

Movements and foraging areas of naïve, recently weaned southern elephant seal pups

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Summary

1. Female southern elephant seals (*Mirounga leonina* L.) expend variable, often large, amounts of their stored body resources on their pups during lactation. There is some evidence that pups with higher weaning masses have a better chance of surviving their first year. But in order to understand what level of maternal investment is required to produce successful pups, we need to understand the behaviour and problems faced by naïve pups before nutritional independence.

2. We used satellite telemetry to track 30 newly weaned pups on their first trip to sea from their natal site at Macquarie Island in 1995 and 1996. Track duration varied from 2 to 179 (mean, 77) days. Seven seals were tracked for the entire duration of their first trip.

3. The movements were grouped into three phases. Phase 1 (mean duration 30 days) was characterized by rapid and directed dispersal from Macquarie Island at daily travel rates of up to 140 km day⁻¹. Phase 2 (mean duration 67 days) consisted of slower travel rates (generally < 20 km day⁻¹) where activity was often centred on localized patches up to 1900 km from Macquarie Island. This phase was sometimes interrupted by bouts of increased travel rate as the seal moved to another patch. Phase 3 (mean duration 42 days) consisted of prolonged increased travel rates as the seals returned to Macquarie or, in one case, Chatham Island.

4. The routes of the tracks to the south-east were very similar. Simulated tracks based on a constant heading of magnetic east, at variable swimming speed, and modified by ocean current vectors produced a pattern similar to, but not identical to, the south-east tracks. The tracks to the west and south were more diverse and meandering.

5. Based on a nearest neighbour analysis, neither sex, year nor weaning mass influenced Phase 1–2 or Phase 2–3 transition locations.

6. Phase 2 tracks were associated in the south-eastern group with the Pacific Antarctic Ridge and in the south-west group, to a lesser extent, with the Indian Antarctic Ridge. The southern limits of Phase 2 tracks in the south-eastern group aligned with the southern Antarctic Circumpolar Circulation front.

7. Using calculated estimates of body composition at weaning and estimates of the rate of utilization of body reserves for the period before animals reach phase 2 of their trip, we estimate that large pups will have reserves remaining to supply their needs whereas pups in the small group are approaching critical limits. However, these estimates are based on several assumptions and extrapolations. More information on body composition of pups at weaning and departure is needed along with behavioural information to clarify the value of maternal expenditure in terms of offspring survival.

Key-words: Argos telemetry, foraging strategy, maternal investment, migration, navigation, reproductive strategies.

Journal of Animal Ecology (2002) **71**, 65–78

Introduction

Phocid seals provide unique opportunities for studying maternal investment strategies (Fedak & Anderson 1982; Costa 1993; Trillmich 1996). The mothers of many species expend a large fraction of their body reserves on their pups each year during their brief lactation period. The requirements for lactation are largely met by stored reserves and the mothers often do not feed from parturition through to weaning, when all maternal care abruptly terminates (Fedak & Anderson 1982; Anderson & Fedak 1987; Oftedal, Boness & Tedman 1987). Southern elephant seals (*Mirounga leonina* L.) exemplify this life-history pattern (LeBoeuf & Laws 1994a). Pregnant females come ashore on a few sub-Antarctic islands, give birth and nurse their pups for an average of 24 days (McMahon *et al.* 1997). After weaning they mate and then abandon their pups, which remain ashore for a further 6 weeks fasting (Arnbom *et al.* 1993). Mothers may vary in mass by a factor of three at parturition but across the entire size range, they expend material roughly proportional to (35%) their mass at that time (Fedak, Arnbom & Boyd 1996). The pups may treble their birth mass during suckling, but weaning mass is strongly dependent on the mother's parturition mass, with the pups of larger mothers weighing up to three times those of smaller ones. The value of such a variable maternal investment can only be understood in terms of the pup's subsequent behaviour.

We would expect the cost of maternal expenditure and the benefit (in terms of pup survival) to be important parameters in determining maternal strategies. Maternal costs are demonstrable in southern elephant seals. Small females that expend a high proportion of their reserves in one year are often missing on breeding beaches the following year (Arnbom, Fedak & Boyd 1997). Furthermore, reserves must be restored quickly since they are required again around 70 days later to sustain the animal over the energetically expensive annual moult in February (Boyd, Arnbom & Fedak 1993). It can also be demonstrated that females appear to be in control of their own expenditure. For example, the rare mothers that feed two pups only expend the amount expected for the mother's size, in spite of presumably facing double the demand from the pups, and mothers adjust their expenditure from year to year, depending on their mass gain between years (Arnbom *et al.* 1997).

We would expect that this large, and apparently costly, maternal expenditure would confer benefit in terms of pup survival. Indeed, McMahon *et al.* (2000) found that southern elephant seal pups that were heavier at weaning (> 135 kg) had higher (72%) chances of first year survival than lighter (< 95 kg) pups (54%). In contrast, LeBoeuf *et al.* (1994b) found no clear relationship between weaning mass and first year survival in northern elephant seals (*M. angustirostris* Gill). However, the extent of the costs and benefits depends upon the situations mothers and pups face at sea. Both must retain sufficient reserves at departure to see them

through the time it takes to swim to sources of food. But while mothers have previous foraging experience, their pups depart naïve, having never been away from their natal island, and do so at a time when their mothers and all other experienced animals have already left.

By the time the pups finally depart the breeding site, they will have lost, on average, 32% of their weaning mass (Arnbom *et al.* 1993). During the post weaning fast, behavioural and physiological developments take place in preparation for life at sea. However, the fast has a likely cost in that the body reserves remaining at departure, to provide for the pup until it finds food, will be diminished. The value of the resources passed to a pup by its mother and the cost of its post-weaning fast will depend critically on the time it takes for pups to locate prey. This in turn is influenced by the predictability of prey distribution, and the information and strategy the pups use to help them locate prey.

Therefore, to understand the costs and benefits of maternal investment in phocid seals, we need to know the proximity (in time and space) of foraging areas from natal areas and have an idea of the problems that naïve pups face in locating these areas and how they might solve them. This is the primary aim of this paper. We used satellite telemetry to study naïve southern elephant seal pups on their first trip to sea from their natal site on Macquarie Island in the Southern Ocean. We describe their initial foraging trips and examine both the intrinsic (sex, weaning mass and year) and extrinsic factors (oceanographic and geophysical features) that may influence foraging areas used and how the pups find them. Finally, we estimate how long body reserves in large and small pups would last in relation to the time it takes them to first find food.

Materials and methods

STUDY SITE

Macquarie Island (54°30' S, 158°57' E) is situated in the Southern Ocean between Australia and the Antarctic continent (Fig. 1). It has an associated southern elephant seal population of approximately 78 000 individuals (Laws 1994), which represents about 12% of the world population of 664 000.

DEPLOYMENT

Forty-four pups were fitted with Argos Satellite Relay Data Loggers (SRDLs, Sea Mammal Research Unit, St Andrews, UK) at Macquarie Island during their post-weaning fast in December 1995 (32) and 1996 (12). Each pup was individually marked and weighed at birth and reweighed at weaning and at the time of SRDL deployment. They were chosen on the basis of sex and the lower and upper quartiles of weaning mass (light < 96 kg and heavy > 135 kg). We code individual seals by their sex and weaning mass. For example, 'HF1' is a heavy female. In addition, we include the

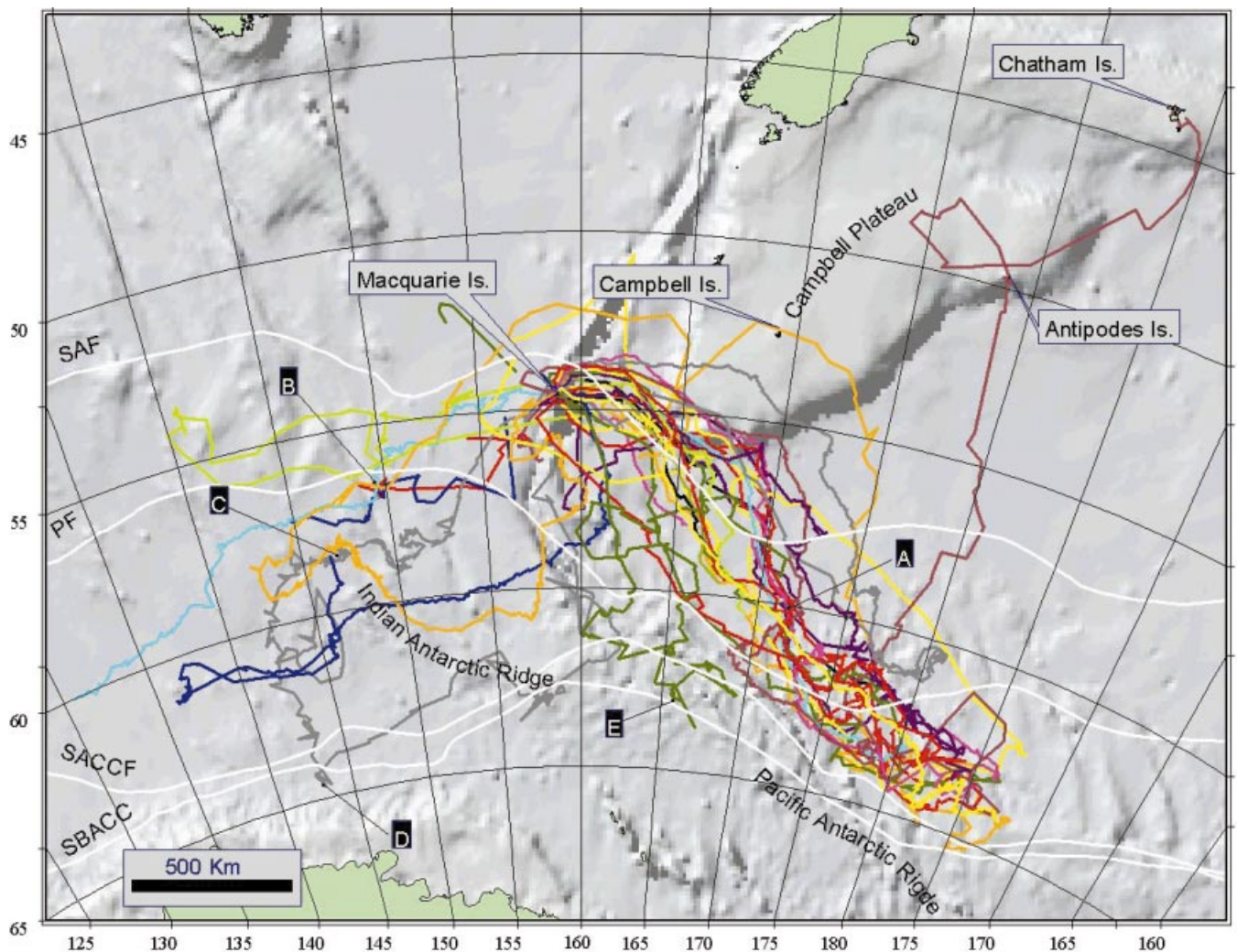


Fig. 1. Tracks of 30 southern elephant seal pups after their first departure from Macquarie Island. The tracks are colour coded by seal (13 colours are recycled). The mean tracking duration was 84.5 days. The bathymetry is derived from the ETOPOS data set (NOAA 1988). The white lines indicate the locations of the Subantarctic (SAF), Polar (PF) and southern Antarctic Circumpolar Circulation fronts (SACCF) and the southern boundary of the Antarctic Circumpolar Circulation (SBACC) as described by Orsi *et al.* (1995). Upper case letters point to locations mentioned in the text.

corresponding Seal Codes used by Hindell *et al.* (1999) who presented the dive information obtained from this study.

Each pup was lightly anaesthetized with an intramuscular injection of Zoletil (Virbac, France) at an intramuscular dose rate of approximately 0.5 mg kg^{-1} body weight (Baker *et al.* 1990). The fur at the site of attachment was dried and cleaned with ethanol and the SRDLs were glued to the fur with a two-part, rapid-setting epoxy resin (Fedak, Anderson & Curry 1983). The SRDLs were placed on the top of the neck just behind the head so that the aerial would emerge when the seal surfaced.

TELEMETRY SYSTEM

The SRDLs consisted of a data logger interfaced to a 500 mW Argos RF unit (model PTT100, Microwave Telemetry, Columbia, MD, USA) (McConnell, Chambers & Fedak 1992). Detailed dive behaviour information were collected and transmitted. The data collection and analysis have been described by Hindell *et al.* (1999). The

SRDL measured $10 \times 9 \times 4 \text{ cm}$, weighed 0.7 kg and could resist pressure to a depth of 2000 m. In order to prolong battery life, the SRDLs switched to an energy-saving mode after 50 days when transmissions were inhibited for 10 out of every 15 h, resulting in a decreased rate of location fixes.

DATA PROCESSING

Argos location fixes were filtered by the algorithm described by McConnell, Chambers & Fedak (1992), using a 'maximum speed parameter' of 2.0 m s^{-1} . The principle of this filter was to reject locations that would require an unrealistic rate of travel to achieve. *Path length* and *daily travel rate* were estimated from mean daily, filtered locations.

MOVEMENT CLASSIFICATION

We classified individual seal tracks into three phases based upon their daily travel rates. The *departure date*

was defined as when a seal had travelled at least 50 km from Macquarie Island. We defined the start of Phase 1 as the departure date and the end when the 5-day running mean of daily travel rates first dipped beneath 20 km day⁻¹. We defined the end of Phase 2 as the date when the 5-day running mean of daily travel rates last rose above 20 km day⁻¹. We defined the end of Phase 3 as the arrival date at Macquarie Island or Chatham Island. These definitions are the same as those used by Hindell *et al.* (1999). We use the phrase 'completed Phase *n*' to indicate that a phase was completed to its end definition, rather than being terminated by SRDL failure or seal death. In this paper 'day *n*' refers to the *n*th day after a seal's departure date.

SPATIAL TESTS

To test whether a nominal variable (*sex* or *year* of deployment) or an ordinal variable (*weaning mass*) influenced the clustering of locations, we calculated a nearest neighbour test statistic. Two sets of locations were considered separately: the terminal locations of completed Phase 1 and of completed Phase 2.

Let D_{ij} be the Euclidean distance between the location of animal *i* and the location of its nearest neighbour, *j*. A measure of nearest neighbour similarity (d_{ij}) is defined for nominal variables as:

$$d_{ij} = \begin{cases} 1 & \text{if the } i^{\text{th}} \text{ location and its nearest} \\ & \text{neighbour have the same value} \\ -1 & \text{otherwise} \end{cases}$$

and for ordinal variables as:

$$d_{ij} = |value_i - value_j|$$

The test statistic (*h*) is defined as

$$h = \sum_{i=1}^n \frac{d_{ij}}{D_{ij}}$$

The test statistic was calculated for the observations (h_{obs}). We then used a re-sampling procedure to estimate the probability (*P*) that h_{obs} could have been obtained from a population where the value of *h* was independent of a given variable. Consider, for example, the nominal variable *sex*. Each animal location was re-assigned a random value of *sex* from the original set of *sexes* and *h* was recalculated. This process was repeated 1000 times and the mean of *h* values (h_{mean}) was calculated. If $h_{\text{obs}} < h_{\text{mean}}$ then *P* was assigned the proportion of the 1000 *h*s from resampling that were less than h_{obs} . If $h_{\text{obs}} > h_{\text{mean}}$ then *P* was assigned the proportion of the 1000 *h*s from resampling that were greater than h_{obs} . The tests were programmed in *R* (Ihaka & Gentleman 1996).

TRACK SIMULATION

In order to examine the possible role of geo-magnetism and ocean currents on the outward tracks from Mac-

quarie Island, we constructed a series of simulated seal tracks. Based on the observed tracks, we constructed a simple rule that the seal should swim due magnetic east. A regional grid of magnetic declinations (the difference between true and magnetic bearing) was constructed from the International Geomagnetic Reference Field (1995) model (Barton 1997). An overlapping grid of ocean current vectors was constructed from the Ocean Circulation and Climate Advanced Modelling Project (Saunders, Coward & deCuevas 1999) at the 100 m depth level for the month of February 1996. The simulated tracks consisted of daily magnetic eastward vectors of 0, 20, 40, 60, 80 or 100 km that were added to the local daily current vector to produce a series of net daily movements.

REMOTELY SENSED DATA

Various remotely sensed data sets were examined using the MAMVIS visualization package (Fedak, Lovell & McConnell 1996) to explore spatio-temporal associations with the seal tracks. Ice concentration data were provided by the EOS Distributed Active Archive Center (DAAC) at the National Snow and Ice Data Center, University of Colorado, Boulder, CO. Sea Surface Temperature data were provided by the NASA Physical Oceanography Distributed Active Archive Centre (DAAC) at the Jet Propulsion Laboratory, California Institute of Technology. Sea colour data were provided by SeaWiFS Project (Code 970-2) and the Distributed Active Archive Center (Code 902) at the Goddard Space Flight Center, Greenbelt, MD 20771.

ESTIMATION OF TIME TO STARVATION

We calculated the approximate time to starvation using estimates of body composition of southern elephant seal pups at weaning and during the post-weaning fast (Carlini *et al.* 2001) and mass loss rate using the equations of Reilly & Fedak (1990) relating total body water to protein and fat. Mean mass loss rates during the post-weaning fast were estimated, separately for the heavy and light categories, from weaning mass and subsequent mass at tag deployment (an average of 38 days later). These mass loss rates were extrapolated to times after departure. Death by protein depletion was estimated to occur when the pup lost 30% of its weaning protein mass (Cahill, Marliss & Aoki 1979). Death by fat depletion was estimated as when fat mass reduced to 10% of body mass (Cahill *et al.* 1979).

Results

TELEMETRY SYSTEM PERFORMANCE

We include here data from the 30 SRDLs (21 in 1995 and 9 in 1996) that provided data once the seal had travelled at least 50 km from Macquarie Island (the *departure date*) (Table 1). An initial high failure rate in some of SRDLs that were originally applied was due primarily

Table 1. Details of the SRDL deployment and tracking of 30 southern elephant seal pups. The departure date was the first day that a seal exceeded 50 km from Macquarie Island. The definitions of the three track phases are given in Results. Summary statistics (mean (SD, SE)), grouped by sex and weaning mass are shown. Summary statistics of durations only include completed phases (durations shown in bold). Durations for uncompleted phases are also shown. Completion of Phase 3 is defined by return to Macquarie or Chatham Island (¹ and ², respectively, in column 'end date'). No SE statistic is given for the 'All' seals category. The date and mass of seals recaptured on their return to Macquarie Island are also shown

Seal	Seal code	Weaning mass (kg)	Departure date	Phase 1 duration (days)	Phase 1–2 transition	Phase 2 duration (days)	Phase 2–3 transition	Phase 3 duration (days)	End date	Total duration (days)	Recovery date	Recovery mass (gain from estimated departure mass) (kg)
HF1	22501–95	136	18 Dec 95	16	03 Jan 96	17	–	–	20 Jan 96	33		
HF2	17215–95	139	18 Dec 95	13	–	–	–	–	31 Dec 95	13		
HF3	5811–95	145	25 Dec 95	36	–	–	–	–	30 Jan 96	36		
HF4	20916–95	151	18 Dec 95	12	–	–	–	–	30 Dec 95	12		
HF5	20917–96	165	18 Dec 96	6	–	–	–	–	23 Dec 96	6		
HF6	28482–96	171	20 Dec 96	46	–	–	–	–	04 Feb 97	46		
HF		151.2 (14.1, 5.8)		16 (–, –)		– (–, –)		– (–, –)		24.4 (16.2, 6.6)		
HM1	17219–95	140	08 Dec 95	27	04 Jan 96	6	–	–	09 Jan 96	33		
HM2	26629–95	141	14 Dec 95	11	–	–	–	–	24 Dec 95	11		
HM3	5814–95	143	09 Dec 95	30	08 Jan 96	68	16 Mar 96	48	03 May 96 ¹	146		
HM4	22500–96	142	17 Dec 96	8	–	–	–	–	25 Dec 96	8		
HM5	26623–96	169	17 Dec 96	16	02 Jan 97	127	09 May 97	36	13 Jun 97	179		
HM		147.0 (12.3, 5.5)		24.3 (7.4, 4.3)		97.5 (41.7, 29.5)		48.0 (–, –)		75.2 (80.9, 36.2)		
H		149.3 (12.9, 3.9)		22.3 (7.3, 3.7)		97.5 (41.7, 29.5)		48.0 (–, –)		47.5 (58.8, 17.7)		
LF1	17217–95	78	06 Dec 95	37	12 Jan 96	51	03 Mar 96	33	05 Apr 96 ¹	121	10 Apr 96	99 (43)
LF2	22486–95	81	02 Dec 95	41	12 Jan 96	31	12 Feb 96	44	27 Mar 96	116	28 Mar 96	87 (32)
LF3	22500–95	88	03 Dec 95	31	03 Jan 96	74	17 Mar 96	40	26 Apr 96 ¹	145		
LF4	26635–95	89	06 Dec 95	28	03 Jan 96	70	13 Mar 96	46	28 Apr 96 ¹	144		
LF5	26625–95	91	05 Dec 95	36	10 Jan 96	43	22 Feb 96	30	23 Mar 96	109		
LF6	2849–95	92	02 Dec 95	41	12 Jan 96	41	22 Feb 96	57	19 Apr 96 ¹	139	14 Apr 96	88 (12)
LF7	26633–95	95	10 Dec 95	11	–	–	–	–	20 Dec 95	11		
LF8	22490–96	93	08 Dec 96	26	03 Jan 97	1	–	–	4 Jan 97	27	19 Sep 97	105 (43)
LF9	20916–96	90	02 Dec 96	11	–	–	–	–	13 Dec 96	11		
LF		88.6 (5.6, 1.9)		34.3 (6.0, 2.3)		51.7 (17.0, 7.0)		45.5 (12.0, 6.9)		91.5 (57.9, 19.3)		
LM1	22483–95	84	05 Dec 95	22	27 Dec 95	92	28 Mar 96	8	05 Apr 96	122		
LM2	22499–95	84	10 Dec 95	30	09 Jan 96	88	06 Apr 96	54	30 May 96 ²	172		
LM3	26628–95	88	02 Dec 95	23	25 Dec 95	69	03 Mar 96	25	28 Mar 96 ¹	117	31 Mar 96	80 (18)
LM4	26627–95	88	10 Dec 95	32	11 Jan 96	32	–	–	12 Feb 96	64		
LM5	22484–95	90	29 Nov 95	23	–	–	–	–	22 Dec 95	23		
LM6	20918–95	92	06 Dec 95	32	07 Jan 96	68	15 Mar 96	35	18 Apr 96	135		
LM7	22490–95	93	13 Dec 95	25	07 Jan 96	60	07 Mar 96	54	29 Apr 96 ¹	139		
LM8	28479–96	85	11 Dec 96	2	–	–	–	–	13 Dec 96	2		
LM9	22483–96	92	05 Dec 96	29	03 Jan 97	29	–	–	01 Feb 97	58		
LM10	26624–96	92	10 Dec 96	39	18 Jan 97	58	17 Mar 97	38	24 Apr 97	135		
LM		88.8 (3.5, 1.1)		29.0 (5.6, 2.0)		72.5 (14.3, 5.8)		37.9 (14.8, 8.5)		96.7 (56.0, 17.7)		
L		88.7 (4.5, 1.0)		31.5 (6.2, 1.6)		62.1 (18.5, 5.3)		44.2 (12.0, 4.5)		94.3 (55.4, 12.7)		
ALL		110.9 (30.8)		29.5 (7.4)		67.1 (24.3)		42.3 (11.0)		77.1 (60.2)		

Table 2. Mean number of locations per day for all seals, grouped by Argos location quality index, and by whether locations passed through the location filter

Argos location quality index	Mean number of pre-filtered locations per day (percentage of total)	Mean number of post-filtered locations per day (percentage of total)
3	0.02 (0.8)	0.02 (0.8)
2	0.04 (1.5)	0.05 (1.9)
1	0.12 (4.1)	0.11 (4.5)
0	0.16 (5.6)	0.15 (6.2)
A	0.69 (24.1)	0.62 (25.4)
B	1.83 (63.8)	1.50 (61.2)
All	2.86 (100)	2.46 (100)

to aerial breakage while seals were still on land. Due to these failures, heavy pups were under-represented in the remaining study sample: heavy females (HF) $n = 6$, heavy males (HM) $n = 5$, light females (LF) $n = 9$, and light males (LM) $n = 10$.

TRACKING DURATION

The mean tracking duration was 77.1 days. The under-representation of heavy pups was exacerbated by the heavier group (especially the females) having shorter tracking durations (mean 47.7, SE 17.8, range 2–179 days) than the light group (mean 94.3, SE 12.7, range 6–172 days).

RATE AND QUALITY OF LOCATION FIXES

Details of location fixes are given in Table 2. The filtering algorithm rejected 13% of locations. There remained an average of 2.46 locations per day, of which 92% were classed as 'of unguaranteed accuracy' (location quality (LQ) 0, A and B (Argos 1989)). For filtered LQs 0, A and B, Vincent *et al.* 2002) estimated 68th percentile latitude errors as 1851, 678 and 3193 m, respectively, and 68th percentile longitude errors as 3029, 909 and 4815 m, respectively.

RECOVERIES

Five study animals were recovered and reweighed at Macquarie Island; four in March–April and one in September. Their mass gain in relation to estimated departure mass varied from 12 to 43 kg (for more detail see Table 1).

OVERVIEW OF MOVEMENTS

All seals dispersed from Macquarie Island to areas up to 1900 km away. There were two main areas, one up to 1900 km to the south-east, and a more diffuse grouping up to 1800 km to the west (Fig. 1). Daily distances from Macquarie Island and travel rates are shown in Fig. 2. Movements were grouped into three phases. Phase 1 was characterized by rapid and directed dispersal from Macquarie Island at daily travel rates of up

to 140 km day⁻¹. Phase 2 consisted of slower travel rate (generally less than 20 km day⁻¹) where activity was often centred on localized patches. This phase was sometimes interrupted by bouts of increased travel rate as the seal moved to another patch. Phase 3 consisted of prolonged increased travel rates as the seal returned to Macquarie Island (or, in the case of seal LM2, Chatham Island). Seven seals were tracked to the completion of Phase 3. Their total path lengths ranged from 2671 to 6509 km, with a mean of 4600 km.

PHASE 1

The mean of the departure dates was 9 December, and they ranged from 29 November to 15 December. The mean duration of completed Phase 1s was 29.5 days ($n = 19$, SD = 7.4) (Table 1). This was equivalent to a mean of 73.2 days (SD = 7.81) post-weaning, and the means for the heavy and light groups were not significantly different (t -test, $t = 1.42$, modified d.f. = 4.12, $P = 0.227$). The tracks were grouped into those that went generally south-east ($n = 20$) or south-west ($n = 10$). For the south-east group the end of Phase 1 was reached after a mean of 71.5 days post-weaning, and for the south-west group at a mean of 79.7 days post-weaning. The difference in the means was not significant ($P = 0.08$).

All seals undertook directed and rapid travel from Macquarie Island (Fig. 3a). Within the first few days between-seal direction of travel was varied. However, by day 5 there was a distinct grouping of tracks which went east and then south-east, and tracks which were more variable in direction, but headed generally to the west and south. These two groupings were usually, but not always, evident by day 5. Two seals (LF5 and LM7) were exceptional in this respect. Both travelled similar routes to the south for the first 10 days, but thereafter LM7 travelled into the south-east grouping while LF5 travelled into the more diffuse west grouping.

Many of the tracks to the south-east showed a high degree of spatial similarity. In one region, 1010 km from Macquarie Island (marked A in Fig. 1), the tracks of six seals (HM1, LF1, LF3, LM1, LM2, LM6) passed within 12 km of each other. Although 12 days separated the first and last passage through this convergence,

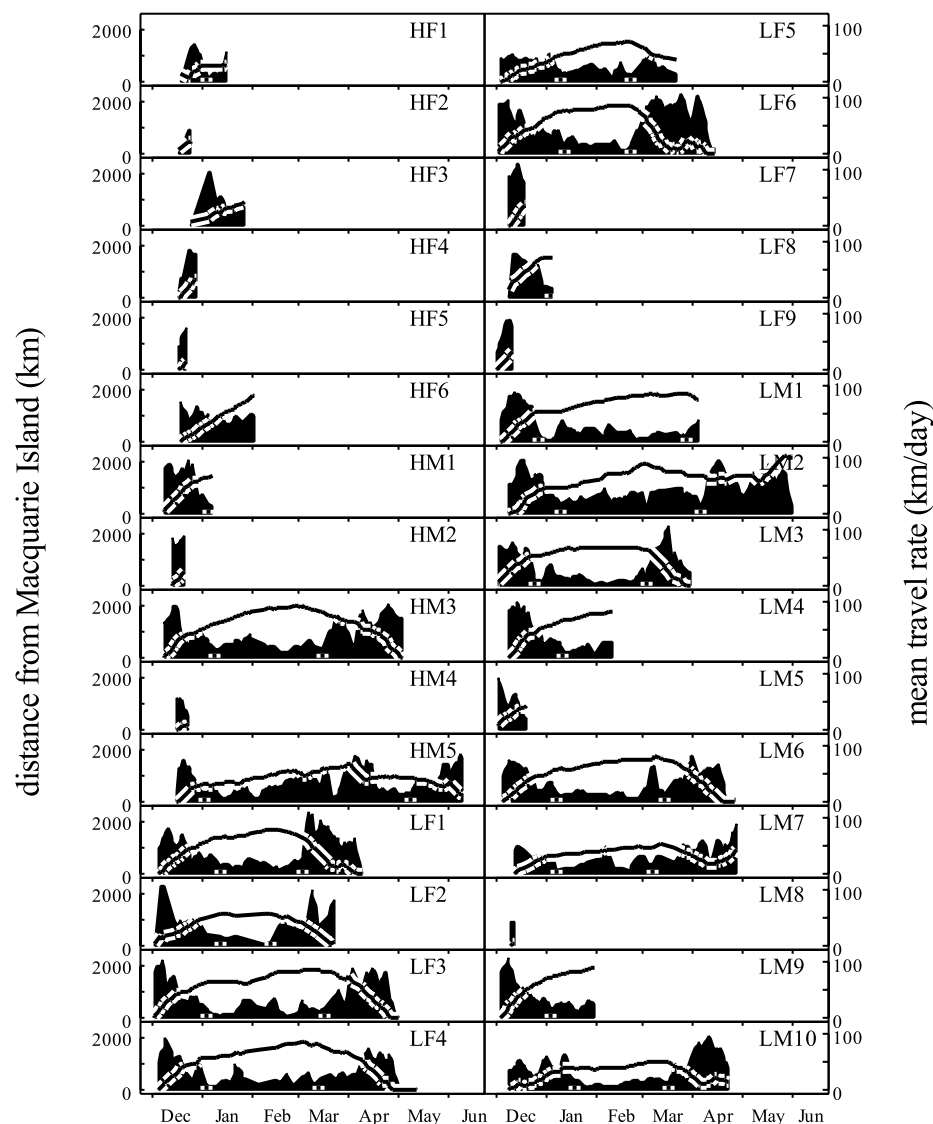


Fig. 2. Distance from Macquarie Island (line) and daily distance travelled (shaded) plotted against month for each of 30 southern elephant seal pups. The vertical lines indicate the Phase 1–2 and Phase 2–3 transition dates (see Results). Note that the plot of distance from Macquarie Island may start before travel rate if there are no locations in the first few days.

two of these seals (LM1 and HM1) did coincide on the same day and their tracks had been within 40 km of each other for the previous 4 days. Although, in general, there was less spatial similarity within the west group of tracks, two seal tracks in particular converged in time and space. Seals HF1 and HF3 remained within 10 km of each other between 13 and 15 January 1996 (marked B in Fig. 1) having previously been hundreds of kilometres apart.

Daily travel rate was frequently in excess of 100 km day⁻¹ and varied between day and seal. Over days 5–10 the mean of the mean daily travel rates for each seal was 88 km day⁻¹ with a SD of 16.6 km day⁻¹. The maximum of the 5–10 day means was 122 km day⁻¹ (seal HM3). The mean path length of completed Phase 1s was 1252 km (SD = 444), and the mean distance of their terminal location from Macquarie Island was 1169 km (SD = 293).

All transition locations from Phase 1–2 in the eastern group were north-east of, but close to, the Pacific

Antarctic Ridge (Fig. 1 and the solid circles in Fig. 3a). The tracks leading to these locations were further to the east of the ridge and did not appear to be related to it. The western tracks were more diverse, but all the transition locations of completed Phase 1s were close to the Indian Antarctic Ridge.

In Fig. 3d we show simulated tracks from Macquarie Island based on swimming speeds between 0 and 100 (in steps of 20) km day⁻¹ at a constant course of magnetic east but influenced by modelled ocean currents at 100 m depth (see Materials and methods). Most of the tracks of the eastern group were aligned with, but to the north-east of, the simulated tracks over the first 500 km down to the southern tip of the Campbell Plateau. Thereafter the seal tracks took a more southerly course and the end locations of Phase 1 tended to the south-west of the simulated tracks.

The results of the nearest neighbour spatial tests are shown in Table 3. The two nominal variables of *sex* and

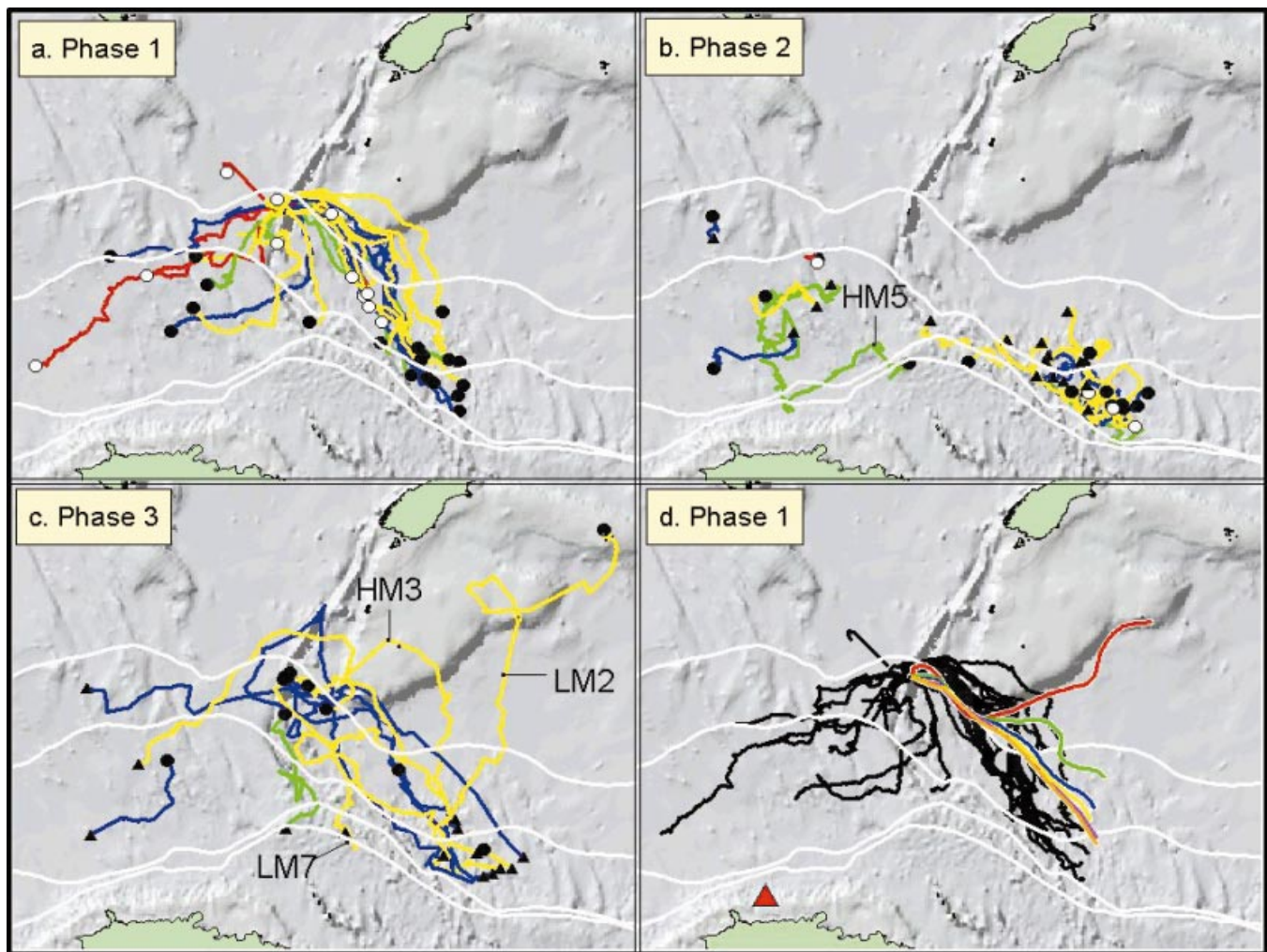


Fig. 3. Tracks of seals shown in Fig. 1 grouped by movement Phase 1 (a), 2 (b) and 3 (c) (see Results). The tracks are colour-coded by the seals' sex-weaning mass code where heavy female (HF) is red, heavy male (HM) is green, light female (LF) is blue and light male (LM) is yellow. The start of each track is shown by a triangle (omitted in (a) since all seals departed from Macquarie Island). A solid circle shows the last location of a *completed* phase. An open circle shows where transmissions terminated before a phase transition. The frontal systems labelled in Fig. 1 are shown in white. Selected seals mentioned in the text are labelled. In Fig. 3d the Phase 1 tracks (black) overlaid with simulated seal tracks at swimming speeds of 0 (red), 20 (green), 40 (blue), 60 (yellow), 80 (purple) and 100 (orange) km day⁻¹ on a constant magnetic bearing of due east. The tracks were truncated at 180° east and covered periods of 55 days at 0 km day⁻¹, 50 at 20, 31 at 40, 21 at 60, 17 at 80 and 14 at 100. The red triangle marks the position of the south magnetic pole.

Table 3. The influence of sex and year of deployment and weaning mass on terminal locations of completed movement Phases 1 and 2 (shown as solid circles in Fig. 3a,b). The nearest neighbour test statistic used is described in Materials and methods. The values indicate the probability that H_0 (the factor does not influence the nearest neighbour index) is true

Terminal locations	<i>n</i>	Sex	Year	Weaning mass
Phase 1	19	0.483	0.095	0.277
Phase 2	13	0.084	0.287	0.272

year of deployment and the ordinal variable of *weaning mass* were examined for their influence on the nearest neighbour statistic (*h*) of the terminal locations of completed Phase 1s and completed Phase 2s. At the $P = 0.05$ confidence level, neither a seal's *sex*, *year*, nor *weaning mass* predicted that of its nearest neighbour at the terminal locations of completed Phase 1.

PHASE 2

The mean of the Phase 1–2 transition dates was 6 January, and they ranged from 25 December to 18 January. The average duration of completed Phase 2s was 67.1 days ($n = 14$, $SD = 24.3$). Travel rates were variable, but slower than in Phase 1, and frequent changes of direction were observed. Periods of slow movement were often interrupted by more rapid travel to a different location. However, there was no apparent overall temporal pattern to this behaviour, both within and between seals.

The direction of travel (Fig. 3b) was variable and meandering in western group. In contrast, travel in the eastern group was directed generally to the south-east, although there were periods of travel of varied direction. This south-east trend generally maintained the seals within a 500-km wide corridor north-east of and parallel

with the Pacific Antarctic Ridge. The mean displacement between the start and the end of Phase 2 in this group was 393 km (SD = 113 km) and the mean path length was 530 km (SD = 182 km).

The distances travelled in Phase 2 by the western group were similar with a mean displacement of 420 km (SD = 180 km) and a mean path length of 474 km (SD = 226 km). Seal HM5 (western group) travelled much further than any other seal, with a displacement of 670 km and path length of 3325 km. Although the western group was more scattered, two seals in particular appeared to be associated with the Indian Antarctic Ridge. The tracks of HM5 and LM10 became more sinuous over this region and they spent a total of 79 days within a 200-km radius circle of the location marked C in Fig. 1.

At the $P = 0.05$ confidence level, neither a seal's *sex*, *year*, nor *weaning mass* predicted that of its nearest neighbour at the terminal locations of completed Phase 2 (Table 3).

PHASE 3

The mean of the Phase 2–3 transition dates was 13 March and they ranged from 12 February to 9 May. The average duration of completed Phase 3s was 42.3 days ($n = 7$, SD = 11.0) and their mean path length was 2246 km (SD = 860). All seals except LM2 started moving back towards Macquarie Island (Fig. 3c). The movements were generally less directed than during Phase 1. Two seals (LF6 and LM10) separately approached within 200–300 km of Macquarie Island and then almost circumnavigated the island at roughly this distance for 3 weeks before making a final approach to the island from the south-east. Of the seven seals that were tracked all the way back to Macquarie Island, six approached (from 100 to 200 km) from the south-east. An eighth seal (LF2) that travelled eastwards from the west group, was tracked to an area 150 km south-east of Macquarie Island before contact was lost. HM3 passed within 20 km of Campbell Island on its approach from the east to Macquarie Island, but there was no evidence that it hauled out there.

A dramatic exception to this pattern of returning to Macquarie Island was seal LM2. From the south-east group, it moved 1500 km north directly towards to the Antipodes Islands and then, after a large loop, 750 km north-east to Chatham Island.

ASSOCIATION OF TRACKS WITH OCEANOGRAPHIC FEATURES

In Figs 1 and 3 we include the positions of fronts and boundaries associated with the easterly Antarctic Circumpolar Current (ACC) (redrawn from Orsi *et al.* 1995). The southern limits of movements (in Phase 2) of the south-eastern group were aligned with the southern ACC front (SACCF). The modal distance of the mean daily locations of the Phase 2 eastern group from

the SACCF was 90 km to the north-east, with a secondary mode at 250 km. There was no obvious association with the Subantarctic (SAF) or Polar (PF) Fronts in this phase.

The seals that moved south-easterly direction during phase 1 moved through water of decreasing sea surface temperature, from about 7 °C near Macquarie to about 2 °C at the end of phase 1. The seals that moved in a westerly direction showed a similar, but less pronounced trend. During Phase 2, most of the eastern group remained within or close to the 2–5 °C isotherm band (*c.* 250 km across). This band was more diffuse to the west of Macquarie Island (> 500 km across) and there was no obvious association with the tracks there. There was no obvious association between SST and the tracks in Phase 3 or between the sea colour (SeaWiFS) images and tracks in any phase.

Two seals visited the margin of the Antarctic pack ice. During the last 3 weeks of April, HM5 (west group) travelled south to the ice margin (D in Fig. 1) and tracked it north-east for the next 6 weeks (Phase 2) before departing north (Phase 3) towards Macquarie Island. LM7 (south-east group) spent the second week of March close to the ice margin (E in Fig. 1), although approximately 500 km to the east of HM5's ice margin tracks.

ESTIMATED TIME TO STARVATION

The mass loss rate during the post-weaning fast for the heavy weaning mass group was 0.93 (SD 0.15) kg day⁻¹, and for the light group was 0.68 (SD 0.09) kg day⁻¹. These two means were significantly different (*t*-test, $t = 5.11$, modified d.f. = 14.6, $P < 0.001$). Using these loss rates and our criteria, the mean estimated time to protein starvation was, for light and heavy animals, respectively, 70.2 (SD 9.0) and 81.1 (SD 8.7) days post-weaning and to fat starvation was 77.9 (SD 9.3) and 113.8 (SD 11.4) days post-weaning.

Discussion

OVERVIEW

The movements of southern elephant seal pups in this study fell into three phases. Phase 1, lasting an average of 30 days, consisted of rapid directed dispersal from Macquarie Island with a mean extent of 1169 km. Phase 2, lasting an average of 67 days, consisted of slower and less directed travel. Phase 3, lasting an average of 42 days, consisted of rapid, but less directed than in Phase 1, travel back to Macquarie Island (for six of the seven seals tracked to the end of Phase 3) or to Chatham Island (for seal LM2). We consider it reasonable to assume that Phase 2 primarily represents feeding. This supposition is supported by LeBoeuf *et al.* (2000), who showed that the proportion of days with reduced travel rate in northern elephant seal tracks was positively related to mass gain between departure and return to land.

The classification of movements into three phases appeared in most cases to be appropriate. However, there were potential difficulties when considering tracks of different durations. For example, in April HM5 increased its travel rate to almost 100 km day⁻¹ for a period of 2 weeks. It then slowed down again and the definition of end of Phase 2 (5-day running mean of daily travel rates *last* rose above 20 km day⁻¹) was not reached until 9 May. If the SRDL had failed in April the definition of end of Phase 2 would have been satisfied on *c.* 1 April. Thus, the end of Phase 2 as assigned may have been premature in seals with a shorter tracking duration. In addition, there was variable reduction in travel rate from seal to seal after their initial fast dispersal from Macquarie Island. HM3 decelerated abruptly while LF7 decelerated slowly. Thus, the date of Phase 1–2 transition was sensitive to the defined threshold of 20 km day⁻¹ in LF7, but less so in HM3. In summary, we regard the three phases of movements to be useful and realistic groupings, while at the same time we regard the exact dates and durations with caution.

COMPARISON WITH ADULT MOVEMENTS

Hindell *et al.* (1991) inferred the tracks of 14 southern adult elephant seals from Macquarie Island using sea temperature data and showed that they may forage up to 4000 km from Macquarie Island. The four males and five of the 10 females in that study seemed to travel to the Antarctic continental shelf, while the five remaining females travelled to the Antarctic Polar Front. None of these adult foraging areas matched well with the Phase 2 areas of the pups in this study. However, additional data provided by Slip *et al.* (1994) show that the area of our Phase 2 south-eastern group is also used by post-moult adult females. Recent tracking studies (SMRU, unpublished) have also suggested that post-moult females sometimes follow similar routes to the south-east group of pup tracks in this study.

The variability in travel rate during Phase 2 was similar to that described for adult elephant seals (McConnell & Fedak 1996; Campagna, Fedak & McConnell 1999; LeBoeuf *et al.* 2000) although the extreme pattern of some adults remaining almost stationary feeding near the seabed on or near the continental shelf was not observed.

INFLUENCE OF INTRINSIC FACTORS ON MOVEMENT PATTERNS

The nearest neighbour spatial test showed no evidence that sex, year, weaning mass or departure day, affected Phase 1–2 or Phase 2–3 transition locations. Sexual segregation of foraging areas has been demonstrated to varying degrees in both southern (Hindell *et al.* 1991; Campagna *et al.* 1995; McConnell & Fedak 1996; Campagna *et al.* 1999) and northern (Stewart & Delong 1990; LeBoeuf *et al.* 1993; LeBoeuf *et al.* 2000) elephant seal adults. Further, LeBoeuf *et al.* (1996)

showed that pups start to exhibit sexual foraging segregation from their third to fourth trip to sea, while Stewart (1997) found segregation was established in males that were 2–4 years old. This segregation has been attributed to the differing energetic requirements of the highly dimorphic sexes in elephant seals (Stewart 1997). While sex may account for a certain degree of variation in choice foraging areas, it appears not to be the whole story. A localized foraging area on the continental shelf off the Falkland Islands used by an adult male from Patagonia (Campagna *et al.* 1999) was very close to an area used by a female from South Georgia (McConnell *et al.* 1996). Thus, sexual segregation may be more apparent within rather than between breeding colonies. Our failure, however, to observe sexual segregation in this study does not detract from the hypothesis that any sexual segregation is driven by differing energy requirements since Bell *et al.* (1997) showed that there was no difference in male and female growth rates of pups returning to Macquarie Island after their first trip to sea. Thus, under this hypothesis, any sexual segregation would not be expected until later in the pups' development.

INFLUENCE OF ENVIRONMENTAL FACTORS ON MOVEMENT PATTERNS

The rapid, directed dispersal in Phase 1 is similar to that of post-breeding and post-moult adult southern elephant seals (Hindell *et al.* 1991; Hindell *et al.* 1992; McConnell *et al.* 1992; Campagna *et al.* 1995; McConnell *et al.* 1996; Campagna *et al.* 1999). McCann (1985) argued that dispersal from South Georgia was driven by insufficient local prey density. It is likely that a similar situation exists at Macquarie Island. The rapid nature of pup dispersal may also act to minimize predation by killer whales (*Orcinus orca* L.) (Guinet, Jouventin & Weimerskirch 1992).

The pattern of dispersal from Macquarie Island formed two groupings: a tight south-easterly group and a more diffuse group to the west. Bornemann *et al.* (2000) also found a close grouping of southern elephant seal pups as they dispersed to the west, avoiding pack and sea ice, from a breeding site at King George Island, off the Antarctic Peninsula. In contrast, most of the adult females in that study were associated with the ice edge. In our study only two pups travelled to the ice edge, and then only for a combined duration of 7 weeks.

The simplest hypothesis to explain the observed south-east pup dispersal from Macquarie Island is that the pups passively drifted in the ocean currents. In the vicinity of Macquarie Island the predominantly easterly Antarctic Circumpolar Current (ACC) is diverted to the south-east by the Campbell Plateau for approximately 700 km. In this region the current can reach speeds of 0.8 m s⁻¹. The path taken by a passively drifting particle at 100 m depth is shown by the 0 m s⁻¹ swimming speed simulated track in Fig. 3d, and it is

clearly inconsistent with the seal track data. However, further inspection of the track data suggests that the addition of the simple rule 'swim magnetic east' may produce trajectories similar to the tracks of the south-eastern group. The resultant trajectories at a variety of swim speeds show a general similarity to the south-eastern tracks, but not sufficiently so to reject the hypothesis that swimming at a constant magnetic bearing plays no role in navigation. The gross role of ocean currents in dispersal thus remains uncertain in the south-east group, but it certainly appears to have no role in the movements of the western group. In another satellite telemetry study, Loughlin *et al.* (1999) hypothesized that the movements of male northern fur seals (*Callorhinus ursinus* L.) in the Bering Sea and North Pacific Ocean were influenced by surface currents. However they concluded that individual seal tracks were, for the most part, independent of surface currents.

The Phase 2 tracks of the south-eastern grouping were within the 2–5 °C sea surface temperature isotherm band. Otherwise, there was no evident correlation with the available remotely sensed sea surface temperature or colour data. However, these data sets were integrated over time and space and may thus have obscured any relationship with smaller scale or transient ocean surface features.

The return route during Phase 3 was generally less directed than the outward Phase 1. The Phase 3 track of seal LM2 was exceptional in that it travelled north in a directed fashion to the Antipodes Islands and then to Chatham Island. Since this seal had never previously been to either of these islands it could not have been making use of a spatial memory map. However, the directed nature of its approach suggests that the seal either sensed the bearing to these islands from many hundreds of kilometres away or that it followed another animal which had been there before.

Seven of the eight seals which were tracked back to, or close to, Macquarie Island approached the island from the south-east, including one animal that had travelled from the western group. This funnelled approach from the south-east was against the prevailing current of the ACC and contrasts with the wide spread of initial departure bearings. Such a pattern of behaviour is consistent with the hypothesis that final navigation back to Macquarie Island involves the detection of a down current, or down wind, chemical signature of Macquarie Island. The use of such olfactory cues has already been suggested in the migration of green turtles (*Chelonia mydas* L.) to Ascension Island (Koch, Carr & Ehrenfeld 1969) and is well documented in salmon (*Oncorhynchus* spp.; Dittman & Quinn 1996). The chemical plume hypothesis could be readily tested by using the techniques of Oliver *et al.* (1998) and translocating pups up and down stream from Macquarie Island.

These south-eastern group Phase 2 tracks were bounded to the south-west by the Pacific Antarctic Ridge. A similar association of elephant seal tracks

with subocean ridges and seamounts has previously been observed by a number of workers (McConnell *et al.* 1996; Jonker & Bester 1998; Bornemann *et al.* 2000). They suggested that seals were attracted to increased prey density due to enhanced production caused by local upwelling. In this study we suggest that the mechanism connecting the Pacific Antarctic Ridge and foraging in Phase 2 is via the influence of the ridge on the eastwards flow of the Antarctic Circumpolar Current (ACC) (Gordon, Molinelli & Baker 1978). The boundary of the ACC, and the positions of the major frontal systems within it (Orsi *et al.* 1995) are shown in Figs 1 and 3, and the southern boundary of the south-east group Phase 2 tracks is clearly aligned close to the southern ACC front (SACCF). We should, however, be aware that Orsi mapped the positions of ACC and its frontal systems using historical records, and that the position of the fronts associated with the ACC can vary significantly through time (Moore, Abbott & Richman 1999; Pakhomov, Ansorge & Froneman 2000; Trathan *et al.* 2000). Thus, there is a degree of uncertainty in the actual position of the ACC fronts and boundaries during our study years. However, Nicol *et al.* (2000) have recently shown the importance of the area to the south of the Southern Boundary of the ACC (SB-ACC) on local productivity at all trophic levels. Tynan (1998) also documented concentrations of krill (*Euphausia superba* Dana) and sperm whale (*Physeter macrocephalus* L.) near the SB-ACC (as mapped by Orsi) and concluded that the SB-ACC 'provides predictably productive foraging for many species, and is of critical importance to the function of the Southern Ocean ecosystem'. Our study suggests that the area around the southern extent of the ACC is also important as foraging grounds for a significant proportion of southern elephant seal pups.

The pattern of tracks we have observed is not random and is likely to be the result of a combination of intrinsic and extrinsic factors. It is difficult to know if the numerous coincidences of tracks that have occurred are the result of chance encounters or some combination of the use of environmental cues and/or communication links with conspecifics or other animals. However, the frequency of such encounters encourages further observation and offers hope that clues to the cues that animals use to locate foraging locations may be gained from them.

IMPLICATIONS FOR MATERNAL INVESTMENT

We have made a preliminary attempt to use the behaviour of naïve pups at sea, in conjunction with estimates of the stored resources they have when they depart, to examine the consequences of maternal expenditure on survival to nutritional independence. We emphasize that this is currently based on a number of assumptions that need further study to refine and validate but we believe it remains a useful exercise. We did not measure body composition in our study animals, but assumed

that their body composition at weaning and the composition of the mass they lost were similar to that reported for southern elephant seals elsewhere by Carlini *et al.* (2001). We make the conservative assumption that pups at sea will use materials at the same rate as they do while ashore. While we expect that energy requirements are likely to be higher at sea, it is possible that opportunistic feeding balances this to some degree. And finally, we assume that 10% body fat reserve and 30% protein loss represent critical levels for survival. It is important that all these assumptions are examined and we hope that their use here will draw attention to their importance.

Several of the implications of this exercise deserve special emphasis. Based on the above assumptions, the time taken for animals to enter Phase 2 (the assumed foraging phase) is very close to estimates of critical time for smaller pups whereas larger ones seem to have a greater margin of safety. The calculations also suggest that protein stores as well as blubber stores should be considered when examining the value of maternal expenditure. While animals adapted to prolonged fasting can reduce absolute and relative protein utilization, adequate protein supplies are nevertheless required during fasting (Dulloo & Jacquet 1999). The consequences of the fat–protein balance at weaning also extend to diving ability. In this same set of pups, Hindell *et al.* (1999) showed that larger pups displayed enhanced diving capabilities, possibly as a result of their greater lean body mass. Thus, the optimal balance of fat and protein resources at weaning may be a complex response to the need to avoid starvation before reaching distant foraging areas and the ability to dive adequately once there. Additional factors such as the role of fat in thermal insulation may also influence this balance. For these reasons and those listed in the paragraph above, detailed studies of body composition in the pup's first year of life seem essential for understanding maternal expenditure strategies.

The function of the post-weaning fast, common in many species of phocids (Arnbom *et al.* 1993) is not clear but it seems likely that it has some important physiological function (Blackwell & Leboeuf 1993; Pattersonbuckendahl *et al.* 1994; Thorson & LeBoeuf 1994; Falabella, Lewis & Campagna 1999) or social (Arnbom *et al.* 1993; Modig, Engstrom & Arnbom 1997) function because it is always present and is expensive in terms of the amount of body stores consumed to support it. It also acts to isolate pups from their mothers and may deny them the opportunity to capitalize on the mothers foraging experience. Our results suggest that the pup's decision when to terminate the fast is a particularly critical and complex one. Arnbom *et al.* (1993) showed that large pups tend to both remain on shore longer and depart heavier, presumably gaining advantage both from the fast and extended survival time at sea before finding food. Animals must leave anticipating a significant further period without food. Physiological signals initiating

departure must therefore come in advance of the acute consequences of fasting, in some way taking into account an expectation of the time to successful foraging.

It seems likely that year-to-year variability in oceanographic conditions (Sharhage 1988) will influence the time it takes pups to find food and the rate at which it can be consumed. Thus, we would predict a significant variability in pup survival – body reserves that are adequate in one year may be inadequate or superfluous in others. Indeed, Hindell *et al.* (1991) have shown that first year survival at Macquarie has ranged from 42–46% to as little as 2% during a period of rapid population decline. In northern elephant seals, LeBoeuf *et al.* (1994b) found that first year survivorship ranged annually between 20% and 49%. However, the response of pup survivorship to oceanographic conditions will depend upon the extra level of maternal expenditure that is provided to insure pups against the consequences of occasional, extreme years. If mothers routinely provide superfluous resources to their pups, a decrease in survivorship would only be apparent in years when the oceanographic conditions were *extremely* unfavourable. The pattern of pup survivorship would be further complicated if the mothers' expenditure was modified by one, or a series of many, unfavourable years. Such a hypothesis is testable with long-term parallel biological and oceanographic studies. Finally, we should be aware that the maternal *cost* would be reduced if the pup were capable of converting any superfluous resources into increased growth, or capacity for growth or subsequent fitness.

There could be a trade-off between the mother's material expenditure on her pup and the information the pup has, either from the mother herself or other sources, to help it find food. If food sources were local, reliable and/or the pups were directed to them by information from their parents, then less reserves may be required to give a reasonable expectation of survival until finding food. In such a scenario mothers could give less, and the value of a large expenditure would be reduced. Thus, pups would not require as large a reserve to survive and an extended post-weaning fast would be less costly. However, if food were distant, patchy and unpredictable the value of a given maternal material expenditure may be greater. The availability of good information and cues to direct pups to food could influence the time and effort needed to find food and thus reduce the level of maternal expenditure required.

In summary, maternal expenditure strategy in southern elephant seals would appear to be a complex response to many factors. However, a necessary key to understanding the importance of these factors is an appreciation of the difficulties faced by naïve pups on their road to nutritional independence in a new and variable environment. The elephant seal population on Macquarie Island has declined markedly since the 1950s (Hindell 1991), and is now less than half what it was. In recent years there has been a steady decline of about 1.6% per year (Hindell, Slip & Burton 1994). A

number of theories have been put forward to explain why the Macquarie and other southern Indian Ocean population are declining while those of the South Atlantic are stable or increasing (Hindell *et al.* 1994). We suggest that, whatever the cause for the decline, the complex relationship between maternal expenditure, pup condition at weaning and long-term trends in oceanic conditions needs to be understood before any convincing conclusions can be drawn. This basic biological information can only come from integrated, long-term studies of seal behaviour and oceanography.

Acknowledgements

This study was funded by the Netherlands Antarctica Program of NWO (Project 751 49 505), the Natural Environment Research Council Sea Mammal Research Unit and the Australian Antarctic Division (Human Impacts Project 1007 and Biological Sciences Project 2265). We are grateful for the essential support and advice from the Australian Antarctic Division at Macquarie Island, especially Dave Slip and Clive McMahon. Beverly A. de Cuevas of the Southampton Oceanography Centre made OCCAM data available to us. Alejandro Orsi kindly provided location data of the oceanographic feature associated with the Antarctic Circumpolar Front. We also acknowledge the helpful referees' comments of Dan Costa and Joachim Plötz.

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Received 17 April 2001; revision received 14 September 2001