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Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea

Mark A. Hindell, Bernie J. McConnell, M.A. Fedak, David J. Slip, Harry R. Burton, Peter J.H. Reijnders, and Clive R. McMahon

Abstract: The ability to forage successfully during their first trip to sea is fundamental to the ultimate survival of newly weaned southern elephant seals (*Mirounga leonina*). However, there is considerable variation in the body mass and fat content of seal pups at weaning, which results in some individuals having larger energy and oxygen stores than others, which may confer advantages on them. The diving behaviour of 21 newly weaned seals was studied using satellite relayed data loggers. Seals were captured at Macquarie Island in December 1995 and 1996, approximately 4 weeks after weaning. Two groups of seals were specifically targeted: a heavy group from the top quartile of weaning masses ($n = 6$) and a light group from the lower quartile ($n = 15$). Most of the seals made dives in excess of 100 m depth and 5 min before final departure from the island. However, for the first 60–80 d, all of the seals exhibited behaviour quite distinct from the patterns reported for older conspecifics, and made relatively shallow (100 ± 39 m; mean ± SD) and short (5.7 ± 1.23 min) dives. During this time the seals spent 74.3 ± 12.6% of each day diving, and the depth of the dives did not follow any diurnal pattern. The diving behaviour of all seals changed abruptly when they started on their return to land. During this time their behaviour was more like that of adults: they made deeper (159 ± 9 m) and longer dives (9.01 ± 1.69 min) than previously, and the dives showed a strong diurnal pattern in depth. There is no obvious explanation for this change in behaviour, although its abrupt nature suggests that it is unlikely to have been due to physiological changes in the seals. The size of the seals at weaning was an important influence on diving behaviour. Heavy weaners made significantly deeper (130 ± 40 m) and longer dives (7.36 ± 0.55 min) than light weaners (88 ± 32 m and 5.04 ± 0.64 min, respectively). This indicates that smaller seals are constrained to some extent by their physiological capabilities, which perhaps requires some individuals to adopt different foraging strategies.

Résumé : La capacité de s'alimenter au cours de leur premier voyage en mer est essentielle à la survie future des jeunes après le sevrage chez l'Éléphant-de-mer austral (*Mirounga leonina*). Cependant, la masse et le contenu en graisses sont très variables chez les éléphants-de-mer au sevrage, ce qui fait que certains individus ont des réserves d'oxygène et d'énergie plus importantes et sont donc peut-être avantagés par rapport aux autres. Le comportement de plongée a été suivi par satellite (SRDL) chez 21 jeunes éléphants-de-mer tout juste sevrés. Les jeunes phoques ont été capturés sur l'île Macquarie en décembre 1995 et 1996, environ 4 semaines après le sevrage. Deux groupes de phoques ont été ciblés plus particulièrement, un groupe d'animaux lourds du quartile supérieur ($n = 6$) et des animaux moins lourds du quartile inférieur ($n = 15$). Avant leur départ définitif de l'île, la plupart des jeunes éléphants-de-mer ont fait des plongées de plus de 100 m de profondeur et d'une durée de plus de 5 min. Cependant, au cours des 60–80 premiers jours de leur vie, tous les phoques ont manifesté des comportements très distincts de ceux de leurs conspécifiques plus âgés en faisant des plongées relativement peu profondes (100 ± 39 m; moyenne ± écart type) et courtes (5,7 ± 1,23 min). Durant ce temps, ils passaient en moyenne 74,3 ± 12,6% de leur temps en plongée chaque jour et la profondeur de leurs plongées ne suivait pas de pattern particulier selon le moment de la journée. Chez tous les phoques, le comportement de plongée a changé abruptement à partir du moment où ils ont commencé leur voyage de retour à terre. Durant ce temps, le comportement des jeunes phoques ressemblait davantage à celui des adultes; leurs plongées étaient plus profondes (159 ± 9 m) et plus longues (9,01 ± 1,69 min) qu'auparavant, et la profondeur des plongées suivait un pattern diurne bien défini. Il n'y a pas d'explication évidente à ce changement, mais son caractère abrupt indique qu'il ne s'agit pas d'une réaction à des changements physiologiques. La taille des phoques au moment du sevrage avait une influence importante sur le comportement de plongée. Les phoques sevrés de masse

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élevée faisaient des plongées significativement plus profondes (130 ± 40 m) et plus longues (7,36 ± 0,55 min) que les phoques sevrés de masse moindre (88 ± 32 m et 5,04 ± 0,64 min, respectivement). Il semble donc que les phoques moins gros soient restreints jusqu'à un certain point par leurs capacités physiques, ce qui oblige peut-être certains individus à adopter des stratégies différentes de quête de nourriture.

[Traduit par la Rédaction]

Introduction

The attainment of nutritional independence is a key period in the life history of all mammals. The transition from total dependence on milk supplied by the mother to independent foraging can lead to an increase in mortality, but many species are buffered by a protracted lactation period and extensive maternal instruction, humans being the most extreme example of this strategy. Phocid seals lie at the opposite extreme of this continuum, having a typically brief lactation period after which the young are abandoned by their mother and learn to swim and hunt without adult input (Bowen et al. 1993; Boness and Bowen 1996).

The 24-d lactation period of the southern elephant seal, *Mirounga leonina,* although short by mammalian standards, is about average for phocid seals (Laws 1956*a*; Arnbom et al. 1993). After weaning, the adult seals depart for remote feeding grounds, leaving the young to spend another 3–9 weeks ashore on the natal island before they in turn leave (Arnbom et al. 1993, 1997). Newly weaned southern elephant seals face a number of critical challenges, amongst which are learning to locate and effectively exploit prey. Unlike pack-ice species of phocids, whose feeding grounds are close to their breeding areas, the feeding grounds utilised by adult southern elephant seals are as much as 1500 km from the breeding grounds (Bester and Pansegrouw 1991; Hindell et al. 1991; McConnell et al. 1992; McConnell and Fedak 1996), so the newly weaned seals must locate suitable feeding areas without maternal guidance. The sole contribution that the mother can make towards the pup's survival is to maximise its size at weaning, in terms of both lean tissue and high-energy blubber. The mass of elephant seal pups at weaning can vary by a factor of more than 2 (McCann et al. 1989; Arnbom et al. 1997), indicating a high degree of variability in the ability of females to supply pups with the crucial energy. There is some evidence that larger pups have higher survival rates than smaller ones (McMahon 1998), but the mechanism that governs this is unknown.

Adult elephant seals forage at considerable depths, often in excess of 500 m (Boyd and Arnbom 1991; Hindell et al. 1991; Jonker and Bester 1994; Slip et al. 1994). This foraging strategy requires them to have the ability to remain submerged for long periods, the duration of which is ultimately determined by the amount of oxygen (O_2) carried and the rate at which it is used (Thompson et al. 1993; Boyd and Croxall 1996; Hindell and Lea 1997). As O_2 stores scale to body size in a linear fashion and O_2 consumption scales to a factor of approximately log 0.75 (Kooyman 1989), larger pups should be able to remain submerged for longer than smaller pups. Individual weaners may therefore have considerably different hunting abilities, from the time they are weaned.

This study examines the first months of independence of a mammal that requires highly developed physiological and behavioural capabilities to locate and capture prey in a large heterogeneous environment (Hindell et al. 1992; McConnell et al. 1992; Slip et al. 1994). We used satellite relayed data loggers (SRDLs) attached to two groups of different-sized elephant seal pups to quantify the interplay of environmental and physiological determinants of their foraging during the critical first 6 months of independent life.

Methods

Deployment

We deployed SRDLs on 44 southern elephant seal pups at Macquarie Island (54°30′S, 158°57′E) before their first trip to sea; 32 SRDLs were deployed in 1995 and a further 12 in 1996.

To assess the influence of body size on diving behaviour, SRDLs were deployed on two groups of seals: a heavy group drawn from individuals in the upper quartile of weaning masses and a light group drawn from the lower quartile of weaning masses. The seals were all weighed at weaning and then recaptured when they were expected to have reached 68% of their weaning mass, which is when young elephant seals typically leave their natal island (Arnbom et al. 1993). Each pup was anaesthetised with an intramuscular injection of Zoletil at a dose rate of 1 mg·kg^{-1} body mass (Baker et al. 1990; Slip and Woods 1996). The hair was dried and cleaned with acetone and the SRDL was attached with a rapid-setting epoxy resin. The SRDL was positioned on the top of the head so that the aerial would emerge when the seal surfaced. The seals were weighed and measured and blubber thickness was measured at five points along the dorsal surface using ultrasound (Gales and Burton 1987; Slip et al. 1992).

Telemetry system

The SRDLs were constructed by the Sea Mammal Research Unit and consisted of a data logger interfaced to a 0.5-W Argos radio frequency unit (Fedak et al. 1996). Data from a depth sensor (0.5 m resolution) and a submergence sensor were used to determine the activity of the seal: "diving" (deeper than 6 m for at least 6 s), "hauled out" (continuously dry for at least 240 s), or "at surface." Distance swum was determined by means of a turbine odometer. Individual dive records included maximum dive depth, distance swum, and dive and previous surface interval durations. Six hourly summary records, including the percentages of time spent diving and at the surface, were also calculated. Dive, haulout, and summary records were stored in memory and selected for transmission so that times of day when the Argos satellites were not available were adequately represented. The unit weighed 0.7 kg, measured 10 × 9 × 4 cm, and could resist pressure equivalent to a depth of 2000 m.

The average daily uplink rate was 11 per day. All locations (i.e., irrespective of location quality) were filtered by the algorithm described by McConnell et al. (1992), using a "maximum daily speed parameter" of 2.0 m·s^{-1}. The purpose of this filter was to reject locations that would require an unrealistic rate of travel to achieve; it rejected 14% of all locations.

Estimation of blubber content

Blubber content of the seals at the time of deployment was estimated using ultrasound (Slip et al. 1992). For 10 seals ultrasound measurements were not made, so blubber content was estimated

using an equation derived using data from the seals in this study for which ultrasound data were available:

$$\% \text{ blubber} = -13.148 + [0.717 \text{ (mass/STL)}], r^2 = 0.851$$

where mass is in kilograms and snout–tail length (STL) is in metres.

Estimation of swimming speed

Swimming speeds were recorded for 17 of the seals. All swimming speeds were calibrated before analysis (Fletcher et al. 1996). To do this a minimum possible swimming speed was calculated for each dive by taking the twice the maximum depth and dividing by the duration of the dive (i.e., the speed the seal would have had to swim if it had travelled vertically down and then immediately vertically back up again). This value was then plotted against the recorded swimming speed during that dive, producing a cloud of points with a distinct lower edge that was taken to represent the region where dives were completely vertical (i.e., where the swimming speed would equal the vertical rates of descent and ascent). The slope of this edge was calculated by taking all the dives with minimum swimming speeds (the x axis) between 0.5 and 1.5 m·s^{-1} and dividing them into 20 vertical slices. The minimum recorded swimming speed in each slice was then regressed against the minimum possible swimming speed (Thompson et al. 1996). These calibrations indicated that the recorded swimming speeds needed to be adjusted by a factor between 0.835 and 3.738. The high correction factors may have been required if those units recorded two, three, or four rather than one count per revolution of the turbine.

Identification of drift dives

A proportion of all dives made were classified as drift dives, in which the seals stopped swimming, or at least swam at a speed below the stall speed of the turbines, for a proportion of their dives. These dives have been well documented in adult elephant seals, and have a distinctive depth and speed profile (Crocker et al. 1996). A plot of swimming speed against dive depth for each seal yielded two distinct clouds of points, a larger group associated with generally higher speeds and a smaller group associated with slower speeds. The latter group consisted of drift dives, their lower overall speeds being due to the drift component of the dive. This pattern has been confirmed by data from adult females whose dive profile and swimming speed were both known (M.A. Hindell, unpublished data).

Aerobic capacity of the seals

The departure mass of each seal was estimated using the body mass at deployment, the number of days it remained at the island after the transmitters were deployed, and an estimated daily rate of mass loss of 0.81 kg·d^{-1} (Arnbom et al. 1993). At this time the seals in the heavy group weighed 90 ± 21 kg (mean ± SD) and those in the light group 58 ± 8 kg (Table 5). Total O$_2$ stores, estimated using total body mass and a value of 0.0603 L O$_2$·kg^{-1} calculated for northern elephant seals of the same age (Thorson and Le Boeuf 1994), were 0.33 ± 0.06 and 0.24 ± 0.03 L for the heavy and light group, respectively. The lean-tissue metabolic rate was estimated by taking a seal of average mass (89 kg) and calculating the total resting metabolic rate (RMR) for an animal of this size (Kleiber 1975). This was then multiplied by a factor 3 to allow for the elevated metabolic rate of young pups (Kretzmann et al. 1993; Lydersen and Hammill 1993a; Burns and Castellini 1996). This value was then divided by the estimate of lean-tissue mass for an animal of that size to generate a mass-specific metabolic rate per unit of lean tissue. For each individual in the study, the metabolic rate was then taken to be the product of this figure and the seal's lean-tissue mass. This method of estimating metabolic rate avoids the necessity of making assumptions regarding the interspecific scaling exponent.

The aerobic dive limit (ADL) was estimated by dividing total O$_2$ stores by this estimate of the metabolic rate. This produced a ADL of 5.47 ± 1.09 and 4.86 ± 0.0.58 min for the heavy and light group, respectively (Kooyman 1989).

Statistical analyses

The time when each dive was made was corrected to local time according to the known latitude of the dive. Data are presented as the mean ± SD throughout. Percentages were reduced to proportions and then arcsine-transformed prior to analysis. Dive parameters between trip phases were compared using General Linear Models (GLMs) with individual included as a covariate to allow for the lack of independence in the data. Comparisons of dive parameters between mass groups were done using nested analysis of variance (ANOVA) with individuals nested within mass group and using the nested-effect mean square as the error term (Zar 1984). Post hoc comparisons were made using Tukey's tests. All analyses were done using SAS (SAS Institute Inc. 1988).

Results

Of the 44 SRDLs deployed, 14 failed before the seals had departed for sea or soon after, apparently as a result of damage to the aerials and other technical faults. For this reason only seals that reached a minimum distance of 50 km from Macquarie Island were included in the analysis. Of the 30 seals that reached this point (Table 1), 11 were from the heavy group (5 males and 6 females) and 19 from the light group (10 males and 9 females).

The mass of the light seals at the time of deployment was 65 ± 5 kg, while the heavy seals had a mass of 109 ± 10 kg (Table 1). The estimated blubber content was 22.7 ± 3.2% for the light group and 37.7 ± 4.2% for the heavy group.

The number of days of dive data ranged from 1 to 176 (Table 1). Thirteen seals were tracked for nearly the full duration of the first foraging trip (139 ± 21 d). Eight of these, of which only two were from the heavy group, were recovered back at Macquarie Island. Returning masses of only six of these seals were collected, and these seals had increased their mass by 25.5 ± 8.17 kg (range 18–37 kg) while at sea. This represents a mean mass gain of 40.8% (range 21.6–59.7%). None of the other seals have been seen since, despite routine searches of the island conducted as part of a long-term demographic study (Australian Antarctic Division, unpublished data).

The seals did not appear to disperse from the island at random. Approximately 70% of the seals went to an area to the southeast of Macquarie Island bounded by 60.6°–63.0°S and 161.1°E–179.8°W (B.J. McConnell, unpublished data). The remaining seals dispersed to the west of the island approximately 56°–61°S and 131°–151°E.

Diving behaviour prior to final departure

Seals left the island 14.4 ± 11.5 d after the transmitters were deployed. Seals in the heavy group took 23.0 ± 11.6 d to leave (Table 1), which is significantly longer than the 9.3 ± 8.2 d taken by those in the light group ($t_{27} = 3.16$, $P = 0.003$). During this time the seals spent, on average, 8.8% of each day diving. There was considerable individual variation, with some seals diving every day and others only rarely, if at all. There was no significant difference in the

Table 1. Morphometric details of the 30 seals for which location and dive data were collected.

Seal ID No.	Sex	Mass at weaning (kg)	Mass at deployment (kg)	STL (m)	Girth (m)	Percent blubber	No. of days to departure	No. of days >50 km
			Light group					
17217_95	F	78	62	1.30	1.02	18.8	6	132
20916_96	F	90	56	1.30	0.97	17.7*	11	10
20918_95	M	92	66	1.32	1.06	25.9	7	141
22483_95	M	84	64	1.26	1.06	23.6	7	122
22483_96	M	92	59	1.29	1.00	19.6*	3	58
22484_95	M	90	65	1.30	1.05	22.7*	23	20
22486_95	F	81	65	1.30	1.07	24.5	1	112
22490_95	M	93	72	1.34	1.02	27.6	16	144
22490_96	F	93	60	1.32	0.98	19.4*	32	32
22499_95	M	84	67	1.31	0.95	20.4	6	174
22500_95	F	88	62	1.30	1.05	25.5	5	145
26624_96	M	92	62	1.27	1.00	21.9*	4	137
26625_95	F	91	65	1.25	1.03	24.3	7	108
26627_95	M	88	62	1.22	1.05	19.9	9	64
26628_95	M	88	62	1.24	1.05	20.2	1	117
26633_95	F	95	72	1.33	1.10	28.9	20	9
26635_95	F	89	68	1.24	1.06	25.1	9	145
28479_96	M	85	69	1.32	1.13	24.3*	10	2
2849_95	F	92	73	1.40	1.08	20.9	1	129
Mean		89	65	1.30	1.04	22.7	9.3	95
SD		4	5	0.04	0.05	3.2	8.2	56
			Heavy group					
17215_95	F	139	101	1.54	1.19	36.3	26	2
17219_95	M	142	98	1.53	1.20	32.4	37	32
20916_95	F	151	120	1.59	1.33	42.4	29	10
20917_96	F	165	121	1.55	1.41	42.8*	13	6
22500_96	M	142	96	1.53	1.15	31.8*	22	6
22501_95	F	136	98	1.50	1.20	35.4	47	35
26623_96	M	169	119	1.52	1.33	43.0*	14	176
26629_95	M	141	108	1.51	1.26	37.7	23	8
28482_96	F	171	120	1.65	1.29	39.0*	16	46
5811_95	F	145	109	1.54	1.23	40.4	20	35
5814_95	M	143	107	1.58	1.20	33.5	6	148
Mean		149	109	1.55	1.25	37.7	23.0	46
SD		13	10	0.04	0.08	4.2	11.6	60

Note: These data are restricted to the animals that were recorded more than 50 km from Macquarie Island. The seals are grouped by size class; the light group is the lower quartile of weaning mass and the heavy group is the upper quartile of weaning mass.

*Blubber was estimated from morphometric data.

proportion of mean time spent diving between the heavy and light groups ($t_{27} = 1.65$, $P = 0.11$). The general trend was for seals to make occasional dives every day, but this pattern became more frequent and represented a greater proportion of the time in the days immediately before final departure. There were exceptions, with several individuals from both the heavy and light group not making any dives until the day that they left the island.

Despite the relatively small amount of time spent in the water during these early days, most seals were capable of making relatively deep and long dives by the time they left the island (Fig. 1). Sixty-two percent of the seals had made at least one dive in excess of 100 m depth before leaving the island, the deepest being 271 m made by seal 5814_95, one of the heavy seals. Eighty-six percent of seals made dives in

excess of 5 min before they left the island, the longest being 12.3 min by seal 17215_95, another of the heavy group.

Daily rate of travel

The daily rate of travel was based on the distance between mean daily locations. The rate of travel for all individuals was initially high, sometimes as high as 140 km·d^{-1} (Table 2), then declined steadily over the first 20–40 d. This initial phase corresponds to the seals dispersing from the island in relatively directed movements (B.J. McConnell, unpublished data). A second phase was characterised by low daily rates of travel, generally less than 20 km·d^{-1}, and lasted for between 60 and 90 d. The final phase occurred when the seals turned towards Macquarie Island and, like the outward phase, was characterised by high rates of travel. For the

Fig. 1. Frequency distributions of maximum dive depth (A) and maximum dive duration (B) for seals during their predeparture period at Macquarie Island.
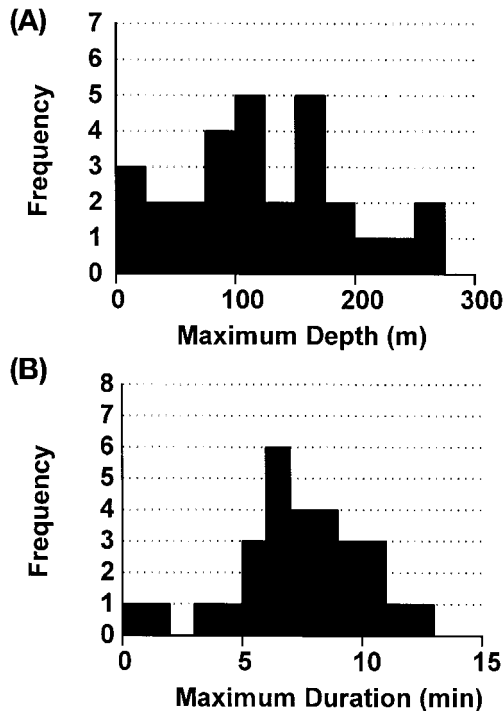
analyses in this study, phase 1 (the outward phase) was taken to end when the 5-d running mean of daily rate of travel first dropped below 20 km·d^{-1}. The end of phase 2 (the foraging phase) was taken to be the last time the 5-d running mean was less than 20 km·d^{-1} (Fig. 2).

There were 21 seals (5 heavy, 16 light) for which there were complete data for phase 1: the daily rate of travel was 47.9 ± 9.0 km·d^{-1} and the phase lasted for 33 ± 8 d (Table 2). The 14 (2 heavy and 12 light) seals that completed phase 2 had a daily travel rate of 17.3 ± 3.5 km·d^{-1} and phase 2 lasted for 60 ± 17 d. For the 13 remaining animals the rate of travel during phase 3 was 54.6 ± 13.4 km·d^{-1} and the phase lasted for 40 ± 20 d.

The duration of phase 1 was not related to the size of the seal ($t_5 = 2.57$, $P = 0.66$), nor was the daily rate of travel related to body size (nested ANOVA, $F_{[1,18]} = 0.493$, $P = 0.492$).

Influence of body size on diving behaviour

Only three seals form the heavy group completed phase 2, which was too few for statistical comparison with the more numerous light group. Therefore, analyses of the influence of body size on diving behaviour were restricted to phase 1, the outward phase, when six of the heavy seals provided data for at least 32 days (Table 1).

Swimming speed and distance swum during dives

The swimming speed of the six seals in the heavy group during phase 1 was 0.9 ± 0.2 m·s^{-1} and for the 10 seals in the light group was 1.2 ± 0.3 m·s^{-1} (Table 3). These values were not significantly different (nested ANOVA, $F_{[1,17]} = 0.77$, $P = 0.40$). Nor did the seals in the heavy group travel significantly farther on their dives than those in the light

group (overall individual value 363 ± 99 m, nested ANOVA, $F_{[1,15]} = 1.75$, $P = 0.21$).

Duration and depth of dives

Seals in the heavy group made significantly longer dives than those in the light group (Table 3): 7.36 ± 0.55 and 5.04 ± 0.64 min, respectively (nested ANOVA, $F_{[1,91]} = 33.86$, $P = 0.0001$). Mean dive depth also differed significantly between the two mass groups (nested ANOVA, $F_{[1,19]} = 4.86$, $P = 0.04$; Table 3). There was more individual variation in depth of dives than in duration, with depths ranging from 21 ± 21 to 133 ± 60 m for the light group and from 73 ± 67 to 167 ± 82 m for the heavy group.

Postdive surface intervals

Both groups of seals spent similar amounts of time on the surface after dives (Table 3), with an overall value of 1.53 ± 0.57 min (nested ANOVA, $F_{[1,19]} = 0.05$, $P = 0.82$). Again there was considerable individual variation, with postdive surface intervals ranging from 1.15 ± 0.65 min for seal 17219_95 to 3.80 ± 2.30 min for seal 22483_96.

All seals had some extended surface intervals, defined here as twice the overall average for an individual seal. For the heavy group, 2.2 ± 0.4% of all dives were followed by an extended surface interval compared with 5.0 ± 3.1% for the light group. These proportions were significantly different (unequal-variance t test, $t_{17} = 3.93$, $P = 0.001$). The two seals that consistently made shallow dives (22496_95 and 26628_95, both from the light group) also had the longest postdive surface intervals (3.8 ± 2.30 and 2.08 ± 1.87 min, respectively) and the highest proportion of extended surface intervals (13.4 and 9.5%, respectively). However, the difference in the proportion of extended surface intervals between the two mass groups was still significant, even when these two animals were excluded ($t_{16} = 4.95$, $P = 0.0001$).

Proportion of time spent diving

The proportions of time spent diving each day were similar for the two groups of seals, the overall value being 69.7 ± 19.3% (nested ANOVA, $F_{[1,17]} = 1.74$, $P = 0.20$). Individual values varied almost twofold, ranging from 21.7 ± 35.7% for seal 26628_95 to 87.2 ± 5.4% for seal 28482_96. There was no significant difference between the proportions of drift dives made by the heavy seals and light seals, with drift dives making up 15.4 ± 5.6% of the total number of dives for each seal (unequal-variance t test, $t_7 = 1.89$, $P = 0.82$).

Diurnal patterns in dive depth

The changes in depth of dives with time of day were not as pronounced during phase 1 as later in the time spent at sea; nevertheless, there were differences between the two mass groups. The dives made by the heavy animals in the 3 h around local midday, 11:00–13:00 (137 ± 69 m), were significantly deeper than those made by the light seals (88 ± 29 m; nested ANOVA, $F_{[1,19]} = 5.17$, $P = 0.03$). However, the depths of dives made at night (23:00–01:00, overall depth 86 ± 35 m) did not differ significantly between the two groups (nested ANOVA, $F_{[1,19]} = 1.48$, $P = 0.24$).

Table 2. Rate of travel (km/day) during each of the three phases of the seal's first trip to sea.

Seal ID No.	Phase 1		Phase 2		Phase 3	
	Mean ± SD	No. of days	Mean ± SD	No. of days	Mean ± SD	No. of days
5811_95	**37.6±30.9**	**35**	—	—	—	—
5814_95	**43.3±17.6**	**36**	**21.6±14.2**	**63**	**60.5±34.1**	**49**
17219_95	**47.1±30.4**	**32**	—	—	—	—
22501_95	**41.0±27.8**	**25**	—	—	—	—
26623_96	**46.2±30.0**	**19**	**29.7±25.1**	**128**	**45.8±26.0**	**28**
28482_96	**44.2±18.0**	**46**	—	—	—	—
2849_95	48.2±27.3	43	17.6±12.0	42	81.1±42.5	45
17217_95	44.9±24.1	38	16.6±9.8	51	61.7±35.5	32
20918_95	44.9±29.2	40	16.3±14.4	72	55.2±28.8	29
22483_95	65.9±31.1	24	16.1±12.0	98	—	—
22483_96	51.7±31.5	32	—	—	—	—
22486_95	41.9±28.9	43	11.8±11.2	45	42.3±24.5	30
22490_95	29.6±17.8	33	20.3±15.5	75	49.4±29.5	36
22490_96	58.9±27.5	31	—	—	—	—
22499_95	57.9±32.8	31	23.8±14.2	44	51.3±32.8	99
22500_95	50.6±33.1	33	16.3±13.1	79	63.1±27.6	33
26624_96	40.3±19.9	41	12.8±7.4	57	59.4±30.9	36
26625_95	38.4±15.5	38	18.3±9.7	45	30.2±17.4	25
26627_95	54.2±33.2	36	—	—	—	—
26628_95	58.2±23.5	26	14.6±12.3	70	69.5±29.1	21
26635_95	60.9±40.0	22	18.0±15.4	67	40.6±27.1	56
Mean	47.9±9.1	34±7	17.3±3.5	60±17	55.0±14.4	42±22

Note: Only data from seals that completed at least phase 1 are included. A dash indicates that a seal failed to complete a phase. Data in boldface type are from animals in the heavy group.

Changes in diving behaviour with time

Thirteen seals (3 heavy and 10 light) were tracked for complete, or nearly complete, ocean trips during their first 6 months of life. During this time there were marked changes in several of the key diving parameters, with a general pattern of stability during the early phases and a distinct increase during phase 3 (Table 4).

Swimming speed during dives

Swimming-speed data were obtained during all three phases for eight individuals. Overall there was no significant difference in swimming speed between the three phases (GLM, $F_{[2,21]} = 0.10$, $P = 0.904$). Combining the data from all three phases produced an overall swimming speed of 1.1 ± 0.2 m·s^{-1}, with individuals' speeds ranging from 0.8 to 1.5 m·s^{-1}. When drift dives were excluded from the data (see below), swimming speed increased by approximately 8%, to 1.2 ± 0.2 m·s^{-1}.

Duration of dives

There were significant differences in the duration of dives in the three phases (GLM, $F_{[2,36]} = 14.44$, $P = 0.0001$), durations during the final phase being significantly longer than in the first two phases. The duration of dives in phases 1 and 2 was 5.46 ± 1.15 and 5.88 ± 1.37 min, respectively (Table 4). This increased to 9.66 ± 1.2.62 min during phase 3. All of the seals showed this pattern, even seal 26628_95, which exhibited no change in overall distance travelled (see below).

Distance travelled per dive

The total distance travelled on each dive was calculated for the individuals for which there were swimming-speed data. In this case there were significant differences between the three phases (GLM, $F_{[2,21]} = 14.58$, $P = 0.0001$). During phases 1 and 2 the distances travelled on dives were not significantly different: 354 ± 76 and 384 ± 98 m, respectively. The distance increased dramatically during phase 3, to 677 ± 196 m. There was also considerable variation among seals, and one seal (26628_95) failed to show this general pattern. This individual swam relatively slowly and travelled relatively short distances on each dive: 246 ± 92, 181 ± 62, and 202 ± 55 m in phases 1, 2, and 3, respectively.

Dive depth

The pattern of dive depth over time was slightly different from that of dive duration. Once again there were significant differences between the three phases (GLM, $F_{[2,36]} = 5.68$, $P = 0.0072$). The depths utilised differed significantly between phases 1 and 2, although these differences were still relatively slight compared with the substantial increase in depth in phase 3: 98 ± 39, 117 ± 48, and 164 ± 47 m, respectively. Although all seals exhibited the general pattern of deeper dives in phase 3, there were considerable individual differences in dive depth, with two seals (22486_95 and 26628_95) consistently making much shallower dives (less than 90 m) than the other seals. The pressure transducer from the SDRL carried by one of these seals was checked after it was recovered and found to be operating properly.

Fig. 2. Examples of the horizontal distance travelled each day by six seals during their entire time spent at sea. The histograms show daily distances travelled and the circles indicate the maximum depth reached by the seal each day. Vertical lines indicate the beginning and end of each phase (see Methods for a definition of phases).
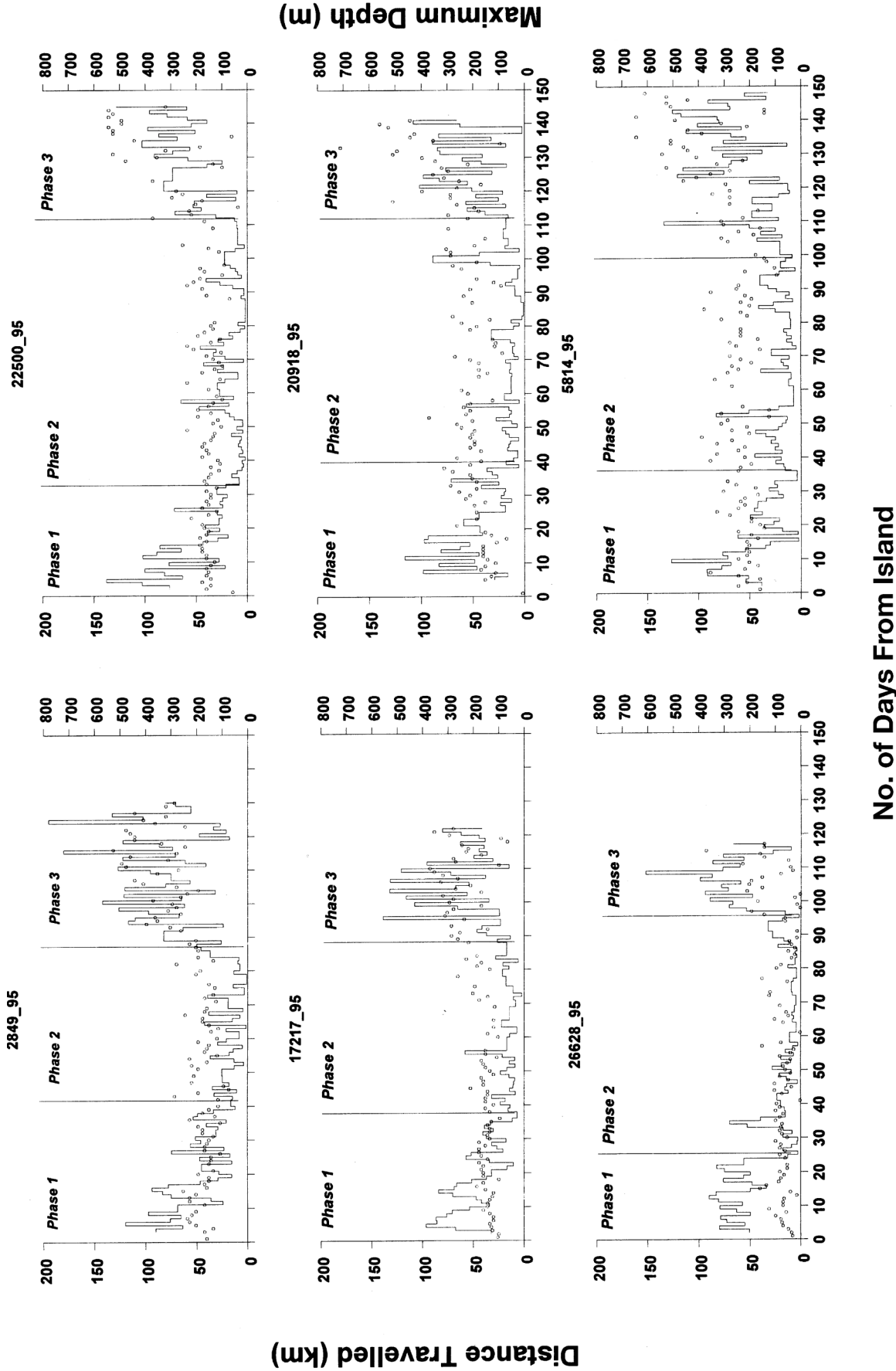
Table 3. Summary dive statistics for all seal that completed phase 1.

Seal ID No.	Mass group	No. of dives analysed	Duration of dives (min)	Depth of dives (m)	Surface interval (min)	Percentage of time spent diving	Swimming speed (m·s^{-1})	Distance travelled per dive (m)	No. of ESIs
17219_95	Heavy	787	6.40±2.06	94±42	1.15±0.65	—	0.80±0.21	260±97	16
22501_95	Heavy	311	7.05±2.00	73±64	1.97±0.87	33.4±38.7	0.78±0.24	326±103	5
26623_96	Heavy	529	7.56±1.63	162±65	1.55±0.89	21.8±35.8	—	—	13
28482_96	Heavy	1625	7.79±2.07	163±72	1.40±0.64	87.2±5.4	1.16±0.27	550±166	33
5811_95	Heavy	550	7.58±1.82	167±82	1.52±0.70	81.9±4.6	1.27±0.45	552±189	15
5814_95	Heavy	1705	7.58±1.81	124±44	1.41±0.83	83.0±4.1	0.95±0.19	424±94	38
Mean ± SD		918±579	7.36±0.55	130±40	1.50±0.27	61±31	0.99±0.22	422±132	20±13
17217_95	Light	2690	5.35±1.37	86±34	1.53±1.04	75.8±5.1	0.96±0.26	298±80	130
20918_95	Light	1520	6.24±1.54	113±43	1.36±0.88	66.2±30.8	0.96±0.22	347±81	53
22483_95	Light	1709	5.05±1.40	76±30	1.21±0.84	79.5±4.4	—	—	73
22483_96	Light	1757	5.21±1.66	93±38	1.31±0.94	84.8±4.6	1.10±0.25	334±95	75
22486_95	Light	403	4.16±1.91	23±18	3.80±2.30	37.7±18.4	1.68±0.59	414±142	54
22490_95	Light	583	4.84±1.14	104±38	1.55±1.03	75.7±5.3	—	—	31
22490_96	Light	1178	5.28±1.61	90±34	1.37±1.00	—	1.08±0.29	333±101	48
22499_95	Light	2005	4.54±1.32	88±36	1.22±0.69	78.5±3.2		—	87
22500_95	Light	1968	4.84±1.43	91±38	1.35±0.73	76.7±6.4	1.06±0.28	271±89	55
26624_96	Light	1859	5.69±1.30	128±55	1.32±0.71	81.9±16.7	—	—	40
26625_95	Light	2690	5.50±1.29	133±60	1.34±0.83	78.6±5.5	1.18±0.37	378±124	81
26627_95	Light	2490	4.29±1.23	73±33	1.29±0.77	70.6±19.8	1.03±0.22	259±78	88
26628_95	Light	1163	3.89±2.39	21±20	2.08±1.87	49.1±16.2	0.95±0.38	246±92	111
26635_95	Light	661	5.77±1.72	99±42	1.19±0.61	83.8±2.7	—	—	21
2849_95	Light	1717	4.99±1.40	104±42	1.31±0.07	77.4±6.4	1.57±0.44	456±140	44
Mean ± SD		1626±722	5.04±0.64	88±32	1.55±0.66	72.3±13	1.16±0.26	334±68	66±30

Postdive surface intervals

The postdive surface intervals (PDSIs) were typically short, with mean individual values ranging from 1.15 to 3.76 min. There no significant differences in PDSI between phases (GLM, $F_{[2,36]} = 0.37$, $P = 0.69$), the overall individual value being 1.7 ± 0.76 min. The seal with the longest PDSI (22486_95) also made the shallowest dives.

Proportion of time spent diving

The proportion of each day spent diving did not change during the first trip to sea (GLM, $F_{[2,36]} = 0.66$, $P = 0.52$): 74.3 ± 12.6% (range 47.0 ± 21.6 – 83.7 ± 6.7%). Individual variation in the proportion of time spent diving was particularly pronounced; one individual (22486_95), which made the shallowest dives and had the longest surface intervals, spent only 47.0 ± 21.6% of its time diving each day.

Diurnal patterns in dive depths

The pattern in the depths of dives made throughout the day varied between the three phases. Dives made during phases 1 and 2 exhibited little variation in depth throughout the day (Fig. 3). The individual depth during phase 1, between 11:00 and 13:00, was 90 ± 35 m compared with 112 ± 46 m at night (23:00–01:00). During phase 3, there was a pronounced increase in the depth of dives made during the day, the individual depth around midday being 227 ± 102 m. Nighttime depths during phase 3 (84 ± 45 m) were the same as nighttime depths during the previous two phases, indicat-

ing that the increase in overall dive depth observed in phase 3 (see above) was due entirely to an increase in dive depth during the day. This general pattern was seen for all seals, even those making very shallow dives during phases 1 and 2.

Drift dives

All seals performed some drift dives, although the proportion declined during the time at sea (Fig. 4). The seals performed the highest proportion of drift dives during phases 1 and 2 (15.0 ± 4.9 and 13.6 ± 7.6%, respectively). In contrast, only 5.3 ± 3.3% of dives recorded during phase 3 were drift dives. There was also a strong time-of-day effect, most drift dives being made at around local midday, with a secondary peak occurring around local midnight. Drift dives were neither unusually shallow, with individual depths ranging between 39 ± 29 and 139 ± 59 m, nor unusually short, with individual depths ranging between 4.35 ± 0.12 and 9.25 ± 0.21 min.

Transition from phase 2 to phase 3

For each seal, the change in diving behaviour from relatively short, shallow dives with little diurnal pattern to longer, deeper dives with a pronounced diurnal pattern occurred over a very few days at or near the end phase 2. The change in behaviour is best detected in the variance of daily dive duration (Fig. 5), which is associated with the seals adopting a diurnal diving pattern. The transition between diving behav-

Table 4. Summary statistics for the 13 seals that completed all three phases of their first trip to sea.

Seal ID No.	Phase	No. of dives analysed	Percentage of time spent diving	Distance travelled per dive (m)	Depth of dives (m)	Duration of dives (min)	Surface interval (min)	Swimming speed (m·s⁻¹)
5814_95	**1**	**1705**	**82.9±4.1**	**424±94**	**124±44**	**7.58±1.81**	**1.41±0.83**	**1.0±0.2**
26623_96	**1**	**776**	**21.7±35.8**	—	**160±64**	**7.64±1.58**	**1.55±0.88**	—
2849_95	1	1717	77.4±6.4	456±140	104±42	4.99±1.40	1.31±0.70	1.6±0.4
17217_95	1	2690	75.7±5.1	298±80	86±34	5.35±1.37	1.53±1.04	1.0±0.3
20918_95	1	1520	66.2±30.8	347±81	113±43	6.24±1.54	1.36±0.88	1.0±0.2
22486_95	1	403	37.7±18.4	414±142	23±18	4.16±1.91	3.80±2.3	1.7±0.6
22490_95	1	583	75.6±5.3	—	104±38	4.84±1.14	1.55±1.03	—
22499_95	1	2005	78.5±3.2	—	88±36	4.54±1.32	1.22±0.69	—
22500_95	1	1968	76.6±6.4	271±89	91±38	8.84±1.43	1.35±0.73	1.1±0.3
26625_95	1	2690	78.6±5.5	378±124	133±60	5.50±1.29	1.34±0.83	1.2±0.4
26628_95	1	1163	49.1±16.2	246±92	21±20	3.89±2.39	2.08±1.87	1.0±0.4
26635_95	1	661	83.8±2.7	—	99±42	5.77±1.72	1.19±0.61	—
26624_96	1	2630	81.7±16.9	—	127±56	5.67±1.31	1.36±0.86	—
Mean ± SD		1578±815	68.1±19.5	354±77	98±39	5.46±1.15	1.61±0.69	1.2±0.3
5814_95	**2**	**1793**	**82.5±7.1**	**440±129**	**135±58**	**7.30±2.22**	**1.30±0.64**	**1.0±0.2**
26623_96	**2**	**4231**	**84.7±9.7**	**258±29**	**176±84**	**8.21±3.85**	**1.61±0.92**	**0.6±0.3**
2849_95	2	774	75.4±6.7	407±116	103±37	5.14±1.62	1.59±0.78	1.4±0.4
17217_95	2	1055	74.9±8.1	351±116	115±35	6.23±1.89	1.76±0.58	1.0±0.3
20918_95	2	1474	80.1±5.8	412±116	137±49	7.01±1.88	1.60±0.55	1.0±0.2
22486_95	2	169	56.2±15.9	443±140	28±21	5.06±2.22	4.06±1.96	1.5±0.4
22490_95	2	1063	76.2±6.2	449±196	130±72	6.03±2.04	1.66±0.97	—
22499_95	2	1308	72.8±5.9	—	96±31	4.17±0.99	1.37±0.52	—
22500_95	2	1828	77.0±6.9	332±112	101±33	5.37±1.62	1.43±0.64	1.1±0.3
26625_95	2	927	78.0±10.6	505±161	181±72	6.79±2.03	1.48±0.76	1.3±0.4
26628_95	2	1363	48.1±13.9	182±62	33±24	3.18±1.87	2.35±2.04	0.8±0.3
26635_95	2	1962	78.1±5.7	412±152	116±32	5.17±1.39	1.33±0.58	—
26624_96	2	2664	84.5±4.4	—	179±74	6.79±1.87	1.52±0.73	—
Mean ± SD		1585±1008	74.5±10.7	381±94	118±48	5.88±1.38	1.77±0.74	1.1±0.3
5814_95	**3**	**899**	**86.0±8.0**	**754±353**	**190±143**	**11.21±5.25**	**1.42±0.81**	**1.2±0.2**
26623_96	**3**	**404**	**85.9±11.0**	**792±403**	**215±166**	**16.63±7.19**	**1.67±0.85**	**0.8±0.3**
2849_95	3	1165	84.4±5.38	698±186	184±94	8.54±2.87	1.36±0.60	1.4±0.3
17217_95	3	612	84.9±5.9	679±272	147±87	9.39±3.69	1.47±0.69	1.2±0.3
20918_95	3	700	87.3±3.7	800±324	191±116	11.38±4.39	1.57±0.60	1.2±0.2
22486_95	3	267	56.0±24.3	762±289	82±97	8.28±4.89	3.51±2.02	1.4±0.5
22490_95	3	856	84.7±6.5	740±396	201±156	8.98±4.98	1.29±0.69	1.5±0.4
22499_95	3	1644	78.5±10.1	—	121±86	5.58±3.06	1.32±0.92	—
22500_95	3	650	84.9±7.5	779±313	175±145	9.86±4.91	1.28±0.42	1.4±0.3
26625_95	3	495	85.9±3.1	743±227	209±93	10.02±3.46	1.47±0.52	1.4±0.4
26628_95	3	277	48.2±22.0	202±55	65±70	7.07±4.20	3.05±2.33	0.5±0.2
26635_95	3	765	88.2±5.0	675±384	190±141	8.78±5.12	1.14±0.65	1.3±0.3
26624_96	3	768	87.1±3.6	—	166±80	9.89±2.82	1.44±0.65	—
Mean ± SD		731±373	73.7±14.8	693±168	164±48	9.66±2.62	1.69±0.72	1.2±0.3

Note: Distance travelled and swimming speed were not available for all individuals, or for all phases for some individuals. Data are grouped according to the three phases of the trip: phase 1 is the outward phase, phase 2 is the "foraging" phase, and phase 3 is the return phase. Values in boldface type are from animals in the heavy group.

iours was typically rapid, taking, on average, 3 d from the last day with low variance to the first day of constantly high variance. The change in behaviour occurred between 17 February and 29 March (mean date 17 March) or 99 ± 17 d after the seals left the island. This is very close to the end of phase 2, which had a mean date of 15 March, or 98 ± 19 d after the seals left the island. There was, however, considerable variation in the timing of both events within seals, with

an average within-seal difference of 13 d. For seven of the seals, the two events occurred within 1 week, and for two seals they occurred on the same day.

Aerobic capacity

The ADL for the heavy seals (5.47 ± 1.09 min) was 1.13 times greater than that for the light seals (4.86 ± 0.58 min; Table 5). Using the models of Ryg et al. (1993) and Boily

Fig. 3. Mean depths of dives made throughout the day (local time) in each of the three phases of time at spent sea.
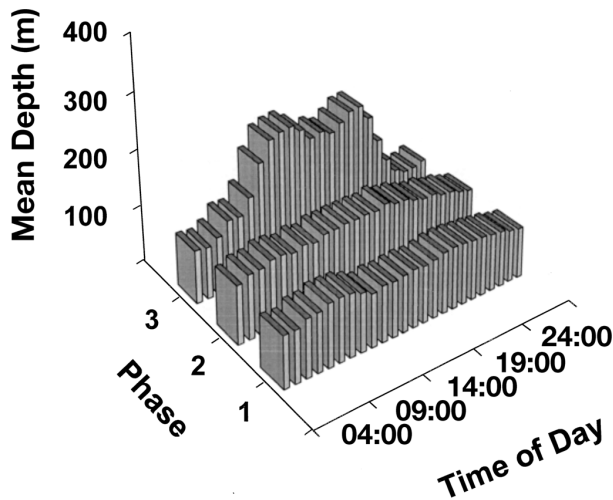
(1995) for seals swimming at 2.0 m·s^{-1} in water at 6°C, the seals in the light group might be expected to lose heat at a greater rate (26.5 ± 1.90 MJ·d^{-1}) than those in the heavy group (18.30 ± 1.22 MJ·d^{-1}). This is 0.65 ± 0.07 times the RMR for the heavy group but 1.27 ± 0.0.07 times the RMR for the light group (Table 5). Although these models make a number of assumptions, for example they use a RMR of 18.3 MJ, which is about half of that estimated for our animals, and need to be validated in controlled experiments, they can still provide the basis for some useful comparisons.

Discussion

The first year of life is a critical time for elephant seals, as it is the period when they experience their highest mortality rate. First-year mortality in southern elephant seals ranges from 50% to as high as 98% (Hindell 1991). This presumably depends on the amount of energy that the seals acquire from their mothers, the ability of the naive seals to locate and capture prey, and their ability to avoid predators (Hindell et al. 1994). Elephant seals make two extended trips to sea during the first year (Laws 1956a, 1956b; Bell et al. 1997). The first lasts for 3–5 months, and the seals often, but not always, return to their natal island. Most weigh little more they did at weaning after their first months at sea, although the relative proportions of lean tissue increase (Bryden 1969; Bell et al. 1997). In northern elephant seals, the relative increase in lean tissue results in an increase in O$_2$ stores, giving the seals greater aerobic capacity on their return (Thorson and Le Boeuf 1994; Le Boeuf et al. 1996).

Our study has revealed two quite fundamental aspects of diving behaviour during these early months that are quite different from the behaviour of adult seals, and which have a bearing on the ability of the seals to hunt for food. The first is the dramatic change in diving behaviour associated with the beginning of phase 3 and the second is the difference in dive duration and depth between the heavy and light seals. A third, and equally important, observation was that there were a number of alternative foraging strategies (perhaps determined by body size) that the young seals successfully employed.

Diving ability prior to departure

By the time southern elephant seal pups depart from their natal island they have been nutritionally independent of their mothers for between 3 and 9 weeks (Arnbom et al. 1993). During this time they rely almost entirely on the store of blubber that they have acquired from their mothers during the 3-week lactation period. Although they do spend some time in the sea during the postweaning fast (Modig et al. 1997), it is doubtful that they have the swimming skills required to catch enough prey to supplement their blubber stores to any great extent. Northern elephant seals undergo considerable physiological changes during this time, with increases in total O$_2$ stores and reductions in diving metabolic rate (Thorson and Le Boeuf 1994). By the time they finally leave the beach, their O$_2$ stores are 73% of those of an adult female (Le Boeuf et al. 1996). Although there are no comparable physiological data for southern elephant seals, both species exhibit increasing proportions of apnoea while sleeping ashore (Kenny 1979; Blackwell and Le Boeuf 1993), which may be linked to increasingly sophisticated metabolic control (Castellini et al. 1986; Blackwell and Le Boeuf 1993; Castellini 1994). In the present study, the duration of dives made during this time increased steadily until, by the time that they left the island, most of the young seals were capable of making dives similar in depth and duration to those made in the subsequent months at sea,. This suggests that, as with northern elephant seals, much of the physiological development required for diving by young elephant seals is acquired prior to their departure (Le Boeuf et al. 1996).

It may be significant that the heavier seals remained ashore for longer than the smaller ones. If the time prior to departure is used for developing swimming and hunting skills, the larger seals will be better swimmers than their smaller counterparts when they eventually leave the beach. Therefore the amount of blubber given to the pup by its mother may have an immediate impact on its potential to survive.

Comparisons with other age-classes

Although they are capable of quite deep, long dives, when they commence their first foraging trip the young seals initially dive in a manner that is quite different to that of southern elephant seals in other age groups (Table 6). The pelagic dives of all other groups of southern elephant seals are typically deep and long and show pronounced diurnal variation in dive depth, daytime dives being deeper and longer than nighttime dives (Hindell et al. 1991; McConnell et al. 1992; Jonker and Bester 1994; Campagna et al. 1995). This pattern is generally interpreted as being a consequence of the seals feeding on diurnally migrating fish and squid or of switching prey at different times of the day (Slip et al. 1994). In the first two phases, the dives of the newly weaned seals were short and shallow, with only slight diurnal variation in depth. Although the general pattern during phase 3 was similar to that of older conspecifics, the young seals at this time still made dives that were much shallower and shorter than those of older seals. The deepest daytime dives of the young seals were also shallower than nighttime dives of the adults (Table 6). On their second trip to sea, seals make dives with durations intermediate between those of the weaners in this

Fig. 4. Mean percentage of drift dives made throughout the day (local time) in each of the three phases of time spent at sea.
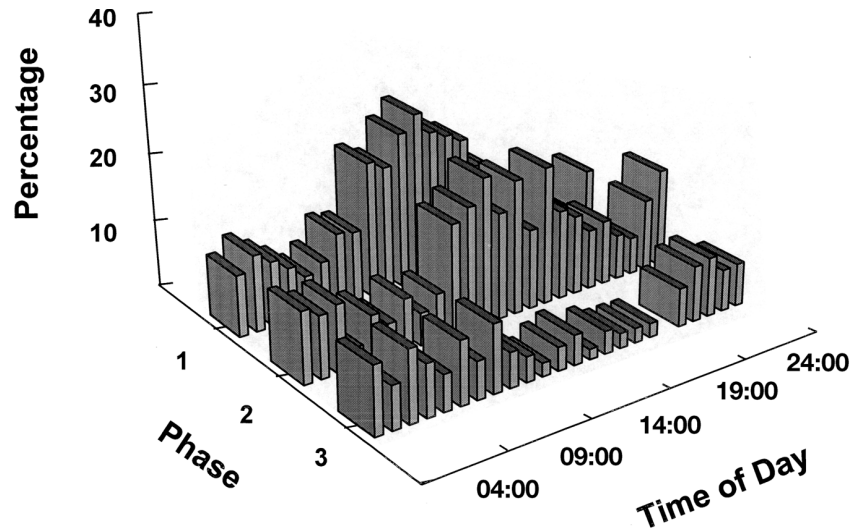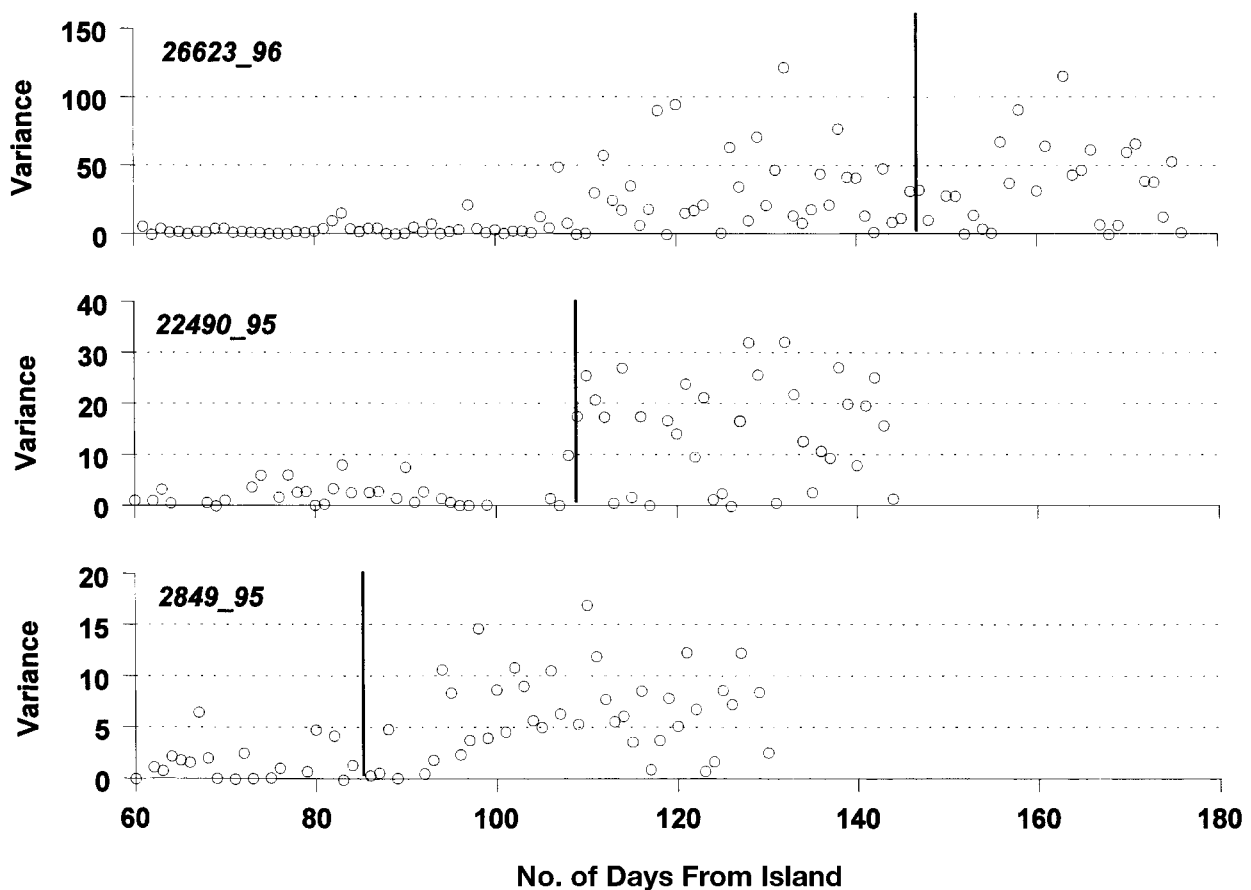

Fig. 5. Three examples of change in the variance of daily dive durations associated with the end of phase 2. The vertical line marks the transition between phases 2 and 3.

study and adult seals (Slip 1997; Irvine et al. 1999). The different diving behaviour of the young seals suggests that they are exploiting different prey to the adults. During phase 1 almost all dives made by weaners were in the first 200 m of the water column. Adults regularly traverse this component of the ocean, but few stop to feed there, even individuals that seem to be in similar regions of the ocean at much the same time of year. Recent studies of the diet of elephant seals at Heard Island indicate that young seals (6 months and older) eat predominantly squid, as do adults, but they eat significantly more *Martialia hyadesi*, and they also eat smaller prey than adults (Slip 1995). Squid tend to move

Table 5. Estimated departure mass, total O_2 stores, resting metabolic rate (RMR), and ADL for each seal in phase 1.

Seal ID No.	Mass group	Mean dive duration (min)	Departure mass (kg)	O_2 stores (L)	RMR (L $O_2 \cdot min^{-1}$)	ADL (min)	Heat loss (MJ·d^{-1})[a]	HL/RMR[b]
17219_95	Heavy	6.40	68	4.10	0.96	4.27	18.8	0.68
22501_95	Heavy	7.05	60	3.61	0.92	3.94	19.6	0.74
26636_96	Heavy	7.56	108	6.49	0.98	6.60	19.1	0.67
28482_96	Heavy	7.79	107	6.45	1.06	6.08	16.2	0.53
5811_95	Heavy	7.58	93	5.60	0.94	5.94	18.6	0.68
5814_95	Heavy	7.58	102	6.16	1.03	5.97	17.7	0.59
Mean		7.33	90	5.40	0.98	5.47	18.3	0.65
SD		0.52	21	1.25	0.17	1.09	1.2	0.07
17217_95	Light	5.35	57	3.45	0.73	4.72	26.1	1.23
20918_95	Light	6.24	60	3.64	0.71	5.13	25.3	1.23
22483_95	Light	5.05	58	3.52	0.71	4.96	27.8	1.35
22483_96	Light	5.21	57	3.41	0.69	4.96	26.5	1.33
22486_95	Light	4.16	64	3.87	0.71	5.44	26.1	1.27
22490_95	Light	4.84	59	3.56	0.76	4.71	24.5	1.12
22490_96	Light	5.28	48	3.32	0.7	2.93	25.3	1.25
22499_95	Light	4.54	62	3.75	0.77	4.85	25.7	1.15
22500_95	Light	4.84	58	3.49	0.67	5.22	26.1	1.35
26624_96	Light	5.69	59	3.54	0.7	5.05	27.3	1.34
26625_95	Light	5.50	59	3.58	0.71	5.01	28.2	1.37
26627_95	Light	4.29	55	3.30	0.72	4.58	29.6	1.42
26628_95	Light	3.89	61	3.69	0.72	5.14	28.7	1.38
26635_95	Light	5.77	61	3.66	0.74	4.96	28.7	1.34
2849_95	Light	4.99	72	4.35	0.84	5.20	22.5	0.93
Mean		5.04	59	3.61	0.72	4.86	26.5	1.27
SD		0.64	5	0.26	0.08	0.58	1.90	0.07
	Heavy/light	1.45	2	1.50	1.35	1.13	0.70	0.51

[a]Estimated daily rate of heat loss.
[b]Ratio of estimated daily rate of heat loss (HL) to RMR.

into deeper water as they get older (Rodhouse et al. 1987; Lu and Williams 1994). Perhaps it is more efficient for adult elephant seals to ignore the smaller squid available in the top 200 m and exploit the larger prey, which provide a higher energy yield per capture.

Other striking differences between the pups and the older age groups are that pups spend relatively less time diving and relatively more time on drift dives. These characteristics have also been described in young northern elephant seals on their second trip to sea (Le Boeuf et al. 1996) and may reflect the limited foraging abilities of these animals. The observation that most drift dives occurred around midday may indicate an inability of the seals to follow the prey as they move down to the deepest part of their vertical migration.

The final important difference between the age groups is the dependence of diving ability on body size. The first-trip seals in our study and the second-trip seals reported by Irvine et al. (1999) exhibited a positive relationship between body mass and dive duration, but in adults, dive duration appears to be independent of body size (Hindell et al. 1992). The fact that there were discernible differences in dive depth and, particularly, duration indicate that the young seals were

regularly diving at or near their physiological limits, but that adults are able to perform normal foraging tasks well within their aerobic capacity.

This may provide a proximate mechanism for several key demographic characteristics of southern elephant seals. There is a considerable difference in inter-annual survival rates of first-year seals (Hindell 1991; Wilkinson 1992). The Southern Ocean is subject to several large-scale variations in oceanic properties, such as El Niño / Southern Oscillation (ENSO) and the Antarctic Circumpolar Wave (White and Peterson 1996), which may render prey more difficult to catch in some years. If younger seals are diving at near the limits of their capacity, inter-annual changes in the vertical distribution of prey of even 50–100 m may place it beyond the reach of the young seals, making diving ability, and therefore maternal expenditure, a key determinant of survival in those years.

It has also been reported that larger weaners have higher survival rates than smaller weaners (McMahon 1998). The ability of larger weaners to dive deeper and for longer than smaller seals may be the proximate mechanism in this differential survival. If so, considerable advantages would accrue to mothers that are able to wean larger pups.

Reasons for size-related diving abilities

A combination of O_2 stores and estimated O_2 consumption rate while diving is often used to estimate ADL (Le Boeuf et al. 1989; Hindell et al. 1992; Lydersen and Hammill 1993b). The estimated ADL for the heavy and light groups varied by a factor of 13%, indicating that the observed 45% difference in dive duration between the two groups is likely to due to factors other than O_2 store alone. One explanation is that the metabolic rates of the smaller seals have been underestimated. The elevated metabolic rates in the smaller seals could be due to the different rates of heat loss between the two groups of seals. The heavy seals had more blubber than the light ones at the time of deployment, which not only would provide these animals with a larger energy store, but would also be a more effective barrier against the cold. During phase 1, the seals would have traversed waters with temperatures between 6 and 2°C at the surface, and would therefore have lost heat at a daily rate of 18.3 ± 1.22 MJ·d^{-1} (or slightly more than half of the RMR) and 26.50 ± 1.90 MJ·d^{-1} (1.27 times the RMR) for the heavy and light group, respectively. This means that the lighter seals would need higher metabolic rates to offset the additional heat lost as a consequence of the thinner blubber layer. However, it is important to note that some small weaners actually put on more mass than big ones (Bell et al. 1997), and in those cases would receive a greater heat increment from digestion.

Determinants of diving in the first year of life

Our data suggest that the young seals do not dive to the depths achieved by seals in older age-classes, and as a result of physiological limitations, may be restricted to feeding in the top 100 m for the first two phases and the top 200–300 m during phase 3.

But physiological limitations are not the only determinants of diving behaviour. The sudden switch from shallow to deep daytime dives in a matter of days at the end of phase 2 is too sudden to be due to rapid increases in O_2 stores. Rather, O_2 stores would be expected to increase during the time at sea, as in northern elephant seals (Thorson and Le Boeuf 1994), and presumably the largest component of this increase would occur during phase 2, when the seals are foraging rather than travelling. Total O_2 stores will be higher at the end of phase 2 than at the end of phase 1, so the seals will have the potential to make longer, deeper dives. However, the differences in dive duration and depth between the two phases are only slight, suggesting that at least towards the end of phase 2, the seals are not diving to their full aerobic capacity. The seals may be responding to the distribution of prey at this time rather than being limited by aerobic capacity.

The changes in behaviour of the seals during their first trip to sea may be explained by interactions between the physiological capability of the individuals and the distribution of the prey. During phase 1, the seal's ADL would have been at its lowest, and the seals could not penetrate the water column as deeply as on their return journey. However, the high rates of daily travel at this time suggest that the seals were predominantly travelling, and the foraging component was relatively small. In this case the duration, and to some extent the depth, of their dives would be dictated predomi-

Table 6. Dive statistics for elephant seals of various age and sex classes from Macquarie Island.

	Mass (kg)	Dive duration (min)	Dive depth (m)	Dive depth during the day (m)	Dive depth during the night (m)	Percentage of time spent diving	Surface interval	Source
Weaners								
Phase 1 (21)	77±21	5.70±1.23	100±39	102±48	86±35	69.7±19.3	1.53±0.57	This study
Phase 3 (13)	128±20	9.08±1.70	160±50	—	—	—	—	This study
Juveniles, second trip (16)	128±20	14.79±2.53	—	—	—	88.7±2.1	3.90±1.90	Irvine et al. 1999
Adult females								
Summer, postbreeding (9)	373±57	20.41±16.3	455±84	—	—	—	2.56±0.31	Slip et al. 1994
Winter, post moult (14)	357±50	26.97±6.75	415±86	—	—	—	2.42±0.34	Slip et al. 1994
Adult males (9)	2031±695	24.93±3.66	439±78	—	—	—	3.75±0.55	Slip et al. 1994

Note: Numbers in parentheses show the number of seals in each study. Values are given as the mean ± SD.

nantly by their O_2 stores and diving metabolic rate. The decrease in the daily rate of travel during phase 2 suggests the seals had encountered an area with accessible prey. The distribution of prey would then become an important determinant of diving behaviour. Because the seals still cannot make long dives, they concentrate on prey distributed in the first 100 m of the water column. Even though successful animals will increase O_2 stores during this phase, it may be that the relatively shallow prey are still the most effectively exploited by them. When the seals leave the foraging areas, they may be traversing areas where prey are more dispersed, but as they now have greater O_2 stores than during the outward phase they can now make deeper dives to search for food.

Significance of individual variation in foraging strategy

Within the light group, two individual seals made short, shallow dives for their entire foraging trip, with no apparent ill effects (although returning masses of these animals were not obtained). These animals foraged in the same general region as other seals that made deeper and longer dives, but were able to find sufficient food to survive despite their very different foraging behaviour. Why the other seals did not exploit this more accessible resource is unclear. Individual differences in foraging strategies have been observed for both adult and juvenile southern elephant seals (Hindell et al. 1992, Irvine et al. 1999), and the results of the present study suggest that the strategies may be learnt at an early stage.

Studies of growth during the first trip to sea have indicated that smaller females grow proportionally faster than larger ones (Bell et al. 1997). Similarly, the body condition of smaller females increases proportionally more during their second trip to sea (Irvine et al. 1999), indicating that a smaller body size is not necessarily a disadvantage, although it may require the use of different strategies for capturing prey. It seems, therefore, that some of the smaller individuals are able to overcome the disadvantage of small body size by adopting alternative foraging strategies. These individuals may therefore tend to be the ones from that size class which survive the critical first trip to sea.

Acknowledgments

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