals and their homing behaviour

Seal tag no.	Sex	Age (months)	Mass (kg)	Recording instruments	Release date	Release site	Time at sea (days)	Hours analyzed
GH817	F	15	134	HR-TDR	27 May 91	HMS (1)	1.6	11.1
GH890	F	22	208	HR-TDR	02 Oct. 91	SEAS (2)	3.8	39.5
GH911	M	22	206	HR-TDR	07 Oct. 91	SEAS (3)	3.7	29.1
GG571	F	34	245	Holter	13 Nov. 91	HMS (7)	1.2	13.3
GH929	M	22	232	Holter	16 Nov. 91	SEAJ (5)	1.1	12.9
GJ325	M	16	177	Holter	03 June 92	SEAJ (6)	1.1	10.1
GJ711	M	16	150	Holter	12 May 93	SEAJ (4)	0.6	5.5

HR-TDR, digital heart rate–time/depth recorder; Holter, analogue electrocardiogram recorder plus digital time/depth recorder; HMS, Hopkins Marine Station; SEAS, at sea from R.V. *Sproul*; SEAJ, at sea from R.V. *David Johnston* (numerals in parentheses correspond with sites marked on Fig. 1).

Table 2. Comparisons of the dive behaviour and heart rate parameters for dives on and off the continental shelf and for all dives

Seal tag no.	Number of dives	Range of dive duration (min)	Mean dive duration (min)	Mean SI duration (min)	Mean % time submerged	Mean depth (m)	Mean dive heart rate (beats min ⁻¹)	Mean SI heart rate (beats min ⁻¹)	Mean dive cycle heart rate (beats min ⁻¹)
On the shelf									
GH817	53	1.7–14.8	7.4±3.1	1.14±0.36	85.6	70±33	48.4±3.8	102.7±5.8	56.2±4.1
GH890	59	2.2–22.5	9.9±4.2	1.49±0.49	86.0	67±37	45.7±2.1	105.2±6.2	53.9±3.1
GH911	17	4.7–18.3	12.0±3.8	1.55±0.29	87.9	96±27	38.2±3.0	115.1±7.1	47.3±3.9
GG571	43	4.8–18.8	12.9±3.9	1.17±0.27	91.2	72±26	38.8±1.7	105.1±1.8	45.0±2.5
GH929	42	1.0–17.7	10.6±4.1	1.02±0.23	89.4	54±37	37.8±2.3	105.5±3.0	44.4±5.6
GJ325	26	6.9–12.0	9.9±1.5	1.41±0.32	87.4	99±19	42.6±2.4	110.9±1.4	51.2±2.4
GJ711	41	2.1–8.3	5.6±1.7	0.81±0.19	86.6	43±37	37.2±3.0	104.8±2.9	46.1±4.2
Grand mean			9.8±2.5	1.22±0.27	87.8±2.0	72±20	41.2±4.4	107.0±4.4*	49.2±4.6*
Off the shelf									
GH817	15	9.7–16.5	12.4±1.9	1.87±0.32	86.9	247±70	42.8±3.3	106.0±0.3	51.1±3.7
GH890	73	10.5–30.8	21.2±4.9	2.10±0.42	90.7	373±74	37.8±4.4	111.9±4.6	44.6±4.0
GH911	70	8.5–31.3	19.6±4.5	2.08±0.31	90.0	377±93	33.4±4.5	111.4±3.3	41.2±5.3
GG571	8	18.7–25.6	22.7±2.7	1.56±0.3	93.6	339±86	31.8±2.5	106.6±1.1	37.3±2.7
GH929	14	11.6–24.2	19.3±3.5	1.24±0.24	93.9	388±149	31.2±3.5	111.4±1.6	38.0±3.2
GJ325	19	12.0–17.7	14.9±1.9	1.64±0.40	90.0	234±39	36.8±4.6	108.1±1.3	43.9±4.0
GJ711	6	8.5–10.1	9.6±0.6	1.50±0.21	86.4	180±37	31.3±6.4	105.1±4.9	41.3±6.0
Grand mean			17.1±4.9†	1.71±0.31†	90.2±2.9†	305±84†	35.0±4.3†	108.6±2.9*	42.5±4.7*†
All dives									
Grand mean			12.6±4.2	1.40±0.39	88.8±2.0	162±89	39.0±4.3	107.3±3.1*	46.6±4.5*

Values are presented as mean ± s.d.

A grand mean is the mean of the individual seal means.

SI, surface interval.

One dive cycle is a dive and the subsequent SI.

*Significantly different from the dive heart rate value for that location (on or off shelf), or for all dives.

†Significant difference between 'on the shelf' and 'off the shelf' value.

Sequential Bonferroni procedure was used to minimise Type 1 errors in the multiple (7) paired *t*-tests performed between locations.

little or no dependence of heart rate on dive duration and the phase of a strong inverse relationship ranged from 9.7 to 18.5 min. Although both the threshold model and the curvilinear model were significantly better descriptors of the relationship than a single linear regression, there was no difference between

the MSE or the RSS of the threshold and curvilinear models. Heart rate in the period 30–60 s after the dive commenced was examined to test whether the general pattern of an inverse relationship between heart rate and dive duration was the result of the seal setting heart rate for a dive of planned duration. No

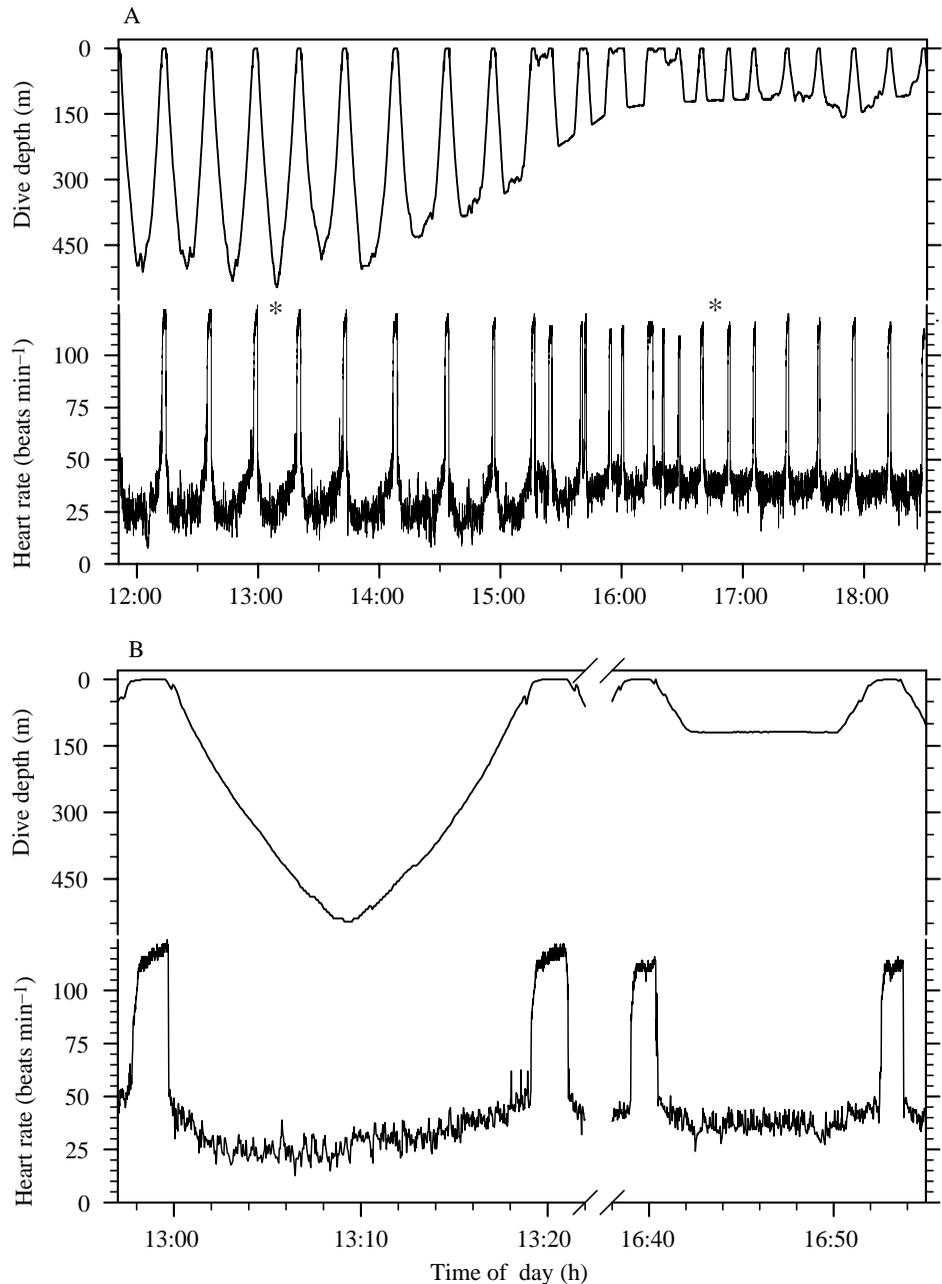


Fig. 2. (A) Dive depth and instantaneous heart rate record of seal GH929. The seal was released at sea at 10:40 h on the day the record was taken. (B) Expanded view of the two marked (*) dives from A to illustrate the difference in heart rate between a V-shaped, deep, long dive and a shorter, shallower flat-bottom dive.

relationship was found between this early heart rate and dive duration. However, six of the seven seals had a significantly negative relationship between heart rate 60–120 s into the dive and dive duration, suggesting that the heart rate–dive duration relationship was partially due to the gradual decrease in heart rate during descent, not the initial level to which heart rate dropped.

Heart rate during apnoea and eupnoea on land

During periods of quiet wakefulness or sleep, the respiratory pattern on the beach was one of alternating periods of apnoea and eupnoea (Fig. 6A). This pattern was repeated for up to 4.5 h when the seals were undisturbed. Mean apnoea duration

ranged from 5.4 to 12.9 min among the four seals, and the maximum apnoea observed was 20.3 min (Table 3). Apnoea/eupnoea cycles on land were compared with those at sea for dives on the shelf, because of the similar mean apnoea durations, as opposed to the longer apnoea durations of dives off the shelf (Table 3). Neither the mean nor the maximum apnoea duration on land was significantly different from the diving, or apnoea at sea, duration. However, the mean eupnoea duration, which ranged from 3.2 to 4.8 min, was significantly longer than the SI, or eupnoea at sea, duration (Table 3). Therefore, the percentage of time spent in apnoea differed significantly between periods at sea and on land. Another striking difference was the lack of any relationship between

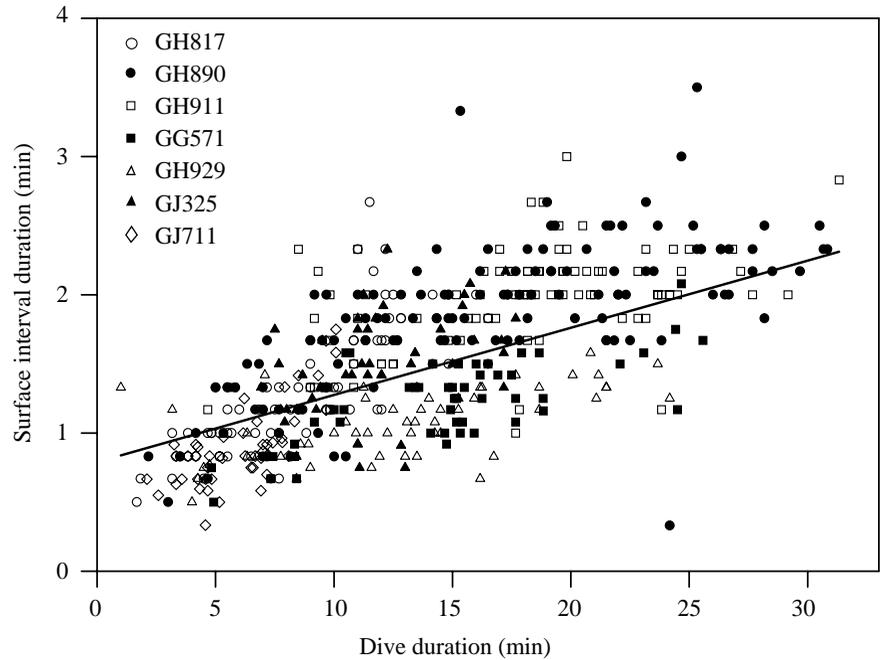
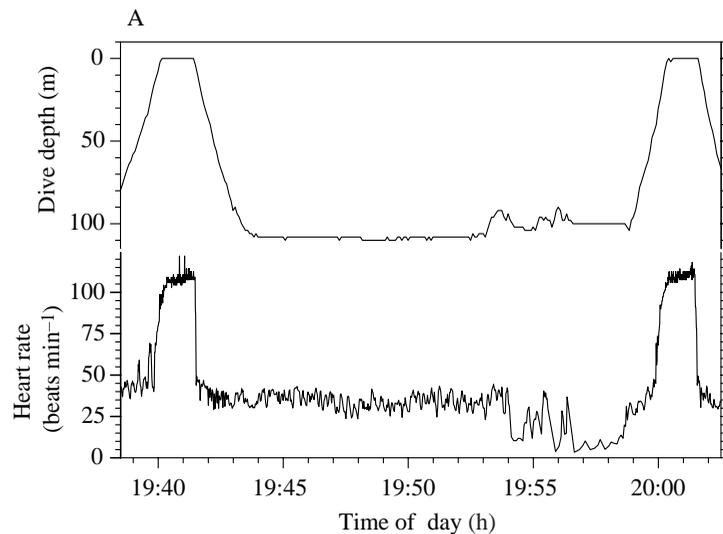


Fig. 3. Surface interval duration plotted against the duration of the preceding dive. Values for each seal demonstrated a significant positive relationship, with r^2 ranging from 0.16 to 0.65. The plotted regression line is the average relationship for all seals and is described by $y=0.79+0.049x$, where y is surface interval and x is dive duration.



B

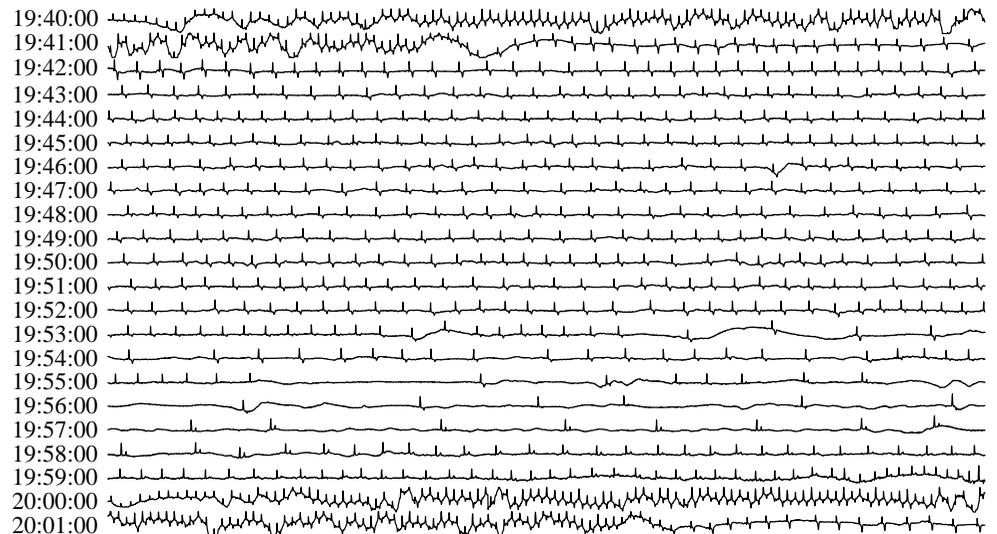


Fig. 4. Dive depth and instantaneous heart rate record from seal GG571. (A) Start time of centre dive, 19:41:29 h; end time, 20:00:06 h; next dive start time, 20:01:38 h. Note that, after ascending for 1 min, at 19:53:39 h, the seal reversed its direction and simultaneously heart rate dropped dramatically. This pattern was repeated 2.5 min later. From 19:53:30 to 19:58:30 h, the mean heart rate was $13.6 \text{ beats min}^{-1}$. (B) The ECG trace for the same period, each line is a 1 min strip. Note the 17.6 s interbeat interval that starts at 19:55:51 h.

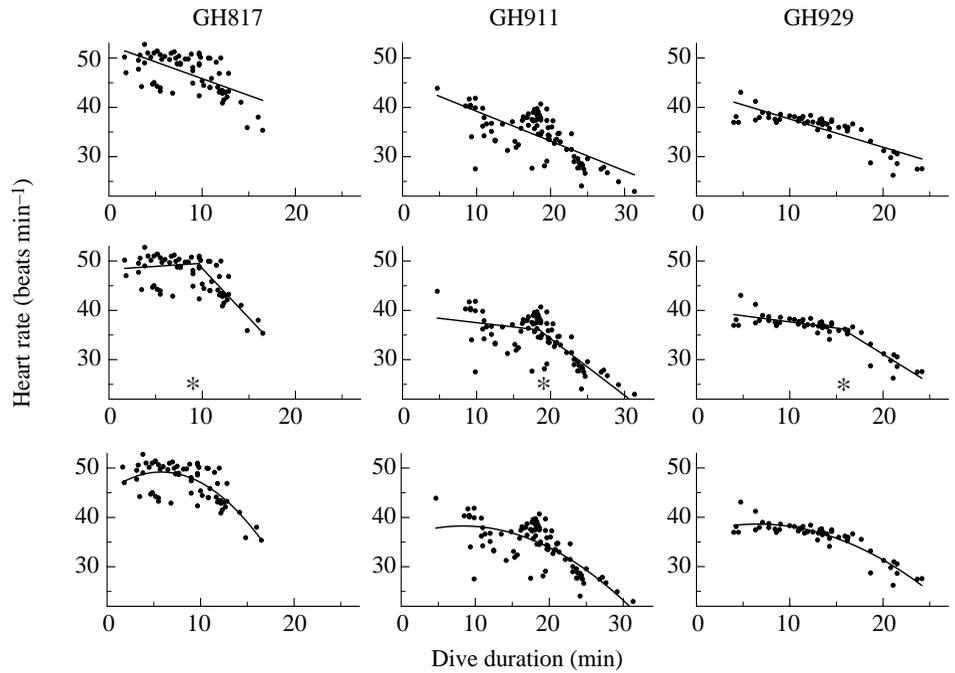


Fig. 5. Mean dive heart rate plotted against the dive duration for all dives of three seals. Top row, single linear regressions fitted to the data. The distributions of the points around the lines are biased, especially on the right-hand side, where all the points lie below the lines. Middle row, two-segment linear regression model fitted to the data, with the thresholds (*) marked on the abscissas. Bottom row, continuous curvilinear model, a second-order polynomial, fitted to the data.

eupnoea duration and the length of the preceding apnoea when on land.

At the start of an eupnoeic period on land, heart rate was 70–80 beats min⁻¹, but it gradually decreased throughout eupnoea as the apparent respiratory sinus arrhythmia became

more pronounced (Fig. 6C). Mean eupnoeic heart rate on land was 65±8 beats min⁻¹ for the four seals and 40% lower than the SI (eupnoea at sea) heart rate (Table 3). By the end of the last expiration in an eupnoeic period, heart rate fell to between 30 and 50 beats min⁻¹, which was close to the minimum heart

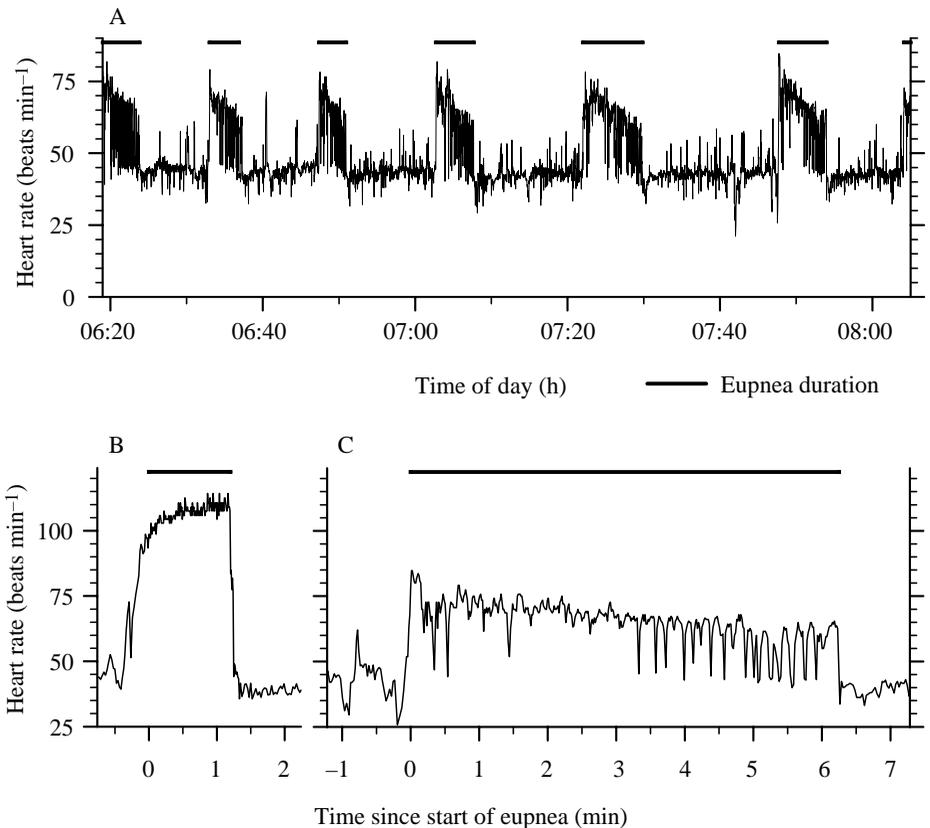


Fig. 6. Heart rate and respiration records for seal GG571; the onset and duration of eupnoeas are indicated by bars above the instantaneous heart rate trace. (A) A 106 min sequence of apnoea cycles on the beach; apnoea duration in chronological order, 9.5, 10.4, 11.8, 14.3, 17.8 and 10.1 min. (B) A 1.21 min eupnoea at sea, which followed a 17.5 min dive, is presented for comparison with a 6.25 min eupnoea on land (C) that followed an 18.1 min apnoea.

Table 3. Comparisons of the durations and heart rates of apnoea and eupnoea at sea (diving on the shelf only) and on land

	Seal GG571		Seal GH929		Seal GJ325		Seal GJ711		Grand mean	
	At sea	On land	At sea	On land	At sea	On land	At sea	On land	At sea	On land
Total no. of apnoeas	43	36	42	21	26	51	41	21	38.0±8.0	32.5±14.4
Mean apnoea duration (min)	12.9±3.9	9.8±3.9	10.6±4.1	12.6±4.9	9.9±1.5	5.4±2.0	5.6±1.7	8.4±3.2	9.7±3.1	9.0±3.0
Maximum apnoea duration (min)	18.8	18.7	17.7	20.3	12.0	9.0	8.3	14.2	14.2±4.9	15.5±5.1
Mean eupnoea duration (min)	1.17±0.27	4.81±1.55	1.02±0.23	4.74±1.78	1.41±0.32	4.16±2.0	0.81±0.19	3.21±1.21	1.10±0.25	4.23±0.74*
Mean % time in apnoea	91.2	65.5	89.4	71.6	87.4	56.2	86.6	71.4	88.7±2.1	66.2±7.2*
Mean apnoea heart rate (beats min ⁻¹)	38.8±1.7	42.5±2.5	37.8±2.3	37.7±2.3	42.6±2.4	54.8±3.6	37.2±3.0	44.5±4.3	39.1±2.4	44.9±7.2
Mean eupnoea heart rate (beats min ⁻¹)	105.1±1.8	60.4±4.3	105.5±3.0	58.6±7.0	110.9±1.4	77.0±5.7	104.8±2.9	64.0±7.8	106.6±2.9	65.0±8.3*
Mean apnoea cycle heart rate (beats min ⁻¹)	45.0±2.5	48.4±2.8	44.4±5.6	43.4±2.9	51.2±2.4	64.5±5.6	46.1±4.7	50.0±4.6	46.7±3.1	51.6±9.1

Values are presented as mean ± S.D.

Apnoea cycle is an apnoea and the subsequent eupnoea.

Sequential Bonferroni procedure was used to minimise Type I errors in the multiple (7) paired *t*-tests.

*Significantly different from the value at sea.

rate of the sinus arrhythmia during the last few breaths (Fig. 6C). Heart rate during apnoea on land was on average 31 % lower than that during eupnoea (Table 3), and the mean was quite stable throughout apnoea, despite frequent arrhythmic oscillations (Fig. 6A). The apnoeic heart rate was significantly different from both the eupnoeic heart rate and the complete apnoea cycle heart rate. Unlike the pattern during diving, there was no relationship between apnoeic heart rate and apnoea duration. The mean apnoeic heart rate on land was not significantly different ($P=0.11$) from the mean diving heart rate (on the shelf), nor was there any difference between dive cycle and land apnoea cycle heart rate ($P=0.20$, Table 3).

Mean daily heart rates on land and at sea

Mean daily heart rate on land was predicted by including the periods of activity (originally excluded) which took place in eupnoea and multiplying the increased proportion of time in eupnoea by mean eupnoeic heart rate and the decreased proportion of time in apnoea by mean apnoeic heart rate. Predicted mean daily heart rate at sea for these four seals was considered to be equivalent to the dive cycle heart rate for dives on or off the shelf. Predicted mean daily heart rate at sea for diving on the shelf ($46.7±3.1$ beats min⁻¹) was not significantly different from predicted mean daily heart rate on land (mean $54.6±9.3$ beats min⁻¹), whereas the predicted mean daily heart rate for diving off the shelf (mean $40.1±3.1$ beats min⁻¹) was significantly lower than the predicted mean daily heart rate on land ($P=0.02$).

Discussion

The translocation method is a suitable and rewarding technique for short-term physiological study of the northern

elephant seal. When the translocated seals were in deep water, their diving pattern was very similar to that observed in naturally migrating juveniles. For naturally migrating juvenile elephant seals, the mean dive depth is $373±77$ m and the mean dive duration is $15.2±2.6$ min (Le Boeuf *et al.* 1996), while in this study the means for 'off-the-shelf' dives were $305±84$ m and $17.1±4.9$ min, respectively. Another advantage of the translocation method is that once the seals are released the effect of the observer's presence is removed. Other methods previously used to monitor the cardiac response to diving in free-ranging pinnipeds have involved the presence of a tracking vessel within 1 km (Fedak *et al.* 1988; Thompson and Fedak, 1993) or the semi-natural environment of an ice-hole surrounded by a laboratory hut and researchers (Kooyman and Campbell, 1972; Hill *et al.* 1987). It is important to reduce or eliminate the effect of disturbance when attempting to record the heart rate response to voluntary submergence because the heart rate response of a seal can be modified by the behaviour of observers (Scholander, 1940; Fedak, 1986).

Despite the voluntary and free-ranging nature of diving in these juvenile elephant seals, their heart rate response appeared to be similar to the response of forcibly submerged adult northern elephant seals (Van Citters *et al.* 1965). However, Van Citters *et al.* (1965) acknowledged that the moderate and gradually developed bradycardia seen in those adult seals may have been due to the lingering effects of anaesthesia. Studies of other pinnipeds have demonstrated a dramatic difference between the heart rate responses to forced and voluntary submergence. Forcibly submerged grey (*Halichoerus grypus*), harbour (*Phoca vitulina*) and Weddell (*Leptonychotes weddelli*) seals immediately reduce their heart rate to 10–15 beats min⁻¹ (Scholander 1940; Irving *et al.* 1941; Zapol

et al. 1979), but these same species respond to voluntary diving with a much more moderate, although just as abrupt, bradycardia, with submerged heart rates usually in the range 30–50 beats min^{-1} (Fedak, 1986; Jones *et al.* 1973; Kooyman and Campbell, 1972). The heart rate response to diving in wild, free-ranging individuals of each of these three species is very similar to the response observed in juvenile elephant seals (Thompson and Fedak, 1993; Fedak *et al.* 1988; Kooyman and Campbell, 1972; Hill *et al.* 1987). A remarkable aspect of the elephant seals' response was the occurrence of extremely profound bradycardia. Occasionally when seals made sudden reversals during ascent and extended the dive, heart rate dropped to levels as low as or lower than those seen in the most extreme responses to forced submergence (Fig. 4). If blood pressure is to be maintained, then instantaneous heart rates as low as 2–3 beats min^{-1} must represent almost complete peripheral vasoconstriction with redistribution of blood and its remaining oxygen supply solely to the anoxia-intolerant tissues of the heart and brain.

Ringed (*Phoca hispida*) and grey seals have also been observed to display very low heart rates during free-ranging dives. Ringed seals diving below ice cover on an experimental pond often reduce their heart rate to less than 10 beats min^{-1} when diving (Elsner *et al.* 1989), and freely diving grey seals sometimes display profound bradycardia even though their access to air is not restricted (Thompson and Fedak, 1993). Mean diving heart rate during grey seal foraging dives that last more than 10 min is always less than 20 beats min^{-1} , and during one 14 min dive mean heart rate was only 6.5 beats min^{-1} (Thompson and Fedak, 1993). Thompson and Fedak (1993) suggested that such bradycardia reflects a reduction in metabolic costs, especially as the seals do not usually swim during the bottom time of these dives. The grey seals were approximately the same size as the juvenile elephant seals in this study, yet the elephant seals routinely made longer dives with higher heart rates. Even during dives as long as 31 min, mean dive heart rate of elephant seals never fell below 18 beats min^{-1} , and while only 6% of the grey seal dives exceeded 10 min, elephant seals exceeded this duration on the majority of their dives. Elephant seals have greater mass-specific oxygen stores than other phocids that have been examined (Thorson, 1993), which may explain why they make much longer dives than grey seals without resorting to such severe rationing of the blood oxygen stores.

It would appear, however, that elephant seals restrict blood flow, as reflected by heart rate changes, to at least some tissues during many dives and that this response is dependent upon the length of the dive. Kooyman (1985, 1989) suggested that the short- to medium-duration voluntary dives of Weddell seals involve little cardiovascular adjustment compared with resting conditions, whereas relatively long dives (>20 min) are more similar to forced submergence with extreme bradycardia and peripheral vasoconstriction. Hill *et al.* (1987) confirmed this prediction for Weddell seals by showing that mean dive heart rate was negatively related to dive duration for dives longer than 20 min, but that there was no correlation for shorter dives.

If elephant seals operate according to Kooyman's (1985) model of the Weddell seal dive response, mean heart rate for short dives should show little or no dependence on dive duration, but beyond some threshold the slope of the relationship should become much steeper. In addition, Le Boeuf and Crocker (1996) showed that when elephant seals are diving on the shelf, they make shorter dives and swim faster than when they are off the shelf. Higher swimming speeds may result in higher heart rates, and we found that both diving heart rate and dive cycle heart rate were higher for dives on the shelf than off. However, swimming speed was not measured in this study, and in laboratory studies both grey and harbour seals showed no dependence of submerged heart rate on swimming speed (Fedak, 1986; Williams *et al.* 1991). Nevertheless, dives performed on the shelf are invariably shorter than those in deep water, which might cause a step change in the relationship between heart rate and dive duration. Although a two-segment linear regression threshold model described the data for five of the elephant seals significantly better than a single regression model, a simpler continuous curvilinear model fitted the data equally well (Fig. 5).

Furthermore, contrary to the suggestion of Kooyman and Campbell (1972) that seals anticipate the duration of a dive and adjust their heart rate accordingly at the beginning of a dive, we found no relationship between heart rate 30–60 s after the dive commenced and dive duration. We did, however, find that such a negative relationship existed for heart rate during the period 60–120 s into the dive for six of the seals. Given that heart rate appears to fall gradually during descent and then levels off or begins to increase if ascent immediately follows (Fig. 2), it appears that elephant seals do not anticipate dive duration but instead adjust their heart rate response throughout a dive. As the seal descends deeper, its heart rate falls to a lower level, so that deeper, longer dives have lower heart rates. This pattern of a gradual and continual adjustment of the heart rate response supports the continuous curvilinear model, rather than a threshold model, to explain the relationship between heart rate and dive duration. Such a continuously graded heart rate response may also represent a gradual reduction in metabolic rate with increasing dive duration. Oxygen consumption measured over a dive plus surface cycle does decline with increasing dive duration in both Weddell and grey seals (Castellini *et al.* 1992; Reed *et al.* 1994). Studies on terrestrial mammals have shown that there is a close match between blood flow and oxygen consumption, at both the cellular and whole-animal levels, from below resting levels up to moderate exercise, and it has been suggested that reduced perfusion may cause a suppression of overall metabolism in large seal species (Hochachka, 1992).

Although the ADL concept has been experimentally verified by lactate measurements in Weddell seals, estimated ADLs have been calculated for many other species of diving vertebrates by measuring available oxygen stores and dividing by either a measured or an estimated diving metabolic rate, without measurements of lactate production (Kooyman, 1989). At least for elephant seals, it would appear that the method of

assuming a single value for diving metabolic rate is not valid. If metabolic rate, like heart rate, is continuously being adjusted, then there can be no single time limit for aerobic dives. Thorson and Le Boeuf (1994) have shown that metabolic rate and dive duration are inversely correlated in juvenile elephant seals voluntarily diving in the laboratory. Therefore, one would not expect to see a threshold for the production of net lactate, but rather lactate concentration in elephant seals might increase continuously with increasing dive duration. If elephant seals are able to reduce metabolic rate through reduced perfusion without an increase in anaerobic metabolism, then the increase in post-dive lactate levels on longer dives may be negligible, which would help to explain how recovery from extremely long dives apparently occurs during very short surface intervals.

Post-dive recovery in elephant seals is probably aided by high surface heart rates and the anticipatory tachycardia before surfacing (Fig. 2). As Thompson and Fedak (1993) pointed out, this anticipatory increase probably reflects a restoration of circulation to tissues that may have been under-perfused during the dive, and such tissues, especially myoglobin-rich muscle, will reduce the P_{O_2} of the blood, thereby maximising oxygen uptake at the beginning of the SI. However, this depletion of oxygen could be detrimental to the oxygen-dependent brain and heart if a seal were forced to reverse its ascent before reaching the surface. This risk may be countered by the benefit of short surface times if the anticipatory tachycardia as well as the very high SI heart rates allow seals to minimise time spent at the surface. Both grey and elephant seals have significantly higher heart rates between dives than do Weddell seals (Thompson and Fedak, 1993; Hill *et al.* 1987), which might partially explain why grey and elephant seals have much shorter surface intervals than Weddell seals.

Another possibility is that grey and elephant seals breathe at a higher frequency during surface intervals than do Weddell seals, although these measurements have only been made at sea for Weddell seals. Milsom *et al.* (1996) reported that, in elephant seal pups, the instantaneous respiratory frequency at the beginning of an eupnoea on land is positively related to the duration of the preceding apnoea. Although juvenile elephant seals respond to the presumably increased respiratory drive of longer dives by breathing for longer, this relationship between SI duration and dive duration has a low slope (Fig. 3) and is not found in adult elephant seals (Le Boeuf *et al.* 1988). Therefore, it would be worthwhile to test whether juvenile and adult elephant seals respond similarly to pups on land and breathe faster after longer dives at sea.

The biggest difference between the heart rate patterns at sea and on land in juvenile elephant seals was the much higher heart rates during breathing at sea (Table 3). The breathing periods were much shorter at sea and were related to the duration of the preceding dive, whereas on land eupnoeic periods were 3.5 times longer and were not related to the duration of the preceding apnoea. Apparently, seals on the beach did not have the same drive to minimise eupnoeic periods as they did at sea. On land, the entrance into apnoea

was accompanied by a drop in heart rate to at least the minimum level observed between breaths near the end of the preceding eupnoea, a pattern previously reported in weaned pups and adult males (Castellini *et al.* 1994a,b). Although heart rate dropped to a similar level at the beginning of dives, the dive response appears to be more complicated than merely a cessation of breathing. If, like freely diving captive grey seals (Reed *et al.* 1994), respiratory tidal volume and flow rate do not vary during the course of an elephant seal's surface interval, then it is unlikely that the immediate drop in heart rate upon submergence is simply due to the physiological response that accompanies the last exhalation. Furthermore, heart rate during apnoea on land did not continue to fall after the first few beats, whereas heart rate at sea declined as the seal descended (Figs 4, 6). There were also differences at the end of apnoeas. While the increase in heart rate at the end of an apnoea on land was probably due to the commencement of breathing, the increase was never as great as that seen at the end of a dive, and the increase in heart rate near the end of a dive always started well before the first breath was taken. Another important difference was that heart rate during diving was inversely related to dive duration, but there was no relationship between apnoea heart rate and apnoea duration on land. During apnoea at sea, elephant seals must always conserve enough oxygen for the heart and brain in case their return to the surface is delayed, whereas on the beach a seal with depleted oxygen stores can always just start breathing immediately. Therefore, the cardiovascular adjustments seen at sea are an important response to diving and not merely to apnoea.

Whether at sea or on land, the heart rate response to apnoea is properly termed a bradycardia. As suggested by others (Belkin, 1964; Kooyman, 1985; Fedak, 1986), we have compared breath-holding heart rate to a long-term mean rate, rather than just to the mean breathing heart rate. Heart rate was significantly lower during dives and during beach apnoeas than the mean daily heart rate at sea or on land, respectively (Table 3). These mean daily heart rate values were even lower than predicted rates based on allometric scaling relationships of terrestrial mammals. The equation presented by Stahl (1967) predicts a resting heart rate of $64.6 \text{ beats min}^{-1}$ for a 193 kg (mean mass of seals in this study) adult mammal, but these diving, exercising juvenile elephant seals had much lower heart rates during individual dives as well as during complete dive and surface cycles. This result might be expected given that phocids tend to have slightly larger hearts and thus larger stroke volumes than other mammals (Bryden, 1972; Drabek, 1977) and, therefore, could potentially produce the same cardiac output with a lower heart rate. However, Ponganis *et al.* (1990) showed that, although harbour seals have a stroke volume during ventilation of 1.2–1.8 times that of resting dogs and goats of similar mass, stroke volume falls by 30–50% during trained dives. If stroke volume also decreases during breath-holding in elephant seals, then their low heart rates cannot be due to their large hearts. An alternative explanation is that the amount of oxygen ejected from the heart on each

beat is greater in elephant seals than in typical terrestrial mammals. Elephant seals have unusually high haematocrits and cellular haemoglobin concentrations, so that a unit of elephant seal blood carries much more oxygen than a similar unit of blood from a terrestrial mammal (Castellini *et al.* 1986; Thorson and Le Boeuf, 1994). These low heart rates may also be simply a reflection of a low field metabolic rate, but this hypothesis awaits testing.

Predicted mean daily heart rate on land was very similar to that at sea. The elephant seal's arrhythmic breathing pattern on land with a low overall respiratory frequency has obvious advantages for water conservation in an animal that is fasting for a month or more (Huntley *et al.* 1984; Blackwell and Le Boeuf, 1993). However, a more important benefit may be the reduction in metabolic rate that potentially accompanies the bradycardia associated with apnoea. Fasting seals clearly have a need for energy and fuel conservation, just as oxygen conservation is important in a diving seal.

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