Antarctic Science 10 (1): 21–30 (1998)

Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island

F.C. JONKER and M.N. BESTER

Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

Abstract: Seasonal movements and foraging areas of postbreeding (n = 9) and postmoulting (n = 3) adult southern elephant seal females from Marion Island were studied using Geolocation Time-depth Recorders. Movements were classified into three phases – an outbound transit phase, distant foraging phase, and an inbound transit phase. The longest residence time of postbreeding females during their foraging migrations was in areas at the outer edge of their feeding range (± 1460 km) both to the north and south of the island, largely within inter-frontal zones south of the Antarctic Polar Front (APF) and between the Sub-Tropical Convergence (STC) and the Sub-Antarctic Front (SAF). Postmoulting females travelled further afield (2122–3133 km distant) to the APF, to inter-frontal zones south of the APF (within the pack ice outer edge), as well as to the Antarctic Continental Shelf. This study provides additional information on the putative function of dive types in relation to the movement phases of elephant seal females from Marion Island. The relative frequency of assumed 'foraging', 'exploratory' and 'transit' dive types, as well as the duration and location of the different phases of movement suggest two seasonal foraging strategies. Sea floor topography could possibly cue the transit phases of both postbreeding and postmoulting females from Marion Island.

Received 30 July 1997, accepted 13 October 1997

Key words: bathymetry, elephant seals, foraging, Marion Island, movements

Introduction

Southern elephant seals, *Mirounga leonina* (L.), including the South Georgia, Macquarie and Kerguelen populations (Laws 1994), breed and moult on islands north and south of the Antarctic Polar Front (APF). Adult southern elephant seals return to sea twice each year for *c.* 2–8 months when they move widely in the Southern Hemisphere often visiting the continents abutting on the Southern Ocean, ranging as far south as the pack-ice region surrounding the Antarctic Continent (Tierney 1977, Murray 1981, King 1983, Bester 1989, Gales & Burton 1989, Laws 1994).

The movements of postbreeding and postmoulting southern elephant seal females from Macquarie Island, South Georgia and Peninsula Valdés (Hindell *et al.* 1991a, 1991b, Boyd & Arnbom 1991, McConnell *et al.* 1992a, Campagna *et al.* 1995, McConnell & Fedak 1996) as well as congeners in the Northern Hemisphere from Año Nuevo Point and San Miguel Island (Le Boeuf *et al.* 1986, 1988, 1989, 1992, Naito *et al.* 1989, DeLong *et al.* 1992, Asaga *et al.* 1994, Stewart & DeLong 1994, 1995) have been described in some detail. However, the pelagic distribution and movements of postbreeding and postmoulting southern elephant seal females from Marion Island, are largely unknown. The present knowledge of the ranging behaviour of southern elephant seals within the Kerguelen Province has been derived almost entirely from sightings of marked animals (Bester 1989, Bester & Pansegrouw 1992).

Although resightings of tagged individuals demonstrated individual movements between sub-populations within the Kerguelen Province (Bester 1988a, Bester 1989, Guinet *et al.* 1992), it is difficult to interpret resighting rates in relation to the distribution of elephant seals at sea (Bester 1989). The development and testing of a geographic–location–time–depth recorder (GLTDR) to study the pelagic movements of northern elephant seals (DeLong & Stewart 1991), permitted a preliminary investigation of the pelagic ranging behaviour of three postbreeding southern elephant seal females from Marion Island (Bester & Pansegrouw 1992).

Since the location and the pattern of diving of elephant seals at sea would reflect the general type of prey consumed (e.g. pelagic or benthic animals), the periodicity of foraging, and the effort expended (Le Boeuf *et al.* 1993, Le Boeuf & Laws 1994), the current study has relevance to possible reason(s) for the continued decline of the Marion Island population (Bester & Wilkinson 1994). This paper describes the seasonal pelagic movements, the free-ranging diving patterns and the locations of foraging of postbreeding and postmoulting southern elephant seal females from Marion Island. The implications of the movements and foraging locations are discussed and compared with those from other breeding populations of southern elephant seals.

Material and methods

Recording instruments

The Geolocation Time-Depth Recorders (GLTDRs), models MK3+ and MK3e (Wildlife Computers, Redmond, Washington, USA) were programmed to record data as soon as the instrumented females entered the water, recording hydrostatic pressure (dive depth) every 20, 30, 60 or 90 s and ambient water temperature at 20, 30, 60, 90 or 300 s intervals. Sea-surface light intensity (SSL) and water temperature (SSTs) were also measured at 20–90 s intervals (of which maximum values were stored) each time the seal surfaced until the memory capacities (256 and 512 kbytes for MK3+ and MK3e TDRs respectively) of the recorders were filled.

The GLTDRs were glued to the dorsal pelage of nine postbreeding and three postmoulting southern elephant seal females at Marion Island (46°54'S, 37°45'E) during their breeding (September–November) and moulting (December–February) seasons of 1990–94, following Bester & Pansegrouw (1992). The recorders were deployed on tagged, adult females which had shown fidelity to Marion Island during previous breeding and/or moulting haulouts. Females were sedated with intramuscular injections of ketamine hydrochloride and xylazine hydrochloride when attaching and recovering instruments (Bester 1988b). Instrument recoveries that took place when moulting was well advanced, involved pulling the entire attachment assemblage off using a hooked staff without sedation of the animal.

Upon retrieval of the recorders, the data were transferred to a personal computer. The GEOLOCATION and DIVE ANALYSIS packages by Wildlife Computers (Redmond, Washington, USA) were used to provide summary analyses of the diving data described by Jonker & Bester (1994). One location was estimated per day from sea-surface light-level readings and based on the highest location quality code available (GEOLOCATION package version 2.0). The daily light-level curves were checked manually (obvious outliers were deleted), and then used to estimate time of dawn and dusk (= civil twilight) from which an algorithm calculated approximate latitudinal and longitudinal position (Hill 1994).

The predicted locations were influenced by the accuracies of civil twilight with variability in air temperature, atmospheric pressure and the duration of a seal's dive (mean dive durations of 24.4 ± 4.4 min, Jonker & Bester 1994) near the civil twilight (Hill 1994) which resulted in predicted error in longitude of 0.25° for each one minute of error in civil twilight (DeLong *et al.* 1992). Errors in predictions of latitude are influenced by both latitude and season as discussed by DeLong *et al.* (1992). Latitudinal locations could not be made from measurements of daylight within several weeks of the autumnal and vernal equinoxes (Hill 1994). Duty cycling (one day on, one day off) was enabled in the case of seal O144 (postmoulting period) to allow coverage of most of the movements before the memory of the recorder (256 kbytes) was filled. Memories of GLTDRs deployed on postbreeding seals O390, R101, O138 and postmoulting seals O144, P537 and G006 were filled while they were at sea.

Additional hydrographical data

General bathymetric charts of the oceans (GEBCO, Hydrographic Office, Canada) were used to obtain information on the geographical positions of submarine topographical features in the region of Marion Island such as the Agulhas Plateau, Agulhas Basin, Southwest Indian Ridge, Mid-Atlantic Ridge, Weddell Abyssal Plain, Enderby Abyssal Plain, and the Ob Bank and Lena Seamount. The tracks of females from Marion Island were plotted independently and then overlaid on an identically scaled bathymetrical chart in order to assess patterns of movements in relation to sea floor topography.

Both satellite images of the position of the northern Antarctic pack-ice edge in the sector 20°W to 40°E during the period 1990–94, obtained from the Navy-NOAA Joint Ice Centre (USA) and information concerning the positioning of frontal systems within the Southern Ocean, obtained from the South African Data Centre for Oceanography (SADCO), were used within the analyses of movements of elephant seal females from Marion Island. Frontal systems defined by Lutjeharms & Valentine (1984) and inter-frontal zones, namely the Sub-Antarctic Zone (SAZ); Polar Frontal Zone (PFZ); the Antarctic Water Zone (AWZ); and the Continental Water Zone (CWZ) following Abrams (1985) were distinguished in this data set.

Classification of movements

The movements of females were divided into three phases based on the location of tracks and residence time in given areas for postbreeding and postmoulting females. In general, the movements of females from Marion Island were defined as follows:

> Phase 1: The period between the departure from the island in a definite one-way directional movement, to the commencement of multidirectional, seemingly haphazard, movement over several days in a defined area(s).
>
> Phase 2: The period of multidirectional, seemingly haphazard movement in a defined area distant from the island.
>
> Phase 3: The period between departure from the defined area of multidirectional, seemingly haphazard movement over several days, to one-way directional movement to, and arrival at, the island.

Foraging grounds (phase 2) of individuals were defined as geographical areas crisscrossed by a high number of tracks (based on daily locations). Transit areas (phases 1 and 3) were defined by single, generally one-way directional tracks (based on daily locations) linking the point of departure/return (Marion Island) and the defined foraging grounds.

Ranging distances

The ranging distance of a female was estimated using a Furuno GPS Navigator which calculated the linear distance between Marion Island and the furthest geographical position reached, not including distance covered at depth of dives or the sum of differences between daily locations of movement (Le Boeuf *et al.* 1992, Stewart & DeLong 1994, 1995).

Classification of dive types

Dive types were categorized (using the DIVE ANALYSIS programme, Wildlife Computers), based on dive configurations as determined by dive depths, dive durations, descent and ascent rates, and bottom times of dives following Le Boeuf *et al.* (1988). Of the seven distinct types (Jonker & Bester 1994) only the major dive types, namely type 3, type 5 and type 7 dives that predominated in this data set, including the predominant type 2 shallow dive (Jonker & Bester 1994), were used within the analyses of movements of females (present study) during the postbreeding and postmoulting migrations from Marion Island. The frequency occurrence of these dive types was expressed as the mean percentage frequency of all dives performed over consecutive five day periods for the total recorded time away from Marion Island.

Results

Movements and foraging grounds

Postbreeding females: Postbreeding females ($n = 9$) between the ages of 4–8 years were tracked for 45–73 days from Marion Island (Table I). Their movements are plotted in Fig. 1. The majority of the postbreeding females remained within ± 1400 km of the island, and spent a large proportion of their time (phase 2) in defined zones. Mean linear distance reached by postbreeding females from Marion Island was 1031 ± 302 km (Table I). Two tracks of seals (O390 and Y333) extended in north-westerly directions and ranged between 600–1300 km from Marion Island. Four tracks of seals (R202, G006 and O138) moved in north-easterly directions, ranging between 722–1150 km, two of which were that of a single seal (R202) which utilized the same area (phase 2) during consecutive (1992 & 1993) postbreeding seasons.

The six tracks of postbreeding females showed long residence times in areas north of Marion Island at 40–45°S, centred around longitudes

a) 15°E (1 track – seal O390) over the Agulhas Basin,

b) 25°E (1 track – seal Y333) over the Agulhas Plateau,

c) 38–46°E (3 tracks – seals G006, R202 for 1992 & 1993) over the Southwest Indian Ridge and

d) 50°E (1 track – seal O138) over and/or adjacent to the Southwest Indian Ridge.

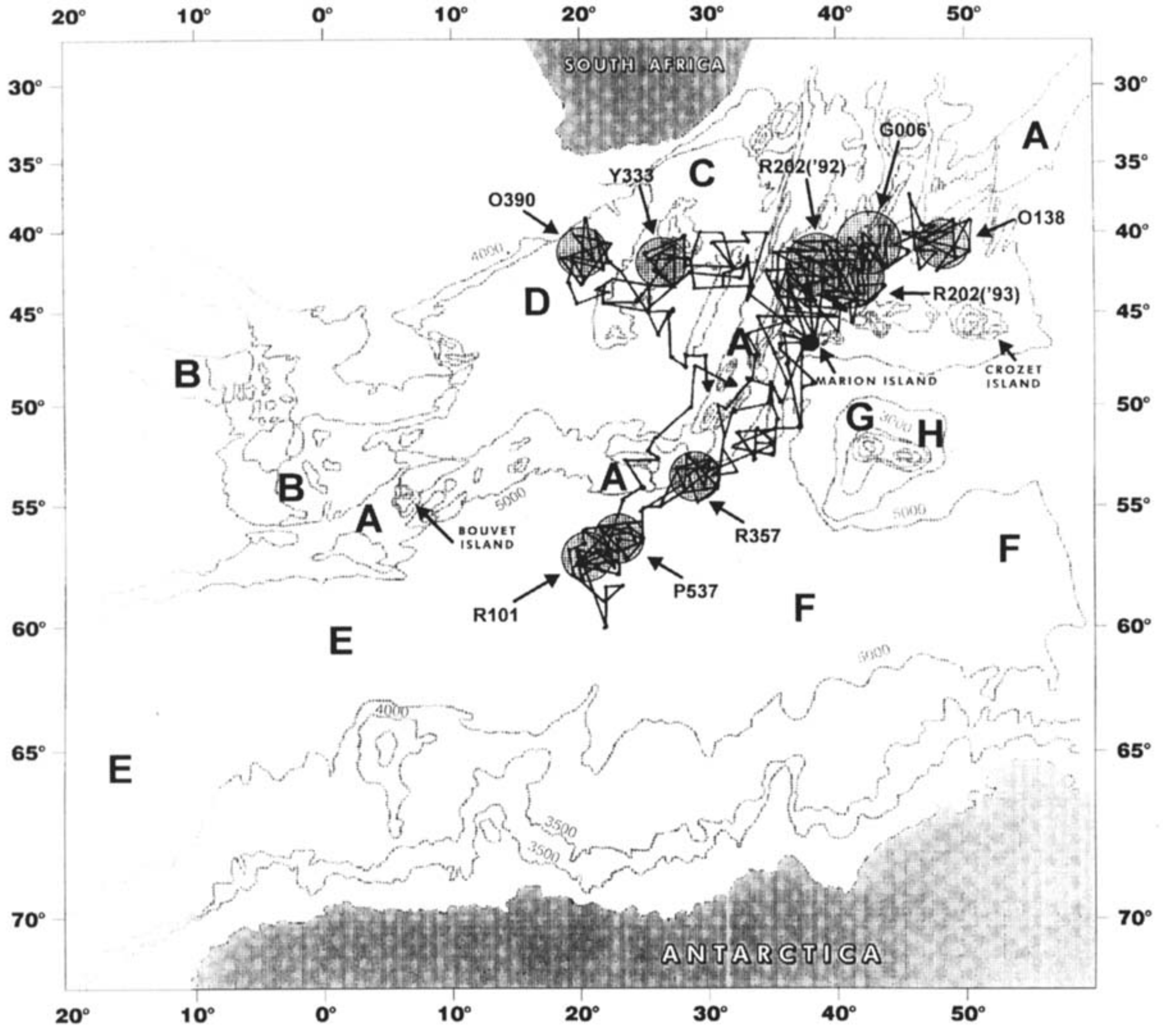
Table I. Direction and the furthest geographical position recorded for southern elephant seal females ($n = 12$) ranging from Marion Island during 1990–94.

Females	Status	Age	Direction away from Marion Island	Furthest position away from Marion Island	Range (km) from Marion Island	Year recorded	Duration of record (days)	Total days at sea	% of the movement period recorded
Y333	pb	6	NW	41.5°S 35.5°E	607	1991	51	51	100
O390	pb	7	NW	41.2°S 24.2°E	1224	1990	53	67	79.1
R357	pb	5	SW	53.5°S 33.5°E	766	1991	45	45	100
R101	pb	4	SW	57.5°S 27.4°E	1393	1990	58	77	75.3
P537	pb	5	SW	56.5°S 23.7°E	1460	1992	51	53	96.2
O138	pb	7	NE	40.9°S 49.2°E	1150	1990	58	67	86.6
G006	pb	6	NE	40.8°S 41.6°E	894	1994	73	73	100
R202(1992)	pb	7	NE	40.8°S 40.8°E	722	1993	69	81	85.2
R202(1993)	pb	6	NE	37.5°S 41.1°E	1068	1992	71	73	97.3
				Mean	1031 ± 302.5			65 ± 12.6	
O144*	pm	8	SW	53.0°S 6.2°E	2379	1991	224	239	93.7
P537	pm	6	SW	71.6°S 18.9°E	3133	1993	201	269	80.1
G006	pm	6	SW	64.7°S 25.4°E	2122	1994	145	258	52.8
				Mean	2544 ± 525.5			255 ± 15.2	

pb - postbreeding NW - north-west
pm - postmoulting NE - north-east
* - duty cycle SW - south-west

All recorded transit phases (phases 1 and 3) of northerly movements of postbreeding seals were tracked over and/or adjacent to the Southwest Indian Ridge (Fig. 1).

Three recorded tracks of seals (R101, P537 and R357) moved south-west from Marion Island and ranged between 766–1500 km. The phases 2 (long residence time) occurred between 50–55°S, centred around (a) 21–24°E (two tracks – seals R101 and P537) adjacent to the Southwest Indian Ridge and extended over the Weddell Abyssal Plain and (b) 30°E (one track – seal R357) occurring over the Southwest Indian



A - Southwest Indian Ridge
B - Mid-Atlantic Ridge
C - Agulhas Plateau
D - Agulhas Basin
E - Weddell Abyssal Plain
F - Enderby Abyssal Plain
G - Ob Bank
H - Lena Seamount

Fig. 1. Movements of nine postbreeding elephant seal females tracked by GLTDR from Marion Island during 1990–94 and overlaid on the bathymetry of the Southern Ocean.

Ridge (Fig. 1). The recorded transit phases (phases 1 and 3) of these southerly movements extended over and adjacent to the Southwest Indian Ridge (Fig. 1).

The north-westerly tracks of seals O390 and Y333 and the north-easterly track of seal G006 (all at 40–45°S) during phase 2, occurred within surface waters ranging between 11.5°C and 14.1°C, whereas seals R202 (recorded during 1992 & 1993) and O138 encountered colder sea surface temperatures ranging between 5.2°C and 8.8°C in their north-easterly tracks during phase 2. Seals R101, P537 and R357 (all at 55–60°S) encountered cold surface waters ranging between 0.8°C and -1.7°C during phase 2.

Postmoulting females: Postmoulting females (n = 3) of 6 and 8 years of age were tracked for 112–201 days (Table I). Their movements are plotted in Fig. 2. All females moved in south-westerly directions from Marion Island. Mean linear distance reached by postmoulting females from Marion Island was 2544 ± 525 km (Table I). Tracks of seal P537 reached a maximum distance of 3133 km from Marion Island, and was distinguished by a recorded dry time of ± 10.4 hours, which indicated a single haulout west of Kapp Norvegia on the Princess Martha Coast, in the eastern Weddell Sea.

Two phase 2 tracks were plotted for seal P537, one of which occurred at (a) 70–72°S centred around 18°W extending over the Antarctic Continental Shelf, and the other at (b) 60–68°S, centred around 18°W–0° longitude over the Weddell Abyssal Plain. The phase 2 recorded for seal G006 occurred at (c) 60–68°S, centred around 22–30°E which extended over the Weddell Abyssal Plain. Both phase 2 tracks of seals P537 and G006 projected within the outer-edge of the Antarctic pack-ice, positioned at 60–65°S during the recording periods of 1993 and 1994, respectively. Phase 2 of seal O144 occurred at (d) 50–55°S, centred around 12–30°E longitude over the Southwest Indian Ridge, and extended over the Mid-Atlantic Ridge. The recorded transit phases (phases 1 and 3) of the postmoulting seals occurred over and/or adjacent to the Southwest Indian Ridge (Fig. 2).

Seals P537 and G006 (at 72–65°S) encountered cold surface waters ranging between -2°C and -0.5°C during phase 2, whereas the track of seal O144 (at 45–50°S) ranged within warmer surface temperatures of between 2.2°C and 4°C.

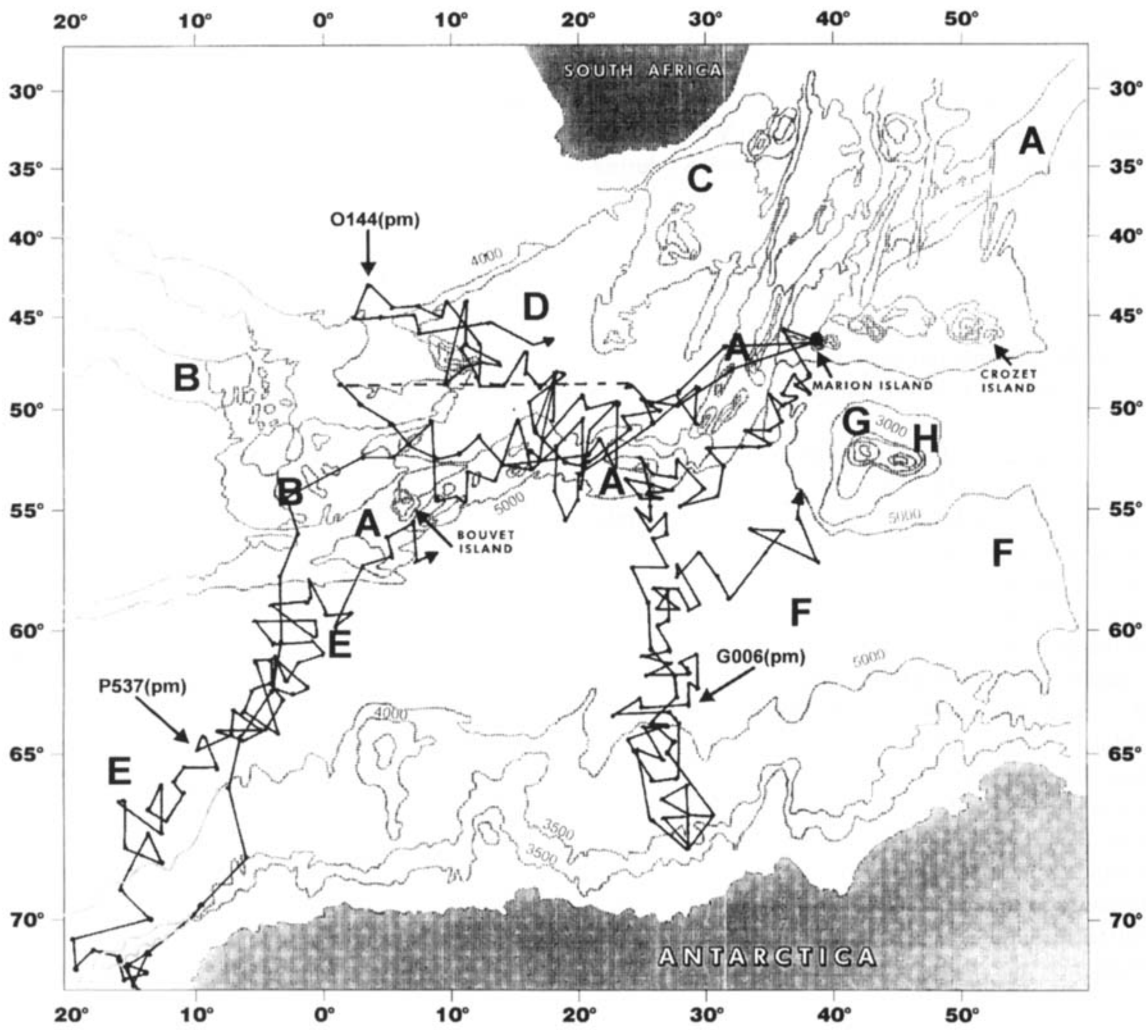
Dive types/phase relationship

The mean percentage time (days) spent by postbreeding females (n = 9) at sea within phases 1, 2 and 3 (15.0 ± 8.3%, 70.8 ± 16.9% and 14.2 ± 8.7% respectively) differed markedly from that of postmoulting females (n = 3), which spent less time in phase 2 (48.9 ± 3.2%) with unequal outbound (phase 1) and inbound (phase 3) transit phases (18.2 ± 12.9% and 32.9 ± 15.3%, respectively) (Table II). The mean proportional contribution of dive types within recorded phases of movement for postbreeding and postmoulting females showed that type 7 dives accounted for the majority of dives followed by type 5, type 3 and type 2 dives (Table II). During both the postbreeding and postmoulting movements of females, the mean proportional contribution of type 5 dives decreased from phase 1 to phase 2, whereas type 7 dives increased. During

Table II. The mean proportion (± standard deviations) of days spent (%) and contribution of the major dive types (%) within the three phases of movement of postbreeding and postmoulting elephant seal females from Marion Island recorded during 1990–94.

Females	Status	Direction away from Marion	Proportion days spent within phases (%)			Mean proportion of dive types within phases (%)											
						phase 1				phase 2				phase 3			
			phase 1	phase 2	phase 3	type 2	type 3	type 5	type 7	type 2	type 3	type 5	type 7	type 2	type 3	type 5	type 7
Y333**	pb	NW	17.6	64.7	17.6	0	10.0	62.5	20.0	0	9.2	22.9	51.9	0	5.1	12.2	62.4
O390	pb	NW	11.9	76.1	11.9	1.0	4.0	19.7	64.0	0.1	5.4	9.7	75.8	-	-	-	-
R357**	pb	SW	14.9	74.5	10.6	12.1	62.7	0.3	8.6	6.3	73.2	1.8	9.7	18.5	54.2		
R101	pb	SW	18.2	63.6	18.2	3.3	12.2	32.1	39.5	0.2	11.9	8.1	71.5	-	-	-	-
P537	pb	SW	30.2	39.6	30.2	3.7	8.3	2.3	79.3	2.1	6.0	4.6	83.3	-	-	-	-
O138	pb	NE	6.0	88.1	6.0	0.3	2.9	4.8	72.8	0.1	8.0	6.7	74.0	-	-	-	-
G006**	pb	NE	6.3	88.9	4.8	9.7	1.5	26.9	61.4	11.2	6.2	9.4	71.7	32.9	0.7	3.5	51.0
R202(1992)*	pb	NE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R202(1993)*	pb	NE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Mean	15.0 ± 8.3	70.8 ± 16.9	14.2 ± 8.7	3.1 ± 3.5	7.1 ± 4.2	22.9 ± 20.0	57.1 ± 20.5	2.0 ± 4.1	7.8 ± 2.4	9.7 ± 6.1	71.6 ± 9.6				
O144	pm	SW	30.5	49.4	20.1	3.1	10.0	5.6	75.0	0.2	0.2	0.7	95.4	-	-	-	-
P537	pm	SW	19.5	51.8	28.7	7.1	2.7	7.8	81.6	0.5	6.8	5.6	84.6	-	-	-	-
G006	pm	SW	4.7	45.5	49.8	10.0	5.5	12.4	70.1	6.8	5.5	9.5	75.4	-	-	-	-
		Mean	18.2 ± 12.9	48.9 ± 3.2	32.9 ± 15.3	6.7 ± 3.5	6.1 ± 3.7	8.6 ± 3.5	75.6 ± 5.8	2.5 ± 3.7	4.2 ± 3.5	5.3 ± 4.4	85.1 ± 10.0				

* - no diving record NW - north-west
** - complete data set NE - north-east
pb - postbreeding SW - south-west
pm - postmoulting



A - Southwest Indian Ridge
B - Mid-Atlantic Ridge
C - Agulhas Plateau
D - Agulhas Basin
E - Weddell Abyssal Plain
F - Enderby Abyssal Plain
G - Ob Bank
H - Lena Seamount

Fig. 2. Movements of three postmoulting elephant seal females tracked by GLTDR from Marion Island during 1990–94 and overlaid on the bathymetry of the Southern Ocean. Broken line connects the known positions of females before and after the vernal and autumnal equinoxes when latitude could not be established.

phase 3 ($n = 3$ females), the frequency occurrence of type 7 dives decreased again whereas type 5 dives increased. The mean proportional contribution of type 5 dives in postmoulting females occurred at lower levels, whereas type 7 dives occurred at proportionally higher levels, than that of postbreeding females (Table II). At the individual level, differences in the frequency contributions of dive types, 2, 3, 5 and 7 were evident within postbreeding and postmoulting females diving behaviour (Table II).

Discussion

Foraging grounds

The utilization of six different foraging areas (four to the north and two to the south) by nine postbreeding elephant seal females from Marion Island seems to indicate no particular pattern in the choice of foraging grounds. However, four out of the six foraging areas (or seven out of the nine tracks) of postbreeding females were positioned along a north-east/south-west line from Marion Island, at an angle parallel to that of the Southwest Indian Ridge (Fig 1a). Not one of the females (*n* = 9) ventured to the east of the SW–NE axis of the Southwest Indian Ridge. Furthermore, the return of a single seal (R202) to the same foraging area during consecutive postbreeding seasons (present study) was similar to movements of three (out of twenty one) northern elephant seal females during the postbreeding migrations of 1991 & 1992 (Stewart & DeLong 1995). Similarly, three seals which were tracked from South Georgia over more than one season, repeated their outward direction of travel in subsequent years (McConnell & Fedak 1996). In addition, three movements of seals from Marion Island used the same northerly routes and foraging areas, and two used similar southerly foraging areas (present study). This suggests that, in at least some instances, certain areas are preferred by individuals, and that the submarine ridges may have cued them during the transit phases.

The mechanisms that seals use to navigate accurately are as yet unknown. However, there has been some speculation that seals could possibly be utilizing bathymetrical and topographical features as navigational cues during movements (Tierney 1977, Burton 1985, Bester 1988b, Gales & Burton 1989, Thompson *et al.* 1991, Wilkinson & Bester 1990), but McConnell & Fedak (1996) could find no obvious topographical features that characterized foraging areas. Although the females from Marion Island did not feed benthically (Jonker & Bester 1994) and the submarine ridges were considerably deeper than the deepest recorded dive, these females performed deep assumed 'exploratory' dives (type 5 dives) at all hours of the day (Jonker & Bester 1994). This could imply that seals probably do not need daytime vision for navigation or orientation as they may be using a number of features to position themselves of which countercurrents (Callahan 1971) and biological productivity (McConnell *et al.* 1992a) could be of importance. All the females in the present study did not use the Enderby Abyssal Plain to the south-east of the island, where no readily locatable oceanographic features occur, excluding the Ob Bank and Lena Seamount (± 800–1000 km distant at depths of 247–3000 m) where elephant seals from an unknown source were seen from Russian trawlers (Bester 1989).

Postbreeding females (present study) that moved to northerly foraging grounds encountered warm surface water consistent with the mean position of the STC at 41°40'S which is recognizable at the sea surface by a mean decrease in temperature from 17.9–10.6°C (Lutjeharms & Valentine 1984), while other northerly foraging areas (*n* = 2) were characterized by surface temperatures consistent with the SAF, which has a mean surface temperature expression of 7°C (Lutjeharms & Valentine 1984). However, close scrutiny of the temperature profile of the water column and daily sea surface temperatures (SSTs) recorded during female dives (Jonker & Bester unpublished data), showed that they foraged in the inter-frontal zones rather than at the STC and SAF as suggested by Bester & Pansegrouw (1992). Similarly, tracks of four postbreeding females from the Patagonia population, which ranged east of Peninsula Valdés (45°W), remained in the temperate waters of the South Atlantic Ocean (in the latitude range 39–50°S), did not seek out frontal systems and did not venture into colder southern waters near the APF (Campagna *et al.* 1995).

Postbreeding females (*n* = 3) from Marion Island, in addition, also foraged in cold waters well south of the APF (found at a mean position of 50°18'S, which is recognizable at the sea surface by a mean decrease in temperature from 4.1–2.5°C, Lutjeharms & Valentine 1984), while postbreeding females from Macquarie Island foraged around the APF (*n* = 3) and in Antarctic waters along the continental shelf (*n* = 5) (Hindell *et al.* 1991a). One postbreeding female from South Georgia was tracked to the APF (McConnell & Fedak 1996) and three were tracked to the continental shelf-area of the Antarctic Peninsula and to Elephant Island (covering distances ≥ 1420 km) (McConnell *et al.* 1992a), one of which moulted there (Fedak *et al.* 1994). Therefore, although the postbreeding females from Marion Island (*n* = 9) used the same open ocean foraging strategy as the Patagonian females, they were foraging within inter-frontal zones (i.e. the STZ and the AWZ) south of the APF, in contrast with the postbreeding females from Macquarie Island (Hindell *et al.* 1991a) and South Georgia (McConnell *et al.* 1992a, McConnell & Fedak 1996) that went to locatable oceanographic and bathymetrical features such as the APF and Antarctic Continental Shelf.

The feeding range of postbreeding females (present study) did not exceed ± 1400 km from Marion Island for the relatively short postbreeding period at sea. It is perhaps significant that frequency occurrences of the predominant assumed foraging dives (type 7 dives) of postbreeding females were the highest at the edge of their feeding range within phase 2 (present study). This might suggest that as soon as suitable levels of prey availability are encountered, they remain in the general area to feed, as hypothesized by McConnell & Fedak (1996) for South Georgia females. Furthermore, the range of 45–77 days at sea between the postbreeding departure and the obligate moult haulout (see Table I), apparently constrained the extent to which the postbreeding females of Marion Island could range. There are no known distant moulting sites, e.g. at islands other than the proximate Prince Edward Island and Iles Crozet or on the Antarctic Continent (Enderby Land being the closest point at

> 2200 km distant), from Marion Island (see Gales & Burton 1989). The movements of postbreeding females from Marion Island (this study) therefore lend support to the hypothesis of Bester (1989), that the foraging range of elephant seals links with the Iles Crozet population (± 1140 km away), but excludes the distant Iles Kerguelen (2640 km) and Heard Island (2740 km) populations which lie to the south-east, an area (the Enderby Abyssal Plain) which was not visited by postbreeding females in this study.

By contrast, the feeding range of postmoulting females (present study) exceeded ≥2122 km from Marion Island to considerably more distant foraging areas which occurred

a) along the Antarctic Continental Shelf near the Princess Martha Coast, in the eastern Weddell Sea,

b) in the inter-frontal zone south of the APF within the AWZ, and

c) around the APF during the postmoulting period of 239–258 days at sea.

Similarly, foraging areas around the APF and over the continental shelf were also sought by postmoulting females from Macquarie Island and South Georgia (Hindell *et al.* 1991a, McConnell & Fedak 1996) as well as inter-frontal zones north and south of the APF by females ($n = 5$) from South Georgia (McConnell & Fedak 1996).

Since foraging locations of postmoulting females from Marion Island in the present study were widely, and more distantly, distributed than that of postbreeding females, it suggests high degrees of pelagic meandering during the postmoulting period, also evidenced by differences in the duration of outbound and inbound transit phases in the latter period. The more constrained foraging excursions undertaken by postbreeding females from Marion Island by contrast, displayed relatively short in and outbound transit phases of similar duration with most time spent within foraging grounds. Similarly, the tracks of females from South Georgia were also generalized into three phases consisting of rapid directed movements away from the island, followed by slower, often meandering travels interspersed with slow or stationary periods, and a rapid directed return to South Georgia (McConnell & Fedak 1996).

Dive types/phase relationship

Phases 1 and 3 of the present study were consistent with transit phases to feeding grounds as dive types 1 and 2, hypothesized to serve as shallow 'transit' dives (Jonker & Bester 1994) increased in the frequency occurrences during these phases. Dive types 3 and 4 were hypothesized to serve as functional 'resting/transit/exploratory' dives, whereas type 5 dives were assumed to serve as deep 'exploratory' dives (Jonker & Bester 1994). Type 7 dives contributed 75% or more of the dive types in each of the dive records in this study, a percentage contribution similar to assumed foraging dive types reported for females in earlier studies (Le Boeuf *et al.* 1986, 1992, Hindell *et al.* 1991b, Asaga *et al.* 1994, Campagna *et al.* 1995). The predominance of type 7 dives (present study), and its particular characteristics (Jonker & Bester 1994), suggests that it serves foraging (Le Boeuf *et al.* 1988, 1992, Hindell *et al.* 1991b, Jonker & Bester 1994).

Since foraging grounds of postbreeding females were located within inter-frontal zones (present study), their foraging grounds were therefore not reliably associated with readily locatable oceanographic features such as the STC, SAF and the APF where primary productivity is high (Plancke 1977, Allanson *et al.* 1981). The frequency of assumed foraging dives within postbreeding foraging grounds were generally lower (interspersed with increased frequencies of assumed 'transit' and 'exploratory' dives) than within the foraging grounds of postmoulting females which were situated at readily locatable oceanographic features. This possibly suggests more opportunistic feeding by postmoulting females *en route* to an area of assumed intense 'foraging/prey pursuit' during phase 2, evident by a concomitant increase in type 7 dives during long residence times in a specific area. Similarly, opportunistic feeding in grey seals also seemed to be an explanation for continuous foraging dive bouts during transit phases (McConnell *et al.* 1992b). Moreover, Hindell *et al.* (1991b) found foraging dives in southern elephant seals to occur the least in the days immediately after departure from the island and periods of reduced travel (phase 2) was hypothesized to occur in areas of increased prey availability (McConnell & Fedak 1996).

We therefore suggest two seasonal foraging strategies for adult females from Marion Island

a) short, directed outbound and inbound journeys to/from circumscribed foraging areas within the inter-frontal zones or open reaches of the Southern Ocean where prey distribution is likely to be unpredictable (El Sayed 1988) but which may attract the same or different individuals during the relatively short postbreeding period, or

b) wide ranging meandering during the relatively long postmoulting period, interspersed with high frequencies of assumed foraging behaviour at separated distant locations which may be readily locatable.

Despite the hypothesized two seasonal foraging strategies, foraging strategy may also be dependent on the diving behaviour of females, e.g. the frequency distributions of foraging dive depths, durations of dives which were on average longer during the postmoulting period than those during the postbreeding period (Hindell *et al.* 1991b, Jonker & Bester 1994), bottom times during diel dive patterns, and the occurrences of Extended Surface Intervals (ESIs) (Jonker & Bester 1994). All these factors could be related to seasonal differences in the type of prey available, as hypothesized by McCann (1985), which may lead to variations in foraging range, location and diving behaviour. Furthermore, these individual differences in diving behaviour and foraging movements not only lie in the interaction between prey availability and the annual energy requirements of populations (Boyd *et al.* 1994) and individual seals, but could be closely correlated with the hydrography and physical characteristics of the water column (Boyd & Arnbom 1991, Hindell *et al.* 1991a, McConnell & Fedak 1996).

Conclusions

Despite overlap in the same geographical areas at sea in some instances, postbreeding and postmoulting females largely displayed different foraging strategies. Foraging excursions of postbreeding females were constrained in time (the short postbreeding period) and choice of alternative moulting haulout sites which could have extended the range of movement. They made short, directed outbound and inbound journeys to/from well circumscribed foraging grounds which promoted extended foraging time. However, foraging areas were located largely within inter-frontal zones where prey distribution is likely to be unpredictable. This is presumably attested to by the high frequency occurrence of hypothesized exploratory dives used during the transit and foraging phases, away from locatable oceanographic features such as the SAF, APF and STC, areas of high primary productivity. Postmoulting females, on the other hand, displayed opportunistic, patchy foraging, meandering between different foraging grounds. They appear to maximize their foraging potential in different locations, some of which are conceivably readily locatable, where assumed 'foraging/prey pursuit' dives predominated. Postmoulting females also range further afield owing to an extended period between moulting and breeding. Prominent ridges north and south of Marion Island could possibly have been used as navigational cues by postbreeding and postmoulting females in the present study during their transit phases.

Acknowledgements

The study was completed under the auspices of the Department of Zoology and Entomology, University of Pretoria. Financial and logistical support was provided by the Department of Environmental Affairs & Tourism on advice from SACAR. We gratefully acknowledge the assistance in the field provided by Hendrik Pansegrouw, Francois Roux, Johan Fourie, Johannes de Lange, Andre La Cock, Greg Hofmeyr, Johannes Klopper and other members of the Marion 47, 48, 49 & 50 relief teams for their support. Thanks are due to Dr Peter Boveng for his help in procuring ice data from the Navy-NOAA Joint Ice Centre (USA). The authors are grateful for the valued comments and suggestions of two anonymous reviewers which greatly improved the paper.

References

ABRAMS, R.W. 1985. Energy and food requirements of pelagic aerial seabirds in different regions on the African sector of the Southern Ocean. *In* SIEGFRIED, W.R., CONDY, P.R. & LAWS, R.M., *eds. Antarctic nutrient cycles and food webs.* Berlin: Springer-Verlag, 466-472.

ALLANSON, B.R., HART, R.C. & LUTJEHARMS, J.R.E. 1981. Observations on the nutrients, chlorophyll and primary production of the Southern Ocean south of Africa. *South African Journal of Antarctic Research*, **10**, 3-14.

ASAGA, T., NAITO, Y., LE BOEUF, B.J. & SAKURAI, H. 1994. Functional analysis of dive types of female northern elephant seals. *In* LE BOEUF, B.J. & LAWS, R.M., *eds. Elephant seals: population ecology, behavior, and physiology.* Berkeley: University of California Press, 310-327.

BESTER, M.N. 1988a. Marking and monitoring studies of the Kerguelen stock of southern elephant seals *Mirounga leonina* and their bearing on biological research in the Vestfold Hills. *Hydrobiologia*, **165**, 269-277.

BESTER, M.N. 1988b. Chemical restraint of Antarctic fur seals and southern elephant seals. *South African Journal of Wildlife Research*, **18**, 57-60.

BESTER, M.N. 1989. Movements of southern elephant seals and subantarctic fur seals in relation to Marion Island. *Marine Mammal Science*, **5**, 257-265.

BESTER, M.N. & PANSEGROUW, H.M. 1992. Ranging behaviour of southern elephant seal cows from Marion Island. *South African Journal of Science*, **88**, 574-575.

BESTER, M.N. & WILKINSON, I.S. 1994. Population ecology of southern elephant seals *Mirounga leonina* at Marion Island. *In* LE BOEUF, B.J. & LAWS, R.M., *eds. Elephant seals: population ecology, behavior, and physiology.* Berkeley: University of California Press, 85-97.

BOYD, I.L. & ARNBOM, T. 1991. Diving behaviour in relation to water temperature in the southern elephant seal: foraging implications. *Polar Biology*, **11**, 259-266.

BOYD, I.L., ARNBOM, T.A. & FEDAK, M.A. 1994. Biomass and energy consumption of the South Georgia population of southern elephant seals. *In* LE BOEUF, B.J. & LAWS, R.M., *eds. Elephant seals: population ecology, behavior, and physiology.* Berkeley: University of California Press, 98-117.

BURTON, H.R. 1985. Tagging studies of male southern elephant seals (*Mirounga leonina* L.) in the Vestfold Hills area, Antarctica, and some aspects of their behaviour. *In* LING, J.K. & BRYDEN, M.M., *eds. Studies of sea mammals in south latitudes.* Northfield: South Australian Museum, 19-30.

CALLAHAN, J.E. 1971. Velocity structure and flux of the Antarctic Circumpolar Current south of Australia. *Journal of Geophysical Research*, **76**, 5859-5864.

CAMPAGNA, C., LE BOEUF, B.J., BLACKWELL, S.B., CROCKER, D.E. & QUINTANA, F. 1995. Diving behaviour and foraging location of female southern elephant seals from Patagonia. *Journal of Zoology, London*, **236**, 55-71.

DELONG, R.L. & STEWART, B.S. 1991. Diving patterns of northern elephant seal bulls. *Marine Mammal Science*, **4**, 369-384.

DELONG, R.L., STEWART, B.S. & HILL, R.D. 1992. Documenting migrations of northern elephant seals using daylength. *Marine Mammal Science*, **8**, 155-159.

EL-SAYED, S.Z. 1988. Seasonal and interannual varaibilities in Antarctic phytoplankton with reference to krill distributions. *In* SAHRHAGE, D., *ed. Antarctic Ocean and resources variability.* Berlin: Springer-Verlag, 101-119.

FEDAK, M.A., ARNBOM, T., MCCONNELL, B.J., CHAMBERS, C., BOYD, I.L., HARWOOD, J. & MCCANN, T.S. 1994. Expenditure, investment and acquisition of energy in southern elephant seals. *In* LE BOEUF, B.J. & LAWS, R.M., *eds. Elephant seals: population ecology, behavior, and physiology.* Berkeley: University of California Press, 354-373.

GALES, N.J. & BURTON, H.R. 1989. The past and present status of the southern elephant seal *Mirounga leonina* (L.) in greater Antarctica. *Mammalia*, **53**, 35-47.

GUINET, C., JOUVENTIN, P. & WEIMERSKIRCH, H. 1992. Population changes, movements of southern elephant seals on Crozet and Kerguelen Archipelagos in the last decades. *Polar Biology*, **12**, 349-356.

HILL, R.D. 1994. Theory of geolocation by light levels. *In* LE BOEUF, B.J. & LAWS, R.M., *eds. Elephant seals: population ecology, behavior, and physiology.* Berkeley: University of California Press, 227-236.

HINDELL, M.A., BURTON, H.R. & SLIP, D.J. 1991a. Foraging areas of southern elephant seals *Mirounga leonina* as inferred from water temperature data. *Australian Journal of Marine and Freshwater Research*, **42**, 115-128.

HINDELL, M.A., SLIP, D.J. & BURTON, H.R. 1991b. The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia:Phocidae). *Australian Journal of Zoology*, **39**, 595-619.

JONKER, F.C. & BESTER, M.N. 1994. The diving behaviour of adult southern elephant seal, *Mirounga leonina*, cows from Marion Island. *South African Journal of Antarctic Research*, **24**, 75-93.

KING, J.E. 1983. *Seals of the world.* London: Oxford University Press, 240 pp.

LAWS, R.M. 1994. History and present status of southern elephant seal populations. *In* LE BOEUF, B.J. & LAWS, R.M., *eds. Elephant seals: population ecology, behavior, and physiology.* Berkeley: University of California Press, 49-65.

LE BOEUF, B.J., COSTA, D.P., HUNTLEY, A.C., KOOYMAN, G.L. & DAVIS, R.W. 1986. Pattern and depth of dives in northern elephant seals *Mirounga angustirostris*. *Journal of Zoology, London*, **208**, 1-7.

LE BOEUF, B.J., COSTA, D.P., HUNTLEY, A.C. & FELDKAMP, S.D. 1988. Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Canadian Journal of Zoology*, **66**, 446-458.

LE BOEUF, B.J., NAITO, Y., HUNTLEY, A.C. & ASAGA, T. 1989. Prolonged, continuous deep diving by northern elephant seals. *Canadian Journal of Zoology*, **67**, 2514-2519.

LE BOEUF, B.J., NAITO, Y., ASAGA, T., CROCKER, D. & COSTA, D.P. 1992. Swim speed in a female northern elephant seal: metabolic and foraging implications. *Canadian Journal of Zoology*, **70**, 786-795.

LE BOEUF, B.J., CROCKER, D.E., BLACKWELL, S.B., MORRIS, P.A. & THORSON, P.H. 1993. Sex differences in diving and foraging behaviour of northern elephant seals. *Symposium of the Zoological Society, London*, **66**, 149-178.

LE BOEUF, B.J. & LAWS, R.M. 1994. Elephant seals: an introduction to the genus. *In* LE BOEUF, B.J. & LAWS, R.M., *eds. Elephant seals: population ecology, behavior, and physiology.* Berkeley: University of California Press, 1-28.

LUTJEHARMS, J.R.E. & VALENTINE, H.R. 1984. Southern Ocean thermal fronts south of Africa. *Deep-Sea Research*, **31**, 1461-1476.

MCCANN, T.S. 1985. Size, status and demography of southern elephant seal (*Mirounga leonina*) populations. *In* LING, J.K. & BRYDEN, M.M., *eds. Studies of sea mammals in south latitudes.* Sydney: South Australian Museum, 1-17.

MCCONNELL, B.J., CHAMBERS, C. & FEDAK, M.A. 1992a. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science*, **4**, 393-398.

MCCONNELL, B.J., CHAMBERS, C., NICHOLAS, K.S. & FEDAK, M.A. 1992b. Satellite tracking of grey seals (*Halichoerus grypus*). *Journal of Zoology, London*, **226**, 271-282.

MCCONNELL, B.J. & FEDAK, M.A. 1996. Movements of southern elephant seals. *Canadian Journal of Zoology*, **74**, 1485-1496.

MURRY, M.D. 1981. The breeding of the southern elephant seal *Mirounga leonina* L. on the Antarctic continent. *Polar Record*, **20**, 370-371.

NAITO, Y., LE BOEUF, B.J., ASAGA, T. & HUNTLEY, A.C. 1989. Long-term diving records of an adult female northern elephant seal. *Antarctic Record*, **33**, 1-9.

PLANCKE, J. 1977. Phytoplankton biomass and productivity in the subtropical convergence area and shelves of the western Indian Subantarctic Islands. *In* LLANO, G.A., *ed. Adaptations within Antarctic ecosystems.* Washington, DC: Smithsonian Institution, 51-73.

STEWART, B.S. & DELONG, R.L. 1994. Postbreeding foraging migrations of northern elephant seals. *In* LE BOEUF, B.J. & LAWS, R.M., *eds. Elephant seals: population ecology, behavior, and physiology.* Berkeley: University of California Press, 290-309.

STEWART, B.S. & DELONG, R.L. 1995. Double migrations of the northern elephant seal, *Mirounga angustirostris*. *Journal of Mammalogy*, **76**, 196-205.

THOMPSON, D., HAMMOND, P.S., NICHOLAS, K.S. & FEDAK, M.A. 1991. Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). *Journal of Zoology, London*, **224**, 223-232.

TIERNEY, T.J. 1977. The southern elephant seal, *Mirounga leonina* (L.) in the Vestfold Hills, Antarctica. *Australian Wildlife Research*, **4**, 13-24.

WILKINSON, I.S. & BESTER, M.N. 1990. Duration of post-weaning fast and local dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. *Journal of Zoology, London*, **222**, 591-600.