# Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean

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**Abstract:** Southern elephant seals (*Mirounga leonina*) are among the most proficient of mammalian divers and are a major component of the Antarctic food web. Yet little is known of their movements or interaction with their oceanic environment. Specially designed satellite-link data loggers allowed us to visualize the 3-D movements of elephant seals as they swam rapidly from South Georgia to distant (up to 2650 km) areas of Antarctic continental shelf. One seal dived continuously to the sea bed in one small area for a month, implying consumption of benthic prey. Dives here were shorter even though average swimming velocity was lower. It is suggested that the physiological requirements of feeding and digestion reduced the aerobic dive limit. Long distance travel to relocatable hydrographic or topographical features, such as shelf breaks, may allow large predators to locate prey more consistently than from mid-ocean searches.

## Introduction

Southern elephant seals have a circumpolar distribution in the Southern Ocean. They breed during October and November on a small number of subantarctic islands and mainland sites in South America (Ling & Bryden 1981, Laws 1984). Approximately half of the adult world population (estimated to be 600 000 (ICSU & SCAR 1991)) breeds at South Georgia (54°S, 36°W) (McCann & Rothery 1988). Their large size and large numbers make them important consumers of Antarctic marine resources. After breeding they spend around 70 days at sea, then come ashore again for *c.* one month to moult (Laws 1956). While at sea, their mobility and diving capabilities make it possible for them to travel great distances and reach great depths. Recoverable time depth recorders (TDR) (Kooyman 1965) have shown that, for the remaining ten months of the year, elephant seals can travel great distances (Le Boeuf *et al* 1988, Hindell *et al* 1991a,b), diving to depths greater than 1500 m, and staying submerged for up to 77 minutes (Stewart & Delong 1990). Dives are punctuated by periods of only 2–3 minutes at the surface (Le Boeuf *et al* 1988, Boyd & Arnbom 1991). This performance can be maintained for weeks at a time.

All of these factors combine to give southern elephant seals the potential to have a major impact over an enormous range of habitats in the Southern Ocean. Although much is known of how they put the resources which they have gathered at sea to use while ashore, little is known about how they exploit the sea or how they are affected by their oceanographic environment. However dramatic the results provided by TDRs, none of these studies have provided high resolution spatial data with which to interpret the behavioural data. As a result, we have little idea of the distribution of southern elephant seals at sea or what they eat, and how, where and

when they eat it.

The aim of this study was to simultaneously monitor the position and dive behaviour of these animals and relate this information, in terms of detailed geographical dispersal and dive behaviour, to physical and biological aspects of the oceanographic environment. This was achieved by the use of a novel transmitter/data logger package, compatible with the Argos satellite system (Argos 1989).

## Materials and methods

### Transmitter packages

A specially designed low power data logger was based on a Dallas DS-5000 microprocessor. Data are obtained from submergence and depth sensors and a velocity turbine. The data logger is interfaced to transmitter units (manufactured by Toyocom, Japan for seals 1, 3 and 4, and Mariner Radar, UK for seal 2) which are compatible with the Argos satellite location system. The timing and data scheduling of transmissions are controlled by the data logger. The minimum interval between transmissions is 40 s. The complete units are contained in an aluminium alloy housing which weighs 1.5 kg in total and is pressure resistant to depths in excess of 1500 m. A complete technical description of the package and the data structures will be published separately.

### Deployment

Four post-breeding female southern elephant seals (Table I) were fitted with data logger/transmitter packages at Husvik, South Georgia. The seals were anaesthetized with an intramuscular injection of Zoletil (Roche) (Baker *et al* 1990)

**Table I.** Weights and tagging dates for the seals studied

| Seal | Weight (kg) | Date |
|------|-------------|------|
| 1 | 506 | 21 Nov 1990 |
| 2 | 362 | 22 Nov 1990 |
| 3 | 315 | 02 Nov 1990 |
| 4 | 414 | 08 Nov 1990 |

at a dose rate estimated to be 1mg kg⁻¹ and then weighed. The data logger packages were glued to the fur on the upper surface of the seals' necks (Fedak *et al* 1983), just behind the head so that the aerial would emerge when the seal surfaced. The aerial pointed forwards at *c.*45° from the longitudinal axis of the seal.

*Data structure and quality control*

Two types of data structure are transmitted, a dive record and a summary record. A dive record consists of an absolute time flag, dive and previous surface durations, maximum depth, and a depth and a velocity profile. A depth profile consists of four depth values measured at times of one, two, three and four fifths of each dive duration. A velocity profile consists of the mean estimated velocity, based on the velocity turbine, for each of five equal intervals of the dive duration between the transmitted depths.

A summary record consists of summary statistics of dive records taken over completed six-hour periods of the day. The starting times of these periods are 00h00, 06h00, 12h00 and 18h00 UTC. The summary statistics include percentages of time spent at the surface and diving, average and maximum depths and the number of completed dives. These records are used primarily to cover periods when the series of dive records received is not continuous.

Two derived parameters from a dive record presented here in Fig. 3 are defined as follows. The *index of dive squareness* is the average of the four depth profile values expressed as a percentage of the maximum depth. A higher index value reflects a more square-shaped dive. The *index of swimming activity* is the average of the middle three velocity profile values. The first and last velocity profile values are omitted to exclude descent and ascent activity. As yet, we have not calibrated the velocity profile values into actual swimming speed values and thus this parameter remains an index of velocity.

The data consisted of behavioural and location information. The integrity of the behavioural data was validated by an error detection and correction code incorporated into each transmission. The Argos system associates a Location Quality Index (LQI) with each location, ranging from three (high expected accuracy) to zero (unguaranteed accuracy), with each location. To remove locations with a large error an iterative forward/backward averaging filter was applied to all locations. A velocity $V_i$ was associated with the ith location where $v_{i,j}$ is the velocity between successive locations

i and j:

$$V_i = \sqrt{\frac{1}{4} \sum_{j=-2, j \neq 0}^{j=2} (v_{i,j+i})^2}$$

Locations with $V_i$ greater than the estimated maximum mean velocity of a seal (3.5 m s⁻¹) were rejected. The filtering process resulted in the rejection of 36%, 48% and 37% of the locations from seals 1, 2 and 3 respectively. Setting the maximum velocity allowed by the filter to 3.5 m s⁻¹ is conservative since overall daily average velocities were always less than 1.5 m s⁻¹. Thus the tracks shown here probably contain more variability than they actually displayed.

Ground truth tests prior to deployment indicated that the location error from the transmitter on seal 2 was between two and four times greater than from the others. This suggests that some of the variability in the track of seal 2 may have been due to location error.

**Results**

The package on seal 4 failed when bitten by a copulating male. The movements of the remaining three animals are shown in Fig. 1. All travelled southwest to sites on the Antarctic continental shelf.

Seal 1 provided detailed information over 70 days. Its track was divided into three phases based on location, movement and dive behaviour. During phase 1 (23 d), it swam 1845 km (average daily velocity across the sea surface
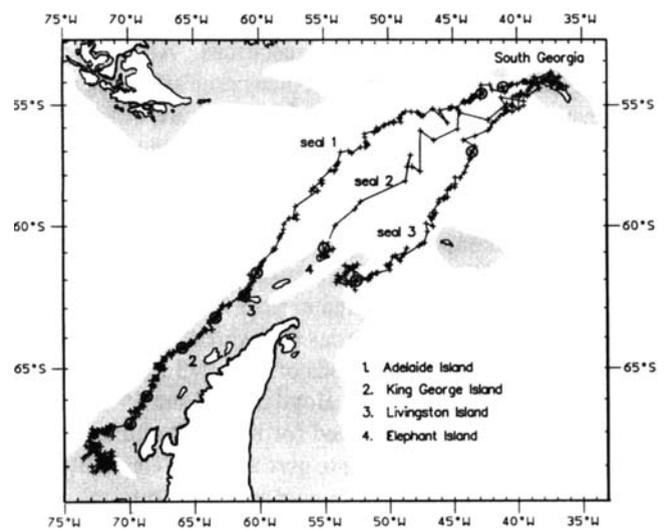


**Fig. 1.** Map of the South Atlantic showing the movements of three post-breeding female southern elephant seals in relation to the continental shelf (hatched area). Locations with a Location Quality Index (LQI) = 0 are shown as a cross and those with a LQI > 0 as a circle. Seals 1, 2 and 3 were tracked for 70, 17 and 20 days providing an average of 9.3, 3.5 and 6.2 valid locations per day respectively.
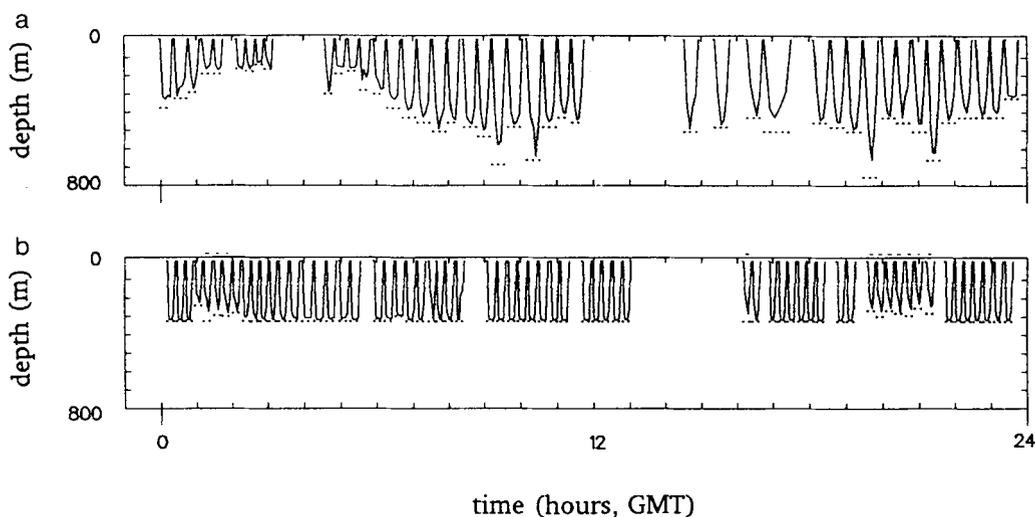
**Fig. 2.** Typical dive depth profiles over 24 hours from seal 1 while in phase 1 (a) and in phase 3 (b). The maximum depth of each dive is shown as a dotted line in the figure. Preceding surface intervals are represented by a horizontal line at zero depth. Breaks in the continuous plot indicate missing data, due primarily to diurnal variation in satellite visibility. Note the variability of dive depth and duration in phase 1 compared with phase 3.

(ADV) 0.93 m s⁻¹) to Livingston Island. In phase 2 (17 d) it hauled out at Livingston Island for 18 h and then swam a further 805 km (ADV 0.55 m s⁻¹) to the southwest, following the continental shelf margin of the Antarctic Peninsula to a location near an underwater canyon 110 km west of Adelaide Island where water depth was 300–400 m. During this phase it spent several periods of up to 12 h at the surface, perhaps on floating ice. During phase 3 (29 d) it remained within 20 km of this location.

Seal 2 swam 1420 km in 16 days (ADV 1.02 m s⁻¹) to Elephant Island where it hauled out. The transmitter failed one day later. It was captured, reweighed and the transmitter removed at a moulting site at South Georgia on 8 February 1991. Seal 3 swam 1435 km in 16 days (ADV 1.03 m s⁻¹) to the continental shelf 110 km southeast of Elephant Island. It remained within a 60 km radius of this area for the next four days after which the transmitter failed. It was sighted on 19 January 1991 at a moulting site on King George Island.

Fig. 2 provides a detailed view of dive profiles from seal 1 on two days typical of phases 1 and 3. Such dive-by-dive data were available from 65% of the animal's track; 6 h dive summaries covered the entire period. A plot of dive statistics is shown in Fig 3. In phase 1 the seal swam in the upper kilometre of the water column. Dive depths (maximum 900 m) and durations (maximum 40 mins) were variable. In phase 2 this variability decreased and frequent dives were made to the sea bed of the continental shelf. Dives made during phase 3, when the animal remained in the small area off Adelaide Island, were shallower and less variable (Fig. 3a) than during phases 1 and 2. The seal tended to swim directly to the bottom and remain there, sometimes swimming slowly, until it returned to the surface (Fig. 3d). These dives involved less swimming activity than those in phases 1 and 2 (Fig. 3e),

yet they tended to be shorter (Fig. 3b) with a smaller proportion of time spent underwater (Fig. 3c). Between days 63 and 65, the seal moved 8 km north, 40 km west and then returned to its starting location. Over these three days all dive parameters (Fig. 3a–e) shifted to values similar to those in phase 1.

## Discussion

Initially, all three seals travelled in a directed manner, with similar routes and speed, over deep water to distant areas of continental shelf. The extended life of the transmitter on seal 1 allowed its subsequent behaviour to be observed. We suggest the following interpretation of its three phases described above. Phase 1 was a transit to feeding grounds, although the variability of maximum depths and dive durations suggests that there was also opportunistic feeding. Phase 2 consisted of slower ADV and dives often to the sea bed. The seal may have been searching for a suitable foraging area or spending more time feeding. Phase 3 reflects targeted benthic feeding. This interpretation is supported in the following arguments.

It is almost certain that seal 1 was feeding over the period it was tracked. In a concurrent study at South Georgia we found that six females gained 1.0–2.3 kg d⁻¹ (seal 2 typified these gains: 141 kg over 78 days, equivalent to 1.8 kg d⁻¹) between breeding and moult. By analogy with female northern elephant seals (*M. angustirostris*) (Le Boeuf *et al* 1989, Sakamoto *et al* 1989), whose weight gain is similar, we estimate that they required 9–20 kg of prey per day; that is 0.6–1.4 tonnes over the 70 day interval between breeding and moult.

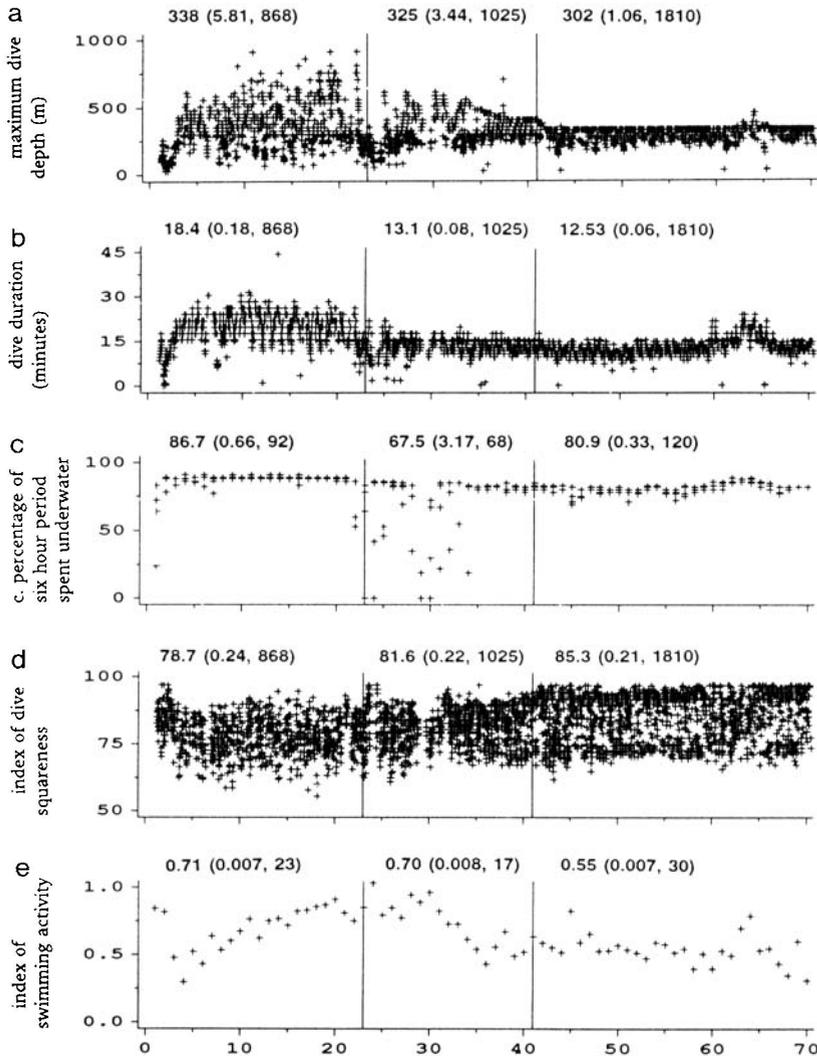Our interpretation of the seal's activity in phase 3 as being

**Fig. 3.** Dive parameters from seal 1 over the 70 day tracking period. Vertical lines delimit the three phases described in the text. Mean, standard error and sample size for each phase, are shown for each parameter. Note that during days 63–65 there was a temporary change in all dive parameters. **a.** The maximum depth attained in each dive. Depth values are accurate to within 5 m at 100 m, to 50 m at 1600 m. The maximum depth of *c.* 910 m was obtained during phase 1. The constant upper limit of depth in phase 3 corresponds to the depth of the sea bed as determined from Admiralty Charts. **b.** The duration of each dive. **c.** The percentage of time within each six-hour summary period that the seal spent underwater. **d.** Index of dive squareness of each dive. **e.** Daily averages of index of swimming activity for each dive.

targeted benthic feeding is consistent with data from stomach samples taken on land in which cephalopods predominate. These included remains from demersal squid and benthic octopods (Rodhouse *et al* in press, Clarke & MacLeod 1982, Laws 1960, Murphy 1914). However, if feeding areas are far from breeding sites these stomach samples may be biased against fish whose remains are retained in the stomach for a shorter period.

Dives in phase 3 were shorter by a factor of 1.5 than in phase 1. For a given depth of dive, more time was spent travelling to and from the surface and the proportion of time spent underwater was 7% less. This behaviour suggests these were not rest dives. For an animal that spends 80–90% of its time underwater, and which might be better referred to as a surfacer than a diver, we would not expect rest dives to be more frequently interrupted by travelling to and from the surface to breathe. Oxygen stores should last longer at rest. Such benthic feeding dives might be shorter if feeding

itself reduced dive duration. Extended periods at the surface were rare during phase 3, implying that the processes of digestion and assimilation were combined with diving activity on a steady state basis, and not put off until breaks in activity. Assimilation of food is known to increase basal metabolic rate up to 1.7 times in another phocid, the harp seal (*Phoca groenlandica*) (Gallivan & Ronald 1981). The increase in metabolic rate due to the specific dynamic effect (Kleiber 1961) is a function of rate of assimilation. We therefore suggest that the seal's aerobic dive limit (ADL) was reduced during phase 3, even though swimming activity was also reduced (Fig. 3e), because the specific dynamic effect of food assimilation increased the rate at which oxygen stores were used. This does not imply that the seal did not feed at all during phase 1, rather that the rate of feeding was greater in phase 3. It is possible that the ADL in phase 3 was not reduced and the seal chose not to approach it because it was not forced to do so by its situation. However, considering the

seal again as a surfacer rather than a diver, it is not obvious why a seal should break off feeding to breathe more frequently than necessary.

All three seals travelled more than 85 km each day for 16–23 days in a directed way to areas of continental shelf. The use of distant foraging areas (associated with the Antarctic Polar Front, continental shelf margin or ice edge) have also been inferred from water temperature data for elephant seals breeding on Macquarie Island (54°S, 157°E) (Hindell *et al* 1991b).

Elephant seal females are long lived animals which invest large amounts of resources in a single pup each year over many years. They must, therefore, locate food reliably each year for many years in succession. Movement away from South Georgia may be explained by the fact that the local shelf area contains insufficient prey items to sustain the local elephant seal breeding population (McCann 1985). There may be an advantage, therefore, in adopting strategies which minimise the risk of yearly failure at the expense of the energetic costs of long distance transits. The physical and chemical conditions around the narrow Antarctic continental shelf, ice edges and the Antarctic Polar Front consistently produce areas of high productivity which attract many top predators (Ainley & DeMaster 1990) and fisheries (Itchii 1990). This contrasts with the open reaches of the Southern Ocean where concentrations of prey are both spatially and temporally very variable and may be associated with unpredictable hydrographic conditions (El-Sayed 1988). If an animal has the energy storage capability (as elephant seals, with their prodigious potential for blubber accumulation, do), the benefit of using distant foraging areas where food is reliably associated with readily relocatable oceanographic features, such as the continental shelf and the Antarctic polar front, may outweigh the costs of transport to these areas. That is, a long swim, perhaps with limited opportunistic feeding en route, may, in the long term, be more productive than pelagic meandering.

Marine mammals impose stringent constraints on technologies for providing information on their biology while at sea. The rigours of their environment, their potentially enormous range and the fact that they spend most of their time below the surface, where both direct observation and electromagnetic telemetry are difficult, requires the use of novel techniques. The development of the data logger and transmitter package has provided a methodology which yields both high quality location and behavioural data. This has permitted, for the first time, visualization of the movements of a marine mammal as it moves freely through the most remote reaches of ocean. It can provide information almost in real time and allow interpretation of the pelagic behaviour in terms of the immediate oceanic environment. The continued successful use of this technique provides a unique opportunity to open up a new window through which to view the behaviour of marine mammals and will impose new demands on the oceanographic data needed to provide overlays for its interpretation.

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