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RESPIRATION AND HEART RATE AT THE SURFACE BETWEEN DIVES IN NORTHERN ELEPHANT SEALS

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Summary

All underwater activities of diving mammals are constrained by the need for surface gas exchange. Our aim was to measure respiratory rate (f_B) and heart rate (f_H) at the surface between dives in free-ranging northern elephant seals *Mirounga angustirostris*. We recorded f_B and f_H acoustically in six translocated juveniles, 1.8–2.4 years old, and three migrating adult males from the rookery at Año Nuevo, California, USA. To each seal, we attached a diving instrument to record the diving pattern, a satellite tag to track movements and location, a digital audio tape recorder or acoustic datalogger with an external hydrophone to record the sounds of respiration and f_H at the surface, and a VHF transmitter to facilitate recovery. During surface intervals averaging 2.2±0.4 min, adult males breathed a mean of 32.7±5.4 times at a rate of 15.3±1.8 breaths min^{-1} (means ± S.D., N=57). Mean f_H at the surface was 84±3 beats min^{-1}. The f_B of juveniles was 26 % faster than that of adult males, averaging 19.2±2.2 breaths min^{-1} for a mean total of 41.2±5.0 breaths during surface intervals lasting 2.6±0.31 min. Mean f_H at the surface was 106±3 beats min^{-1}. f_B and f_H did not change significantly over the course of surface intervals. Surface f_B and f_H were not clearly associated with levels of exertion, such as rapid horizontal transit or apparent foraging, or with measures of immediately previous or subsequent diving performance, such as diving duration, diving depth or swimming speed. Together, surface respiration rate and the duration of the preceding dive were significant predictors of surface interval duration. This implies that elephant seals minimize surface time spent loading oxygen depending on rates of oxygen uptake and previous depletion of stores.

Key words: respiration, heart rate, surface interval between dives, diving behaviour, elephant seal, *Mirounga angustirostris*, marine mammal, swimming, aerobic dive limit, pinniped.

Introduction

Diving marine mammals must surface for gas exchange, a necessity that affects all their aquatic activities. By rapidly exchanging O_2 and CO_2, seals can minimize surface times and maximize submergence times for foraging (Kooyman, 1982; Fedak et al., 1988). In species that dive during horizontal travel (Thompson et al., 1991; Le Boeuf et al., 1992), movements and migrations to foraging areas are most efficient when time under water is maximized. This is because the highest energetic cost of swimming occurs within a few body lengths of the surface (Hertel, 1966). Moreover, minimizing surface time in nearshore waters may reduce the probability of attack by surface predators such as white sharks *Carcharodon carcharias* or killer whales *Orcinus orca* (Le Boeuf and Crocker, 1996). For these reasons, animals such as elephant seals, *Mirounga* spp., spend as much as 90 % of their time at sea submerged (Le Boeuf and Laws, 1994).

Rapid gas exchange is facilitated by the ventilatory tachycardia and increased ventilation that occur during surfacing (Gallivan, 1981; Hill et al., 1987; Fedak, 1986; Williams et al., 1992; Andrews et al., 1997; Hindell and Lea, 1998). This allows the pathways for oxygen delivery to be primed when the rate of oxygen intake is highest. The terminal airways of phocid seals are only moderately reinforced (Denison and Kooyman, 1973) compared with those of diving otariids, potentially limiting flow rates at low lung volumes during expiration (Drabek and Kooyman, 1984) and requiring longer surface times for oxygen loading (Williams et al., 1991).

The aim of this study was to record respiratory rate (f_B) and heart rate (f_H) at the surface between dives in free-ranging adult and juvenile northern elephant seals *Mirounga angustirostris*. Although the free-ranging diving behavior of the elephant seal has been studied extensively, little is known of the normal f_B and f_H during surface intervals, especially in relation to homing, migration and foraging.

Background information

Northern elephant seals dive deeply (modal depths 400–600 m), for long periods (mean 20–22 min) and virtually continuously during 2- to 8-month biannual foraging migrations from rookeries in central and southern California across the northeastern Pacific (Le Boeuf et al., 1988, 1993, 2000; Stewart and DeLong, 1995; Stewart, 1997). Between dives, elephant seals remain stationary with only the anterior part of the head and snout breaking the surface to allow breathing (Davis et al., 1993; Le Boeuf and Crocker, 1996; Williams et al., 2000). Over 98 % of the surface intervals recorded are less than 5 min in duration (Le Boeuf et al., 1988). Among these, the mean surface interval is 2.4 min for migrating adult females, 2.9 min for migrating adult males (Le Boeuf et al., 2000) and 2.0 min for migrating juveniles of both sexes, 9–27 months of age (Le Boeuf et al., 1996). Similar surface intervals have been recorded in homing juveniles, i.e. seals returning home to their rookery after being translocated from the rookery and released at sea (Fletcher et al., 1996; Webb et al., 1998b). The surface intervals of all elephant seals are usually less than 3 min long, even following maximum-duration dives and maximum-depth dives (Le Boeuf et al., 1988; Hindell et al., 1992; Slip et al., 1994). This suggests the use of aerobic metabolism during diving.

If oxygen uptake is limiting, we might expect animals to spend longer periods at the surface for gas exchange after longer dives that use a greater proportion of the oxygen reserves. If surface intervals are invariant, we might expect f_B and f_H to be higher after longer dives. Alternatively, if seals maximize the time submerged on every dive, then differences in individual dive durations might reflect differences in diving metabolic rates, not the degree of depletion of oxygen reserves. We would then expect surface f_B and f_H to be relatively invariant despite similar surface intervals. Lastly, we might expect f_B and preceding dive duration to affect the time spent at the surface between dives. This last possibility is perhaps the most reasonable as it only requires the animal to leave the surface when gas exchange has been completed.

Fletcher et al. (1996) recorded f_B and f_H acoustically during surface intervals of three homing juveniles, 1.4–1.8 years old. The mean breathing rate ranged from 22.0 ± 1 to 24.6 ± 1.6 min^{-1}. Surface f_H ranged from a mean of 117 ± 1 to 121.6 ± 0.9 beats min^{-1}, approximately 80 % higher than surface f_H recorded by analogue electrocardiogram (ECG) recorders from captive juveniles in a metabolic tank (Webb et al., 1998a). Andrews et al. (1997) used custom-designed dataloggers and Holter monitors to record f_H in homing juveniles, 1.3–2.8 years old. They confirmed that f_H at the surface is high, 107 ± 3 beats min^{-1}, and showed that mean f_H during dives, 39 ± 4.3 beats min^{-1}, declines by 64 % from surface rates. Hindell and Lea (1998) recorded a decline in mean f_H from 65–95 beats min^{-1} at the surface to 34 ± 23 beats min^{-1} while submerged in a free-ranging adult southern elephant seal, *M. leonina*.

Materials and methods

Subjects and instrumentation

In the spring and autumn of 1996, we translocated six juvenile elephant seals *Mirounga angustirostris* (1.8–2.4 years old) from the Año Nuevo mainland in central California to a release site near Pioneer Seamount, 90 km to the northwest and 60 km west of the continental shelf break. We used this method (Oliver et al., 1998) to examine their behavior as they returned to the rookery, which took 1–4 days. We attached the following instruments to the dorsum of each seal: (i) a custom-made time/depth recorder (TDR) (Datagrabber, Santa Cruz, California, USA) for recording the diving pattern, (ii) a Sony TCD-D8 digital audio tape recorder (DAT) enclosed in an aluminum housing (17.1 cm×12.7 cm×6.7 cm) with an external hydrophone (High Tech, Inc. HT1-SSQ-41b) that recorded the sounds of respiration and heartbeats at the surface, and (iii) a VHF transmitter (Advanced Telemetry Systems, Asanti, MN, USA) to facilitate recovery of the animals on the rookery (Fletcher et al., 1996; Crocker et al., 1997). The TDRs recorded depth with a resolution of ±1 m every 10 s throughout the period at sea. Relative velocity was sampled every 10 s using a Logtron paddle wheel (Flash Electronic GmbH, Dachau, Germany) attached to the dive recorder. Swimming speed was calibrated using the method of Blackwell et al. (1999). The DATs were programmed to record low-frequency sounds (frequency response 20 Hz to 14.5 kHz, 32 kHz sampling rate) continuously for 4–8 h after release, depending on the length of the tapes used.

The juveniles were captured at the Año Nuevo rookery and transported by truck to the Long Marine Laboratory, where they were weighed and measured. Seals were initially immobilized with an intramuscular injection of Telazol. Immobilization was maintained using intravenous injections of ketamine-HCl. Instruments were attached using 10 min marine epoxy (Evercoat Ten-set, Fibre-Evercoat Co., Cincinnati, OH, USA) or neoprene rubber cement to the hair (Le Boeuf et al., 1988; Fletcher et al., 1996). The following day, the seals were transported by ship to the release site and released. All seals returned to the rookery within 4 days, were again immobilized, weighed and measured, and the instruments were recovered.

In the spring of 1997, we deployed a similar set of instruments on three migrating adult males. In addition, an Argos satellite tag was attached to the top of the head for tracking their movements and location (Le Boeuf et al., 2000). The DAT attached to one male (Bop) was controlled by a Tattletale Lite datalogger (Onset Computer Corp., Pocasset, MA, USA) that turned the DAT on for 20 min every third day at 08:00 h, beginning 14 days after attachment. On two other adult males (Tra and Roc), we deployed acoustic dataloggers or Compact Acoustic Probes (CAPs) (Burgess et al., 1998). CAPs contained a hydrophone and a pressure transducer in a 36 cm long, 10 cm diameter cylindrical housing. Within the housing were a programmable Tattletale 7 data-acquisition engine (Onset Computer Corp., Pocasset, MA, USA) and a 340 Mbyte hard disk. The CAPs were programmed to record low-frequency sounds for 20 min (approximately one dive cycle) at 08:00 h every day beginning with departure from the Año Nuevo rookery. With the 20 min acoustic sampling interval, we recorded 0–2 surface intervals. In addition, diving depth was sampled at 30 s intervals throughout the entire migration.

The migratory tracks of the three adult males were calculated for their entire periods at sea using the locations provided by Argos (Le Boeuf et al., 2000). The entire tracks, including the location of the surface intervals sampled acoustically for f_B and f_H, are shown in Fig. 1. The types of dives preceding each sampled surface interval were categorized according to their shape and function as serving transit or foraging (Le Boeuf et al., 1992, 1993).

Summary dive statistics for all subjects, consisting of dive depth, dive duration and surface intervals, were calculated from the diving records (Le Boeuf et al., 1993). Mean swimming speed was calculated for juveniles from all samples excluding zero-speed samples at the surface.

TDR records were used to expedite the location of the surface intervals in the acoustic record (Fig. 2A). Acoustic recordings of surface intervals were then downloaded from the digital recording devices and analyzed using Canary 1.4 spectral analysis program (Cornell University, Ithaca, New York, USA). A spectrogram was generated for each surface interval (Fletcher et al., 1996). Each surface interval (acoustic record or waveform) was then filtered using a 30–90 Hz band-pass filter, and then amplified, if needed, to enhance detection of both breaths and heart beats (Fig. 2B,C). The beginning, end and duration of each surface interval to the nearest second, as well as the number of breaths and heartbeats, were determined using visual and auditory cues. The duration of 25 breaths (the expiratory/ inspiratory cycle) from five surface intervals of each seal and the between-breath interval were measured to the nearest second. Each surface interval time spectrum was analyzed both as a unit and subsampled to look for changes across the surface interval. Subsamples were defined as follows: the first consisted of the first 15 s in the surface interval; the second and third consisted of 15 s intervals centered in the second and third quartiles of the surface interval; the fourth consisted of the last 15 s in the surface interval.

For one juvenile (Sox), the acoustic record was so muffled that only the breathing rate could be determined during surface intervals.

Values are presented as means ± S.D.

Results
Juveniles
On average, juveniles breathed 41.2±5.0 times at the surface at a rate of 19.2±2.2 breaths min^{-1} during surface intervals with a mean duration of 2.6±0.3 min (means ± S.D., Table 1). Mean breath duration (inspiration/expiration cycle) was 1.66±0.11 s, with a mean of 1.62±0.85 s between breaths. Mean f_H at the surface was 106±3 beats min^{-1}. f_B and f_H did not change significantly over the course of the surface interval ($F=<1.18$, d.f.=3,16, $P>0.05$). Mean surface interval, f_B and f_H were not significantly correlated with departure mass ($t=<0.50$, d.f.=4, $P>0.05$).

f$_B$ *and* f$_H$ *in relation to diving behavior*
The relationship between the measured surface variables and diving duration, depth and swimming speed of previous and subsequent dives varied greatly from one seal to another (Table 2). f_B and f_H were positively and significantly correlated in three juveniles but there was little association between these variables in the other two.

f_B did not vary significantly as a function of mean swimming speed during the previous dive among any of the juveniles (Table 2). f_H varied significantly as a function of mean swimming speed during the previous dive in two of the five juveniles ($F=>5.9$, d.f.=1,21, $P<0.05$); the function was positive in one seal (96N2) and negative in the other (Marlin).

The regression of f_B on preceding or subsequent dive duration or dive depth was significant for three of the six juveniles ($F=>13$, d.f.=1,21, $P<0.05$), being positive in each case (Table 2). The regression of f_H on the duration and depth of preceding or succeeding dives was positive and significant for two juveniles, 96N1 and Marlin ($F=>11.0$, d.f.=1,21, $P<0.05$). For each seal whose f_B or f_H varied significantly as a function of previous or subsequent dive duration or dive depth, the relationships were generally similar (Table 2). That is, f_B was equally associated with previous dive duration as with subsequent dive duration (e.g. Sox), and f_H was similarly associated with dive duration as with dive depth (e.g. 96N1).

f_B decreased significantly with surface interval duration in two juveniles (Marlin $r=-0.64$, d.f.=21, $P<0.01$; Sox $r=-0.72$, d.f.=20, $P<0.01$). Correlation coefficients for other juveniles were not statistically significant. f_H increased significantly with surface interval duration for 9601 ($r=0.88$, d.f.=6, $P<0.01$) and decreased significantly for Marlin ($r=-0.59$, d.f.=21, $P<0.01$).

Relationships were more consistent when a multiple regression approach was used. This approach revealed that surface interval duration could be predicted on the basis of respiration rate and the duration of the preceding dive (Table 3). This relationship was significant for all the juveniles. The maximum depth of each dive exhibited a high degree of colinearity with dive duration in all subjects. For this reason, only dive duration was used in multiple regressions. The addition of swimming speed to these regressions did not significantly increase their predictive value.

Marlin and Sox seemed to have the highest level of exertion as indicated by their high swimming speeds, long dive durations and great dive depths (Table 1). Nevertheless, the number of breaths taken at the surface by these animals was near the mean for the group. Marlin seemed to balance his f_B, which was high, with his surface interval duration, which was brief. In contrast, 96N1 and 96N2 appeared to have low levels of exertion. They had the slowest swimming speeds, long surface intervals (96N2) and relatively short dive durations and shallow dive depths. Their f_B and f_H values were low, especially those of 96N2.

Adult males
On average, adult males breathed 32.7±5.4 times at the surface, at a rate of 15.3±1.8 breaths min^{-1} (Table 4). This was 20 % slower than the breathing rate of juveniles. f_B was similar

among the three males, as was the mean surface interval duration, 2.2±0.4 min. As in juveniles, f_B did not change significantly over the course of the surface interval (F=2.26, d.f.=3,8, P>0.05). Mean breath duration was 2.19±0.19 s, with 1.88±0.60 s between breaths, 16–32 % higher than these values in juveniles. Mean f_H at the surface was 84±3 beats min^{-1} and did not change significantly over the surface interval (F=0.48, d.f.=3,8, P>0.05). Mean f_H of adult males was significantly slower than that of juveniles (t=−4.52, d.f.=6, P<0.05).

f_B and f_H in relation to diving behavior

Male Tra traveled further and faster than other males during his migration to the Aleutian Islands, averaging 98.1 km day^{-1}, and his dives were deeper and of longer duration (Fig. 1A; Table 4). His maximum dive duration was 30.3 min. Relative to other males, this male was racing to his destination. Despite an apparently high level of exertion, his f_B, breath duration and inter-breath interval were intermediate to other males and his f_H was the lowest of the three. His surface intervals were only
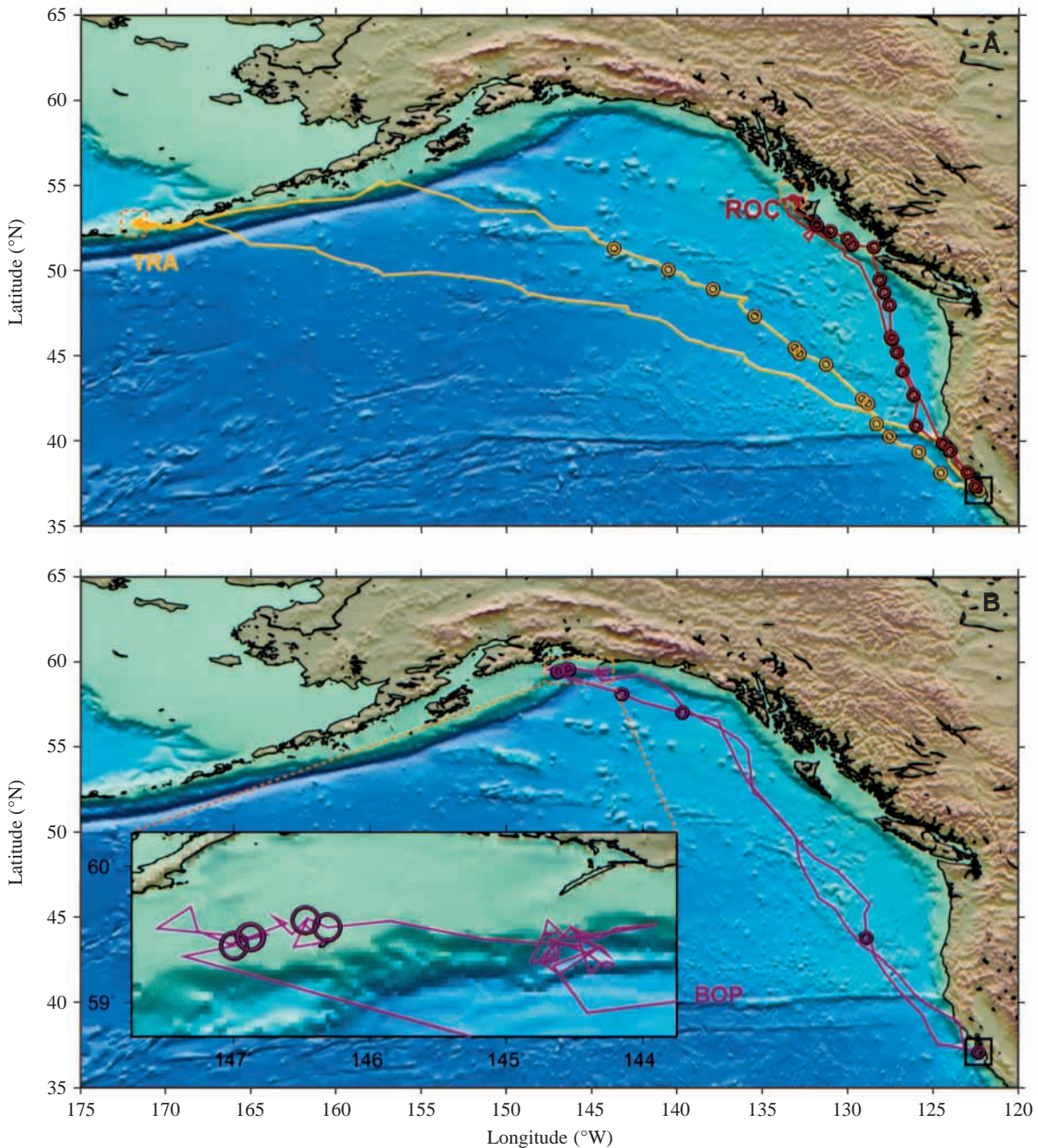
Fig. 1. Migratory tracks of three adult male elephant seals (Roc, Tra and Bop) indicating the starting point at Año Nuevo, California (solid line, open square), acoustic sampling sites (open circles) and the focal foraging area where males spent the majority of their time foraging (dotted line, open squares or rectangle). Because two surface intervals were sampled at some sites, the number of acoustic sampling sites indicated is less than the total number sampled (Table 1).

slightly longer than those of the other males, and surface interval duration and the previous dive duration were not significantly correlated ($r=0.39$, d.f.=20, $P>0.05$). The regression of f_B or f_H on preceding or subsequent dive duration or dive depth was not statistically significant, functions reflected by the correlation coefficients given in Table 2. f_B and f_H were not significantly correlated.

In contrast, Roc traveled slowly on his migration to the Queen Charlotte Islands, averaging 71.5 km day^{-1}, and making short-duration, relatively shallow dives (Fig. 1A; Table 4). His longest dive was 22.7 min. Compared with the performance of Tra, this male exhibited a low level of exertion. Nevertheless, his f_B and f_H at the surface were similar to those of the other males. His surface interval durations, however, were the shortest of all the males, and there was a significant positive correlation between surface interval duration and the previous dive duration ($r=0.82$, d.f.=24, $P<0.05$). His mean breath duration was the shortest and inter-breath interval the longest

of the three males. The regression of f_B on preceding or subsequent dive duration or dive depth was not statistically significant. The regression of f_H on the duration and depth of preceding or succeeding dives was positive and significant ($F=>37$, d.f.=1, 24, $P<0.05$; Table 2). f_B and f_H were not significantly correlated (Table 2). f_H and surface interval duration were positively correlated ($r=0.67$, d.f.=24, $P<0.05$).

Bop's performance was intermediate to the other two males in terms of travel speed, mean dive duration and mean dive depth (Fig. 1B; Table 4). His longest dive was 26.5 min. The first four surface intervals sampled were while he was in transit; the last five surface intervals sampled were obtained once he had reached his destination west of Middleton Island in the northern Gulf of Alaska and was evidently foraging. It was clear that this male had reached his destination from his satellite location and because his horizontal transit speed declined abruptly after having averaged 78 km day^{-1} in transit. We assume that he began foraging at this time because his
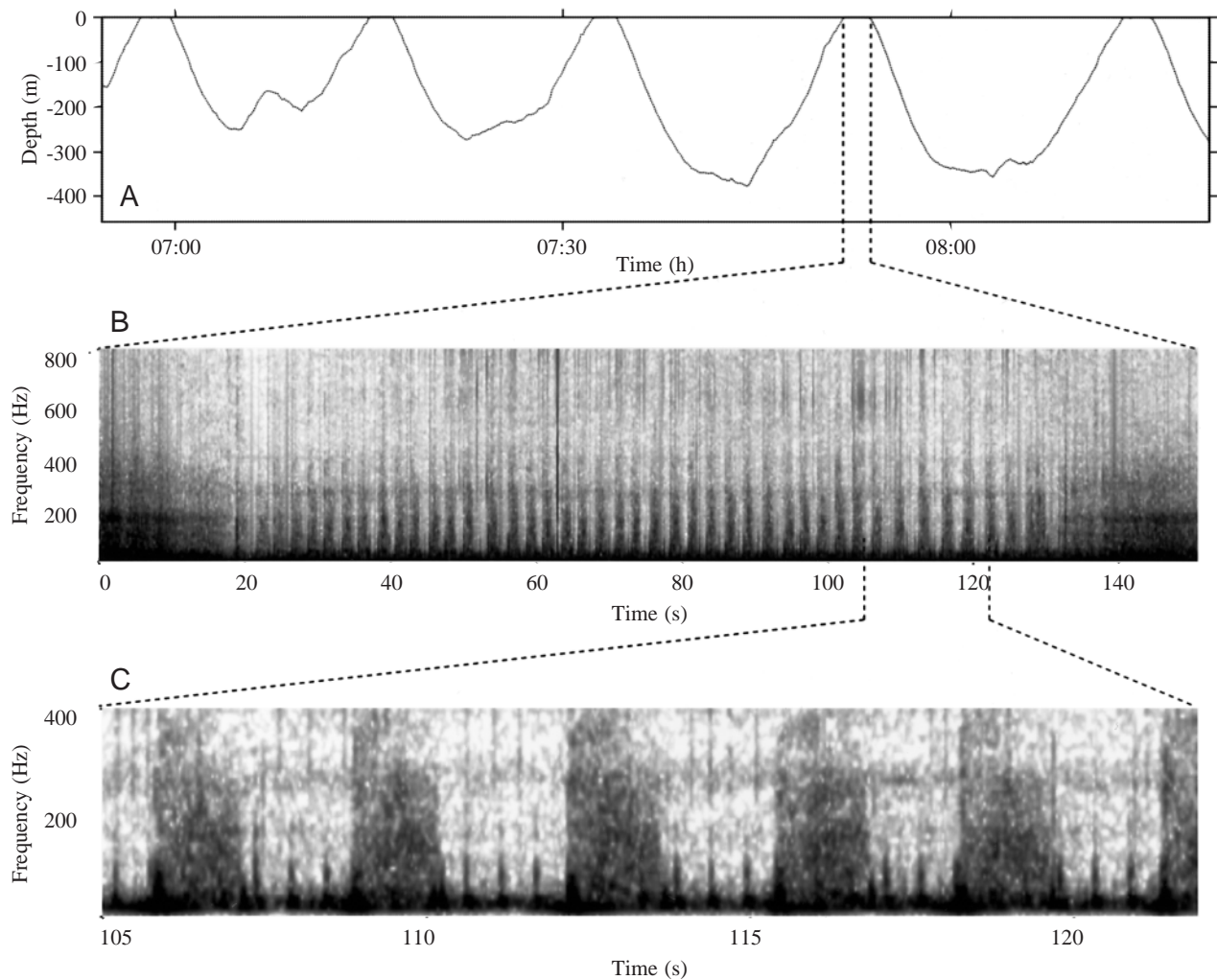
Fig. 2. A diagram of the measurement of key variables showing (A) a typical sequence of four dives from a juvenile diving record indicating diving depth, dive duration and surface interval, (B) a spectrogram of one entire surface interval showing the breathing pattern measured as 43 breaths in 112 s or 23 breaths min^{-1} and (C) an enlarged segment of the surface interval showing five respiratory cycles each lasting approximately 1.4 s with heartbeats interspersed between the breaths and superimposed on them at the rate of approximately 2 beats s^{-1} or 120 beats min^{-1}.

Table 1. *Mean respiration and heart rate at the surface of homing juveniles in relation to mean swimming speed, duration and depth during the previous dive*

Juvenile (sex, age in years)	Mass (kg)	Duration (min)	N	Surface interval — Breaths and **heart beats**				Rate ($\mathrm{min^{-1}}$) in 15 s quartiles of dive				Dive before surface interval		
				Number	Rate ($\mathrm{min^{-1}}$)	Duration (s)	Interval (s)	First	Second	Third	Fourth	Swimming speed ($\mathrm{m\,s^{-1}}$)	Dive duration (min)	Dive depth (m)
96N1 (F, 2.4)	236.5	2.1±0.26	11	38.5±4.5 **214±24**	18.3±1.8 **102±4**	1.77±0.10	1.79±0.98	19.6±2.2 **98±5**	19.5±2.0 **101±4**	18.4±2.8 **102±4**	18.2±3.2 **104±4**	1.19±0.13	15.7±3.3	339±64
96N2 (M, 2.4)	250.4	3.5±0.36	10	43.8±3.4 **336±37**	12.6±1.2 **96±3**	1.99±0.16	2.68±02.10	13.4±1.6 **93±4**	13.6±1.5 **95±2**	12±1.5 **98±2**	15.2±2.4 **101±3**	1.26±0.12	17.0±1.2	359±46
9601 (F, 2.4)	237.6	2.1±0.31	8	45.6±7.1 **233±39**	22.2±2.2 **113±3**	1.60±0.09	1.20±0.37	20.0±3.8 **105±1**	22.8±2.1 **111±2**	21.0±3.0 **114±3**	22.5±2.1 **116±3**	1.32±0.11	18.0±5.5	301±122
Card (M, 1.8)	163.1	2.0±0.43	29	33.6±6.5 **219±46**	17.0±1.7 **110±2**	1.82±0.13	1.98±0.76	18.2±2.6 **104±3**	18.1±3.1 **108±3**	15.8±2.6 **112±3**	17.2±2.1 **114±3**	1.34±0.12	15.2±2.1	332±57
Marlin (?, 1.8)	213.3	1.8±0.21	23	43.7±4.4 **199±20**	24.4±3.0 **110±4**	1.33±0.10	0.96±0.35	23.7±2.6 **109±7**	24.8±2.7 **111±3**	24.0±3.5 **112±4**	23.9±4.2 **112±4**	1.48±0.08	18.7±2.6	384±80
Sox (F, 1.8)	163.4	2.1±0.28	22	42.0±4.2 **233±39**	20.4±3.2 **110±4**	1.46±0.08	1.08±0.56	20.9±3.5 **102±4**	23.1±3.7 **105±3**	21.1±4.1 **108±3**	20.2±4.4 **112±4**	1.57±0.11	18.0±2.2	373±41
Grand mean		2.6±0.31		41.2±5.0 **240±33**	19.2±2.2 **106±3**	1.66±0.11	1.62±0.85	19.3±2.7 **102±4**	20.3±2.5 **105±3**	18.7±2.9 **108±3**	19.5±3.1 **109±3**	1.36±0.11	17.1±2.8	348±68

Values are means ± s.d.
Heart beat statistics are in bold type.

Table 2. *Correlation coefficients between behavior at the surface and in preceding and succeeding dives with varying depth, duration and swimming speed, and between heart rate and breathing rate at the surface*

Age category and name	Number of surface intervals	Correlation between breathing rate ($\mathrm{min^{-1}}$) at surface and:					Correlation between heart rate ($\mathrm{min^{-1}}$) at surface and:					
		Previous dive duration	Previous dive depth	Previous swim speed	Succeeding dive duration	Succeeding dive depth	Previous dive duration	Previous dive depth	Previous swim speed	Succeeding dive duration	Succeeding dive depth	Breathing rate ($\mathrm{min^{-1}}$)
Adult males												
Tra	22	0.20	0.36		0.01	0.49	-0.35	-0.39		0.28	-0.33	0.04
Bop	9	-0.09	0.48		-0.16	0.48	-0.30	-0.17		0.11	-0.13	0.71*
Roc	26	-0.21	-0.08		-0.15	-0.05	0.78*	0.74*		0.78*	0.72*	0.11
Juveniles												
96N1	11	0.74	0.81*	-0.54	0.83*	0.82*	0.94*	0.93*	-0.64	0.96*	0.92*	0.91*
96N2	10	0.62	0.11	-0.27	0.15	0.50	0.09	0.56	0.79*	-0.08	-0.23	-0.08
9601	8	0.65	0.76	-0.40	0.09	0.42	0.82	0.58	-0.02	0.17	0.49	0.13
Card	29	-0.34	-0.08	0.04	-0.04	0.05	-0.15	-0.43*	0.17	-0.14	0.10	0.42*
Martin	23	0.39	0.62*	-0.32	0.65*	0.70*	0.56*	0.58*	-0.47*	0.64*	0.80*	0.69*
Sox	22	0.67*	0.76*	-0.25	0.66*	0.60*						

An asterisk denotes significance at $P<0.01$.

Table 3. *Multivariate regression equations of surface interval duration versus preceding dive duration and surface respiration rate for all seals*

Seal	Regression equation	F	r^2	P
Juveniles				
96N1	$SI=209+0.02t_D-5.52f_B$	10.6	0.73	<0.05
96N2	$SI=247+0.22t_D-20.51f_B$	13.2	0.79	<0.05
9601	$SI=232+0.06t_D-8.03f_B$	10.9	0.81	<0.05
Card	$SI=176+0.04t_D-5.65f_B$	3.8	0.23	<0.05
Marlin	$SI=174+0.001t_D-2.65f_B$	7.1	0.41	<0.05
Sox	$SI=189+0.03t_D-4.80f_B$	12.1	0.56	<0.05
Adult males				
Tra	$SI=140+0.04t_D-4.03f_B$	3.8	0.29	<0.05
Roc	$SI=100+0.08t_D-4.11f_B$	30.7	0.73	<0.05
Bop	$SI=353+0.05t_D-9.92f_B$	3.7	0.55	0.08

SI, surface interval duration (in s); t_D, dive duration (in s); and f_B, respiration rate (in breaths min^{-1}).

Table 4. *Mean respiration and heart rate at the surface of migrating adult males in relation to mean horizontal travel speed, duration and depth during the previous dive*

Adult male	Departure mass (kg)	Duration (min)	N	Surface interval								Horizontal travel speed (km day^{-1})	Previous dive duration (min)	Previous dive depth (m)
				Breaths and **heart beats**				Rate (min^{-1}) in 15 s quartiles of dive						
				Number	Rate (min^{-1})	Duration (s)	Interval (s)	First	Second	Third	Fourth			
Tra	1296	2.29±0.27	22	34.5±4.4	15.1±1.4	2.23±0.15	1.72±0.32	15.8±2.2	15.5±2.1	15.4±1.8	14.5±1.7	98.1	25.9±3.2	408±110
				183±19	**80±2**			**78±3**	**79±2**	**81±2**	**80±2**			
Bop	1081	2.18±0.60	9	33.8±6.6	15.9±2.5	2.42±0.33	1.75±0.69	16.0±2.4	16.4±2.4	16.2±2.1	15.6±2.4	78.0	20.2±3.8	272±102
				224±48	**91±3**			**87±5**	**91±3**	**92±4**	**93±3**			
Roc	1148	2.03±0.40	26	29.7±5.3	14.8±1.4	1.91±0.10	2.16±0.78	15.5±1.9	15.6±1.7	14.8±2.1	13.4±2.0	71.5	17.6±3.9	236±152
				164±36	**81±3**			**75±3**	**82±3**	**84±3**	**82±4**			
Grand mean		2.17±0.42		32.7±5.4	15.3±1.8	2.19±0.19	1.88±0.60	15.8±2.2	15.8±2.1	15.5±2.0	14.5±2.0	82.5	21.2±3.6	305±121
				190±34	**84±3**			**80±4**	**84±3**	**86±3**	**85±3**			

Values are means ± S.D.
Heart beat statistics are in bold type.

dives changed from the V-shaped transit or A type, that maximizes horizontal distance covered (Le Boeuf et al., 1992), to the flat-bottomed type E variety, suggestive of benthic foraging (Le Boeuf et al., 2000). Breath duration and inter-breath interval, however, were 28 and 31 % higher, respectively, while foraging than during transit. There were no significant differences in the following surface variables during transit and when the seal was on his focal foraging area: surface interval duration ($t=-0.77$, d.f.=7, $P>0.05$), the number of breaths during surface intervals ($t=-2.08$, d.f.=7, $P>0.05$), f_B ($t=-0.51$, d.f.=7, $P>0.05$) and f_H ($t=-0.88$, d.f.=7, $P>0.05$). There was no significant correlation between surface interval duration and the previous dive duration ($r=-0.44$, d.f.=7, $P>0.05$). The regression of f_B or f_H on preceding or subsequent dive duration or dive depth was not statistically significant (Table 2). Unlike the other two males, the variables f_B and f_H were positively and significantly correlated.

Relationships among surface interval duration, dive duration and respiratory rate, like that of juveniles, were more consistent when a multiple regression approach was used (Table 3). This approach reveals that surface interval duration in adult males can be predicted from respiration rate and the duration of the preceding dive. Regression equations were significant for all adults except the male with the smallest sample size (Bop, $P=0.08$).

Discussion

As expected, surface f_H was considerably elevated over reported diving f_H, and respiration rates were considerably higher than that reported for animals on land. For juveniles, the mean f_H of 106 ± 3 beats min^{-1} at the surface that we report is 172 % higher than the mean diving f_H of 39 ± 4.3 beats min^{-1} reported by Andrews et al. (1997). If the relationship between surface f_H and diving f_H were similar in adult males, we would expect the diving f_H to average approximately 31 beats min^{-1}. This is similar to the mean overall f_H of 34 ± 23 beats min^{-1} recorded during submergence in an adult female southern elephant seal (Hindell and Lea, 1998). The surface respiration rates we recorded at sea were much faster than those recorded between bouts of apnea on land, 2.3 times faster than that of juveniles and 3.4 times faster than that of adult males (Blackwell and Le Boeuf, 1993).

These data on free-ranging juveniles and adult males indicate that there is no strong link between f_B and f_H at the surface and physical effort expended or anticipated. The duration of the previous dive, perhaps indicating the level of oxygen stores depleted, and the surface f_B determine the time that the animal spends at the surface for gas exchange. This supports the idea that animals maximize the rate of gas exchange to minimize surface time (Kramer, 1998). The level to which previous dive duration contributed to the ability to predict surface interval varied considerably among the animals, suggesting variation in the extent of oxygen reserves used during dives or in diving metabolic rate. Despite relatively invariant and short surface intervals, surface

intervals did vary significantly with dive duration and f_B. For the majority of the animals, neither variable alone significantly predicted surface duration. It is important to note that the range of this surface interval variation was usually less than 1 min, and this relationship would probably be obscured by the 30 s sampling interval used in most studies of free-ranging elephant seals.

All seals exhibited a steady respiratory pattern, and f_H that did not change significantly during the course of surface intervals. In adult males, these rates remained steady regardless of their activity. f_B and f_H at the surface were indistinguishable between adult males with high and low levels of exertion, as indicated by horizontal travel speed, diving duration and diving depth. f_B and f_H at the surface also appeared to be independent of diving activity, remaining unchanged as one adult male shifted from horizontal transit to stationary diving and apparent foraging. This implies either that the diving effort for these activities was similar or that diving effort is not reflected by f_B and f_H at the surface.

f_B at the surface was not significantly correlated with swimming speed during the previous dive in any of the juveniles. The data on juveniles are more equivocal in other respects, being characterized by great variation among individuals. It is not clear whether these individual differences are functional or simply due to differences in sex, age or mass, experience in homing behavior, short-lived differences between individuals caused by the stress of translocation or individual strategies of locomotion and homing. Nevertheless, we assume that f_B and f_H at the surface in homing juveniles are similar to those of juveniles during migration because of similarities in surface interval duration and diving behavior (Oliver, 1997). Mean surface interval duration in 1.8-year-old juveniles during homing in the present study was 1.97 ± 0.31 min ($N=3$) compared with 1.80 ± 2.5 min ($N=9$) in juveniles of similar age during migration (Le Boeuf et al., 1996).

f_B during the inter-dive interval may not reflect the level of exertion because the rate of oxygen uptake for a given respiration rate may be affected by previous depletion of stores or by the characteristics of a given respiratory cycle. Webb et al. (1998a) observed that the surface oxygen consumption rate of juveniles in the laboratory increased with increases in dive duration, while surface interval duration remained unchanged. This increase in the rate of oxygen replenishment following long dives could have been brought about by increases in oxygen concentration gradients, by increases in f_B or by increases in tidal volume. The data were not collected in such a way that these alternatives could be distinguished. Craig and Påsche (1980) found slight but significant increases in tidal volume with increasing oxygen consumption rate in harbor seals *Phoca vitulina*, while Reed et al. (1994) showed that both f_B and tidal volume in gray seals *Halichoerus grypus* increased following long dives. One possible explanation for the lack of association between f_B and diving activity in some seals in this study is that, to minimize surface intervals, seals alter the amount of oxygen

they take in with each breath rather than their breathing rate and/or that depleted oxygen reserves contribute to more efficient loading at a given respiration rate.

The fact that dive duration helped predict surface duration has a number of interesting implications. If the seals were maximizing the submerged time of all dives and maximally depleting oxygen reserves to a similar level, we would not expect dive duration to have any effect on the time spent at the surface, which would then depend primarily on minute volume and extraction efficiency at the surface. In this case, variation in dive duration would primarily reflect differences in diving metabolic rate while using a fixed oxygen store before surfacing. We would expect changes in surface duration with increasing dive duration only if anaerobic metabolism was used. Since dive duration does affect, to some degree, the time spent loading oxygen, this implies some variation in the degree of oxygen stores used. While the sample sizes in the present study are small, a larger sample would allow us to examine over what range of dive durations this impact on surface interval exists. One would predict that, as dive durations increase, this relationship would disappear as oxygen reserves are depleted and alterations in diving metabolic rate confound the relationship between dive duration and oxygen utilization.

This finding is particularly interesting in elephant seals because they appear frequently to exceed estimates of their aerobic dive limit (ADL). Hindell et al. (1992) suggested that elephant seals must reduce their metabolic rate below resting metabolic rate in 40 % of dives to remain aerobic. A model advanced by Davis and Kanatous (1999) suggests that Weddell seals, *Leptonychotes weddelli*, and elephant seals make prolonged dives that routinely approach their ADL by optimizing oxygen stores in the blood and muscle by adjusting cardiac output and convective oxygen transport in the blood according to the level of exertion. The bulk of the data in the present study were obtained from animals that were in transit, either returning to Año Nuevo (juveniles) or rapidly moving towards foraging areas (adult males). It has been suggested that these negatively buoyant animals use a passive gliding phase during some portions of transit dives (Williams et al., 1996, 2000). In fish, this strategy can result in a 50 % reduction in oxygen utilization for a given horizontal distance covered (Weihs and Webb, 1983). If swimming behavior makes transit diving particularly efficient, the animals may be under less pressure to extend dive times by maximally depleting oxygen stores. In this case, seals are not maximizing submerged foraging time and may instead be maximizing the energy efficiency of horizontal travel. From this perspective, it is interesting that the one animal in which the multiple regression of dive duration and f_B on surface interval duration was not quite significant was the animal that reached its foraging grounds while the instrument was still sampling.

We recommend the acoustic method for obtaining information on surface respiration and heart rate in other diving mammals. The acoustic method of measuring heart rate should be validated against electrocardiogram methods for measuring heart rate in free-ranging animals. The method operates for long periods compared with methods that rely on skin-surface electrodes connected to heart-rate recorders or electrocardiogram recorders to obtain data on cardiac function (e.g. Fedak et al., 1988; Andrews et al., 1997; Hindell and Lea, 1998). At their best, the latter yield detailed data on f_H at the surface and during diving, but many attempts fail or recordings are short-lived because the electrodes become dislodged or malfunction. Future studies on respiration and heart rates at the surface can dramatically increase sample sizes obtained by interfacing acoustic instruments with time/depth recorders and only sampling acoustics at the surface. This is particularly important for acquiring data during foraging periods that follow long migrations from the deployment area. Obtaining heart rate during diving using this method is more problematic because of flow noise, but heart rate can be obtained using signal processing (Burgess et al., 1998). The complexity of this process, however, makes it impractical for large sample sizes.

The absolute values for f_B and f_H that we present may prove useful in the future for modeling the diving metabolic rate of elephant seals. Combining knowledge of diving performance and surface activity with estimates of minute volume and oxygen extraction efficiency may allow accurate estimates of metabolic rate at sea.

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