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Diving behaviour and foraging ecology of female southern elephant seals from Patagonia

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Abstract

We asked if non-gestating, adult female southern elephant seals, *Mirounga leonina*, from Península Valdés, Argentina, forage on the wide continental shelf off the peninsula during the post-breeding trip to sea (PB females), or whether they forage in deep water, where gestating, post-moult (PM) animals have been shown to do. More than 16 600 dives were recorded with geographic-location time-depth recorders deployed in five PB females. Data were compared with about 19 500 dives from six gestating, PM animals. Four satellite transmitters linked to the Argos system were deployed in PB (2) and PM (2) animals. During both trips females displayed continuous, deep, and long-duration diving. PB females crossed the shelf in 3–7 days, spending 89% of the recorded time at sea over waters deeper than 200 m. A diel pattern in the frequency distribution of dives/hr, dive depth and dive duration was apparent in both PB and PM individuals beyond the continental shelf. Deeper and longer dives were observed during daylight hours, consistent with feeding on dielly-migrating prey. PB females concentrated their foraging effort in temperate waters of the SW Atlantic, between 36° and 46°S and up to 1200 km from shore. PM females travelled further, reaching ~50°S and 2281 km east from the rookery. The longest migration was a PM trip of 11 600 km. Females from Península Valdés, the only colony for the species with an increasing birth rate, do not feed near or south of the Antarctic Polar Front, where most seals from more southerly stable or decreasing rookeries forage.

Introduction

Female elephant seals of the genus *Mirounga* make two foraging trips per year between one-month-long stays on traditional rookeries to breed and moult their pelage (Le Boeuf & Laws, 1994). The foraging trip after breeding lasts about 70 days and the one after moulting lasts eight months, the entire gestation period. During these migrations, females of both species of elephant seals, southern (*M. leonina*) and northern (*M. angustirostris*), ranging in age from juveniles to adults, forage in deep water, hundreds of thousands of kilometres from their breeding or moulting areas (Hindell *et al.*, 1991*a* and *b*; McConnell *et al.*, 1992; Jonker & Bester, 1994; Le Boeuf, 1994; Le Boeuf *et al.*, 1996; McConell & Fedak, 1996).

Post-moult (PM), gestating female southern elephant seals departing the rookery at Península Valdés, Argentina, moved quickly over the broad Patagonian shelf (345–630 km wide), crossing it in 2.5 days (Campagna *et al.*, 1995). They did not appear to begin foraging until reaching deep water beyond the continental shelf break, at depths exceeding 200 m. PM Patagonian females exhibit the same continuous, deep, long-duration diving pattern as seals from other colonies (see references above), as they forage in temperate waters of the South Atlantic Ocean. The aim of this study was to investigate the foraging behaviour of adult females during the post-breeding migration and expand the information for the first weeks of the post-moult trip.

Specifically, we asked whether non-gestating, post-breeding (PB) females show the same diving pattern and forage in the same location in deep water as gestating PM females, or whether they forage on the continental shelf either exclusively or en route to deep water. As the reproductive condition of the female may affect the diving behaviour (Hindell *et al.*, 1991*b*; Le Boeuf, 1994), PB females might be more likely than PM females to forage in the shallow waters of the shelf. First, the Patagonian shelf supports a biomass of fishes and squid that may serve as prey for seals

(Patterson, 1987; Rodhouse, 1988; Rodhouse *et al.*, 1995). Second, since the energy cost of lactation is higher than the energy expenditure during the moult (Boyd *et al.*, 1994), females that lose 40% of their body weight during four weeks of nursing and fasting (Deutsch *et al.*, 1994), and that have only two months at sea to recover it, might be expected to feed as soon as possible, i.e., on the nearby continental shelf, at least on their way out to deep water. Therefore, a comparison of the diving pattern on and off the shelf, within and between pelagic phases, would reveal effects of reproductive condition on foraging behaviour.

Methods

We deployed geographic-location time-depth recorders (GLTDRs; Wildlife Computers, Redmond, Washington) and VHF transmitters (Advanced Telemetry Systems, Bethel, Minnesota) on eight PB females at Punta Delgada, Península Valdés (42°45′S; 63°38′W), at the end of the lactation period, three in October 1993, and five in October 1994 (Campagna *et al.*, 1993). For comparative purposes, and to augment the sample of PM individuals studied by Campagna *et al.* (1995), we deployed similar instrument packages on two females (PM-A and PM-F) at the end of the moult (February 1994). Data on these females were summarized together with diving information on four additional PM individuals reported in Campagna *et al.* (1995). One female was recorded during both the post-breeding (PB-A) and the post-moult (PM-A) seasons. The unit of one PB female (PB-B) recorded depth only up to 450 m preventing estimates of mean and maximum dive depths.

To validate travelling routes determined with GLTDRs, two PB and two PM females were instrumented with 0.5 watt Argos-linked ST6 Platform transmitter terminals (PTTs) (Telonics, Mesa, Arizona) in October 1996 and January 1997, respectively. PTTs were programmed to repeat the transmission signal every 40 s while the seal was at the surface.

Females were immobilized with Telazol (Aveco Co. Inc., Fort Dodge, Iowa; Baker *et al.*, 1990) and the GLTDRs were attached with marine epoxy (Evercoat Ten-set, Fibre-Evercoat Co., Cincinnati, Ohio) on the dorsal midline above the shoulders (Le Boeuf *et al.*, 1988) while satellite tags were glued to the top of the head to facilitate transmission of location as the animal surfaced between dives.

The Argos satellite system (Service Argos, Inc., Toulouse, France and Landover, Maryland) was employed to determine locations at sea. Location data were filtered based on a maximum transit velocity of 3.0 m/s. Argos provides a Location Quality (LQ) for each location fix. The percent of each LQ category in this study after filtering for transit velocity was: Class 3 (to within 150 m)= 0%, Class 2 (150–350 m)=0.4%, Class 1 (350–1000 m)=2.6%, Class 0 (>1000 m)=19.4%, Classes A and B (unguaranteed)=77.6%.

GLTDRs were programmed to collect data as soon as the animal entered the water, recording dive depth every 20 or 30 s, ambient temperature at 3 or 10 min intervals, and ambient light levels at 15 min intervals. Instruments from PB females were recovered when they returned to moult 70–78 days later. Instruments from PM females were recovered when the latter returned to reproduce seven to eight months later. GLTDRs deployed on PM females recorded diving activity during the first two months at sea. Analysis of diving records and classification of dive types followed the methodology of Le Boeuf *et al.* (1993) and Asaga *et al.* (1994). We classified all consecutive dives at the beginning and at the end of the records that were less than 200 m as being on the continental shelf. Daily light-level curves were matched with sea-surface-temperature (SST) data to estimate migratory paths and location of foraging areas (Hindell *et al.*, 1991*a*; DeLong *et al.*, 1992; Hill, 1994) SST data corresponded to the same period when the seals were at sea. Weekly sea-surface temperature data were obtained from the NASA Physical Oceanography Distributed Active Archive Center and the Jet Propulsion Laboratory, California Institute of Technology (http://podaac-www.jpl.nasa.gov).

Results

The working GLTDRs from PB animals provided a record of 16 673 dives during 271 female-days at sea, encompassing the complete 2–2.5 months of the PB pelagic phase. This was compared with a record of 19 453 dives for PM individuals recorded during 336 female-days at sea (Table 1).

The data do not provide support for the hypothesis that PB females forage over the continental shelf. All females crossed the shelf in seven days or less (mean 4.2 days), spending 89% of the recorded time at sea over deep water (Table 1). PB females crossed the continental shelf quickly, as indicated by a significantly faster mean diving rate and shorter mean dive duration over the shelf than off it ($t=6.93$, -7.13, respectively, $df=8$, $P<0\ 05$). These differences on and off the shelf were even greater for PM females, whose man diving rate was almost twice as fast on the shelf as over deep water, and whose dives were 55% shorter than the dives beyond the shelf. The transition from shallow ($\sim$100 m) to deep waters (>300 m) was abrupt and fast (3–15 dives; 0.8–5.5 hr). The behaviour on the shelf was similar in the outgoing and incoming legs

Table 1. Summary statistics from diving records of post-breeding and post-moult female southern elephant seals on and off the continental shelf

	On Shelf (1)									Off Shelf								
Female	No. dives	Days recorded	Mean dive/hr	Mean depth (m)	Max. depth (m)	Mean dur. (min)	Max. dur. (min)	Mean surf. int. (2) (min)	No. surf. int. (>5 min)	No. dives	Days recorded	Mean dive/hr	Mean depth (m)	Max. depth (m)	Mean dur. (min)	Max. dur. (min)	Mean surf. int. (2) (min)	No. surf. int. (>5 min)
Post breeding																		
PB-A (3)	275	3.9	2.9	79	136	19	30	1.3	0	2268	37.8	2.4	594	1218	22.3	59	1.7	1
PB-B	267	3.2	3.4	83	178	15	33	1.2	9	3314	54.8	2.5			21.9	48	1.8	7
PB-C	292	3.4	3.4	78	166	14	32	1.3	36	2169	37.7	2.3	640	1122	23.3	53	1.7	7
PB-D	599	7.0	3.5	85	182	15	29	1.5	0	2977	54.5	2.2	450	996	24.4	91	1.9	11
PB-D (r)	592	6.9	3.5	77	198	15	43	1.2	19									
PB-E	316	3.5	3.7	84	156	14	34	1.7	7	3343	55.6	2.5	586	1104	22.1	98	1.6	20
PB-E (r)	261	2.6	4.1	73	198	12	31	1.2	8									
Total	2602	30.8								14 071	240.6							
Mean	349	4.2	3.4	82	163	15.5	31.5	1.4	10.4	2814	48.1	2.4	561	1110	22.8	69.8	1.7	9.2
SD	125	1.4	0.2	17	16	4.0	1.7	0.5	13.3	504	8.4	0.0	215	78	6.0	20.7	0.6	6.2
Post moult																		
PM-A (3)	254	3.0	3.4	78	166	16	28	1.3	0	2576	50.2	2.1	429	1016	26.2	102	1.8	13
PM-B	245	2.2	4.4	70	194	12	23	1.2	0	3686	67.5	2.2	431	971	24.7	79	1.5	12
PM-C	230	2.4	3.8	64	114	14	28	1.4	0	3915	64.7	2.5	417	1039	21.9	63	1.7	29
PM-D	303	2.7	4.6	61	126	12	30	1.0	7	3808	60.7	2.6	476	1072	21.3	76	1.4	24
PM-E	222	2.5	3.5	82	190	16	56	0.9	0	3409	65.7	2.1	488	994	26.1	61	1.6	6
PM-F	289	2.6	4.4	71	128	12	20	1.4	0	516	10.7	1.9	460	988	27.5	59	2.5	8
Total	1543	15.8								17 910	319.8							
Mean	257	2.6	4.0	70	153	13.4	31.1	1.2	1.1	2985	53.3	2.2	449	1013	23.9	73.3	1.6	15.3
SD	29	0.2	0.4	25	31	4.1	11.6	0.4	2.6	1188	19.8	0.2	176	33	8.5	14.8	0.6	8.3
Total	4145	46.6								31 981	560.4							
Mean	299	3.3	3.7	77	157	14.6	31.3	1.3	5.3	2907	50.9	2.3	491	1052	23.4	71.7	1.7	12.5
SD	98	1.2	0.5	22	26	4.2	8.6	0.5	10.2	945	15.9	0.1	199	73	7.6	17.8	0.6	8

(1) Means and SDs calculated only for the departing leg of the foraging trip; (r); returning leg of the foraging trip.
(2) Excludes surface intervals longer than 5 min.
(3) Same individual.

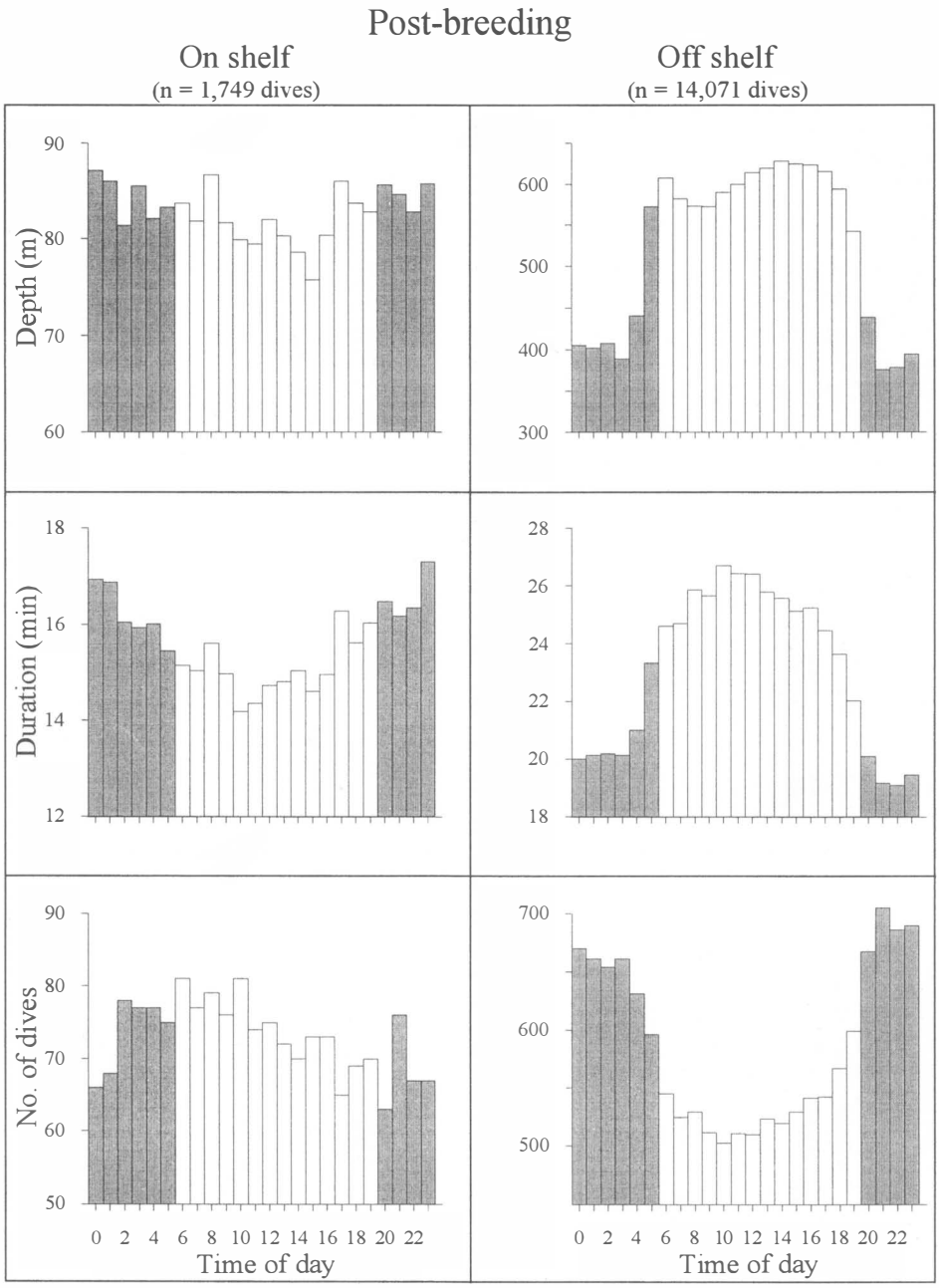

Figure 1(a).

of the pelagic trip (Table 1: females PB-D and PB-E).

Off the shelf, PB and PM females had a similar diving pattern (Table 1). Duration of dives and surface intervals were not significantly different ($P<0.05$). Mean dive depth was 111 m deeper for PB females, a significant difference with PM animals ($t=3.3$, $df=8$, $P<0.05$; Table 1). Surface intervals longer than 5 min were rare on and off the shelf for both pelagic phases of the annul cycle.

Over deep water females were probably foraging in the water column on dielly-migrating prey. Dives

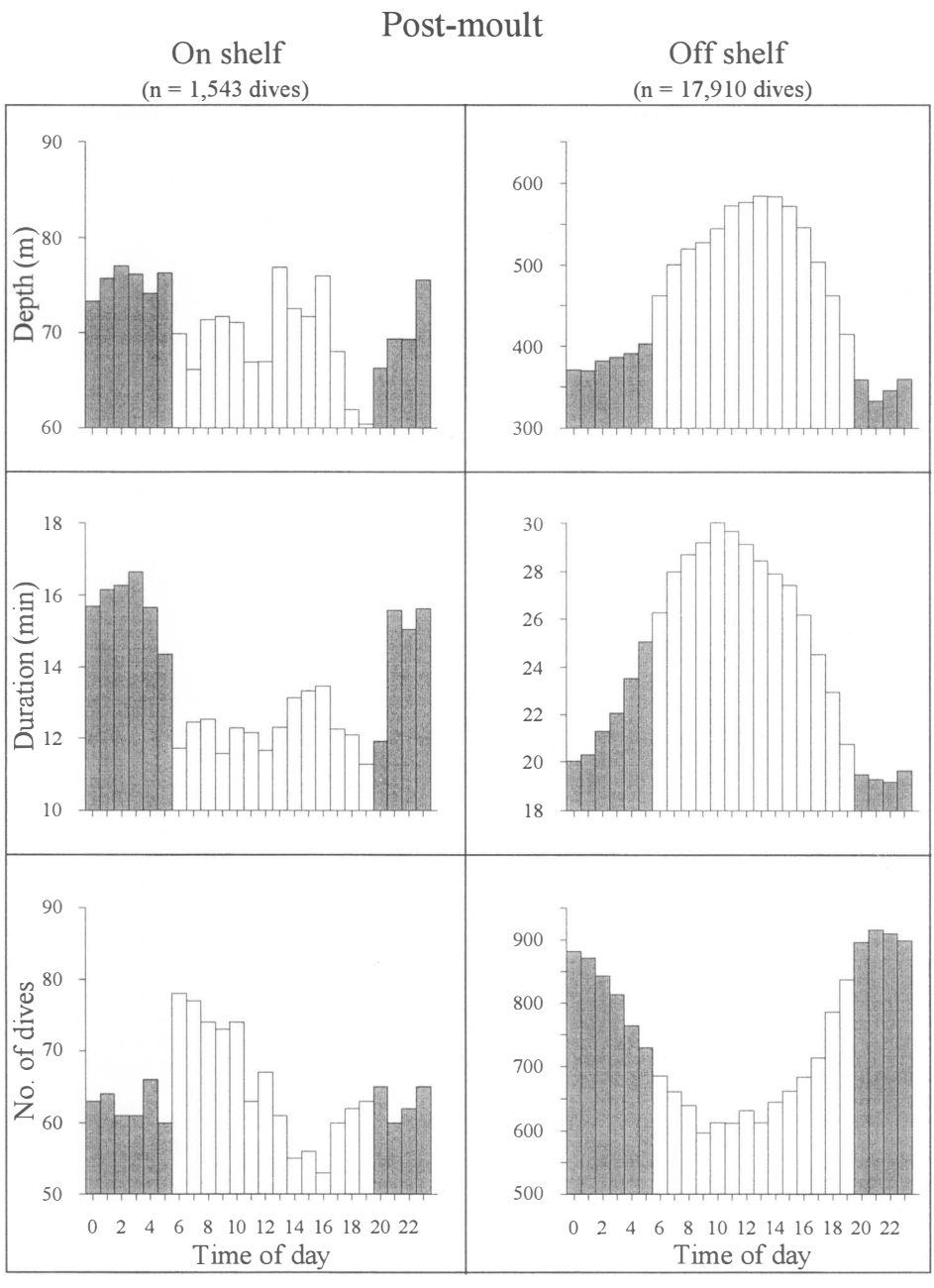

Figure 1(b).

Figure 1. Frequency distribution of number of dives and histograms of mean dive depth and dive duration of all dives, on and off the shelf, of post-breeding and post-moult females as a function of time of day.

of a shape assumed to represent pelagic foraging (Asaga *et al.*, 1994), were absent in diving records of PB females over the continental shelf, but they were the most common dive type beyond the continental shelf, 58.2 ± 21.2% of dives. A diel pattern in the frequency distribution of dives/hr, dive depth and

Table 2. Length of the migration route for post-breeding and post-moult females. The last two animals of each group carried satellite transmitters. Only PM-H yielded a record of the entire post-moult trip

Season and individual	Estimated travel dist. (km)	Mx. dist. offshore (km)	Days recorded at sea	Trip length in days (date at sea)
Post-breeding				
PB-A	2182*	813	42	68 (Oct 17–Dec 24)
PB-B	4933*	1223	58	71 (Nov 7–Jan 18)
PB-D	4899*	1012	69	69 (Oct 24–Jan 1)
PB-E	4277*	1003	62	62 (Oct 20–Dec 21)
PB-F	4798	1110	64	64 (Oct 19–Dec 22)
PB-G	5535	968	75	75 (Oct 17–Dec 31)
Mean	4438	1022	62	
SD	1072	126	10	
Post-moult				
PM-B	5729*	939	70	234 (Feb 3–Sep 24)
PM-D	5206*	1799	63	251 (Feb 12–Oct 20)
PM-E	4656*	1329	68	? (Feb 6–?)
PM-G	2321	916	43	225 (Feb 6–Sep 19)
PM-H	11 599	2281	233	233 (Jan 29–Sep 19)
Mean	5889	1453	95	
SD	3052	524	69	
Mean	5097	1218	77	
SD	2320	424	50	

*Estimates using GLTDRs (Hill, 1994).

dive duration on the shelf was apparent in both PB and PM individuals beyond the shelf (Fig. 1). Dives were deeper during the day than at night. Conversely, most dives on the shelf reached the bottom of the sea and no clear diel pattern emerged in these parameters as a function of time of the day (Fig. 1).

Once females went beyond the shelf they remained clear of it until they returned to land to moult. Geolocation and satellite location data showed that PB females concentrated their foraging effort in temperate waters of the SW Atlantic Ocean, within 36° and 46°S and up to 1223 km away from land (Fig. 2, Table 2). The largest distance travelled by a PB female was 5535 km (Table 2, PB-G in Fig. 2). The tracks of PB females occurred in the same general area as those of PM females (Fig. 2). PM females reached further south ($\sim$ 50°S) than the more temperate PB individuals (Fig. 2).

The satellite-instrumented females provided detailed locations at sea. Both PB and PM females travelled directly eastwards towards deep water, crossing the continental shelf in a similar time to the GLTDR individuals (Fig. 2; Table 1). One PB individual (PB-F; Fig. 2) travelled north and remained in a deep-water area of localized activity, along the continental margin, for about one month. She reached 36°49′S, the northernmost location recorded for all females. She then travelled southwards for about 21 days before crossing the shelf back to Península Valdés in four days. The other PB female (PB-G; Fig. 2) behaved similarly and remained in the same overall areas described for PB animals using the geolocation technique. The mean estimated total travel distance during the PB trip from satellite instrumented females (PB-F and PB-G) was 5167 km, which was similar to travel distances estimated from GLTDR females during a similar period at sea (Table 2).

The two PM individuals carrying satellite tags travelled directly eastwards to deep waters of the SW Atlantic Ocean (Fig. 2). For one of these females (PM-G), we recorded the first 43 of the 225 days she spent at sea. She travelled east, crossed the shelf in five days and remained the rest of the time in deep waters up to 49°S. The last locations showed her at the edge of the continental shelf (Fig. 2). The best record was obtained for PM-H for which we obtained locations for the eight months she spent at sea. During 233 days at sea, she reached 35°7′W, a distance of 2281 km east from Punta Delgada (Table 2, Fig. 2). This is the most pelagic location ever recorded for any adult male or female from Península Valdés. PM-H travelled an estimated distance of 11 599 km and spent 65% of her time at

sea in waters deeper than 5000 m. During most of her time at sea she was more than 1500 km away from Península Valdés, while most other satellite-tracked females were less pelagic (Fig. 3).

Discussion

PB females from Península Valdés followed the prevailing deep-water foraging pattern of PM, non-gestating, individuals (Campagna *et al.*, 1995). Their behaviour was consistent with the general pattern described for female southern and northern elephant seals from other colonies (McConnell *et al.*, 1992; Jonker & Bester, 1994; Le Boeuf, 1994; Slip *et al.*, 1994; McConnell & Fedak, 1996).

The initial and final periods of the pelagic trip reflected time spent over the continental shelf. Females from Península Valdés provide a record of almost 3300 dives on a shelf less than 100 m deep in most of its range. The behaviour on this shallow shelf differed from the rest of the record in dive rate, depth and duration but was alike in the pattern of continuous diving. The shorter duration of dives on the shelf for PB and PM females is consistent with the prediction that seals swimming faster utilize oxygen at a higher rate and hence exhibit an elevated dive rate and relatively shorter dive durations (Davis *et al.*, 1985; Williams *et al.*, 1991).

The dive rate on deep waters of 2.2 to 2.4 dives/hr for PB and PM females, respectively, was similar to the 2.5 dives/hr reported for females from Macquarie Island (Hindell *et al.*, 1991*a*). PB females did not show, however, a difference in dive duration from PM ones during deep dives (mean = 22.8 vs 23.9 min), as described for Macquarie Island (Hindell *et al.*, 1991*a*) and Año Nuevo females (Le Boeuf, 1994).

A diel pattern of dive depth and duration in both PB and PM individuals beyond the shelf is indicative of mid-water foraging following prey whose vertical distribution varies with time of day (Le Boeuf *et al.*, 1989; Hindell *et al.*, 1991*a*). This is congruent with the fact that D-type dives, which are assumed to represent pelagic foraging (Le Boeuf *et al.*, 1993; Type 1 dives in Hindell *et al.*, 1991*a*), were the most common dive type beyond the continental shelf. Conversely, the majority of the dives on the shelf were either flat-bottomed dives, limited by the topography of the ocean floor, or dives containing small vertical excursions. A lack of a diurnal pattern and the uncommon occurrence of D-type dives over the shelf suggests either benthic foraging on prey that would not exhibit vertical migration or, more likely, travelling to foraging grounds.

Geolocation tracks (Hill, 1994) and satellite locations support the conclusion that during both pelagic phases of the annual cycle, adult Patagonian females feed in temperate water of the southwestern Atlantic Ocean and do not reach the Antarctic Polar Front (APF). Seals from other colonies travelled widely, and there is some overlap in the foraging areas of individuals of the most extensive studied colonies (McConnell & Fedak, 1996). However, most elephant seals from populations other than Península Valdés forage around or south of the APF (Boyd & Arnbom, 1991: Hindell *et al.*, 1991; Bester & Pansegrouw, 1992; McConnell & Fedak, 1996). Females from Macquarie Island forage just off the Antarctic Continental Shelf or near the APF (Hindell *et al.*, 1991). Some females from South Georgia Island travelled extensively and some individuals visited locations in the open ocean at the latitude of Península Valdés or even near the Falkland (Malvinas) Islands (McConnell & Fedak, 1996). Most individuals, however, feed south of the APF and on the Antarctic continental shelf. PB females from Marion Island disperse widely around the island, north and south of the APF (Bester & Pansegrouw, 1992).

Differences in the foraging areas that may be associated with dissimilar demographic parameters. Península Valdés is the only colony of the species that does not feed in subantarctic or antarctic waters and that has increased in pup production during the last 20 years (12 000 pups in 1996; Campagna & Lewis, 1992 and unpublished data). Other southern elephant seal populations have decreased or remained stable during the last decades (Laws, 1994; Hindell *et al.*, 1994; Boyd *et al.*, 1996). Only individuals from the South Georgia colony forage close to locations described for animals from Península Valdés. A PM female from South Georgia reached the edge of the continental shelf, northeast of the Falkland (Malvinas) Islands (McConnell & Fedak, 1996), an area visited by foraging adult males from Península Valdés (Campagna, Fedak & McConnell, unpublished data). Another PM female from South Georgia reached 42°S (McConnell & Fedak, 1996), visiting an area that was about 1500 km east of the easternmost location of female PM-H.

Sex differences in foraging behaviour and potential foraging areas have been described for both species of elephant seals (Hindell *et al.*, 1991*b*; Le Boeuf, 1994; McConnell & Fedak, 1996). Male northern elephant seals from Año Nuevo Island tend to migrate farther north and west than females and forage along the continental margins (Le Boeuf, 1994). Male southern elephant seals from Macquarie Island spend most of their time over the Antarctic Continental Shelf (Hindell *et al.*, 1991*b*), and males from South Georgia Island stayed close or centred their activity on the island at the edge of the continental shelf (McConnell & Fedak,

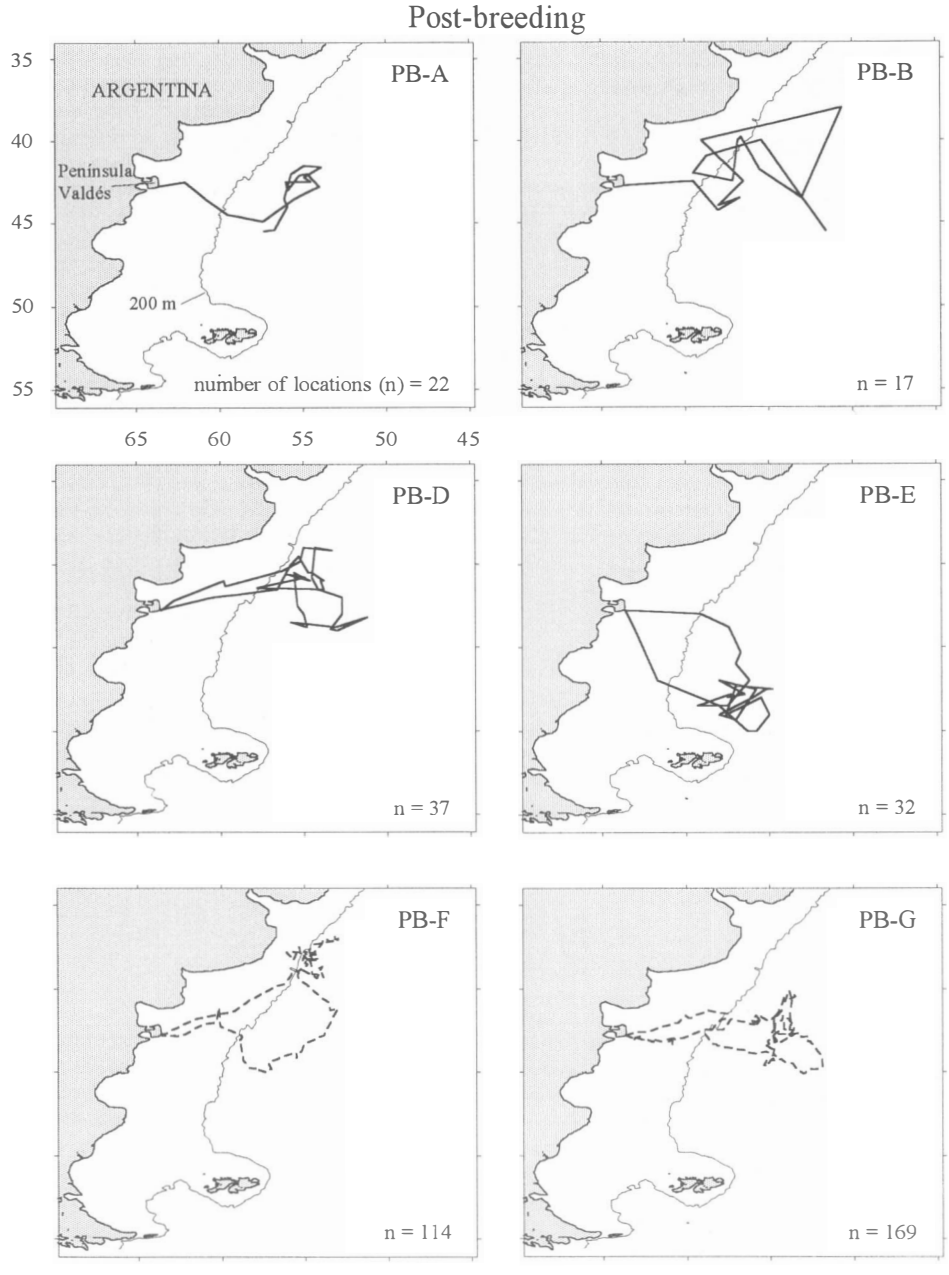

Figure 2(a).

1996). Preliminary results on at-sea locations of adult males from Patagonia deploying satellite transmitters (Campagna, Fedak & McConnell, unpublished data), suggest that females are more pelagic than males. Adult males do not travel to the open ocean but forage along the border of the continental shelf (Campagna, Fedak & McConnell, unpublished data). Some females, like males, apparently exploit topographical features such as shelf breaks, that may allow seals to locate prey more predictably (e.g., PB-F; PM-B). However, other individuals travel long distances

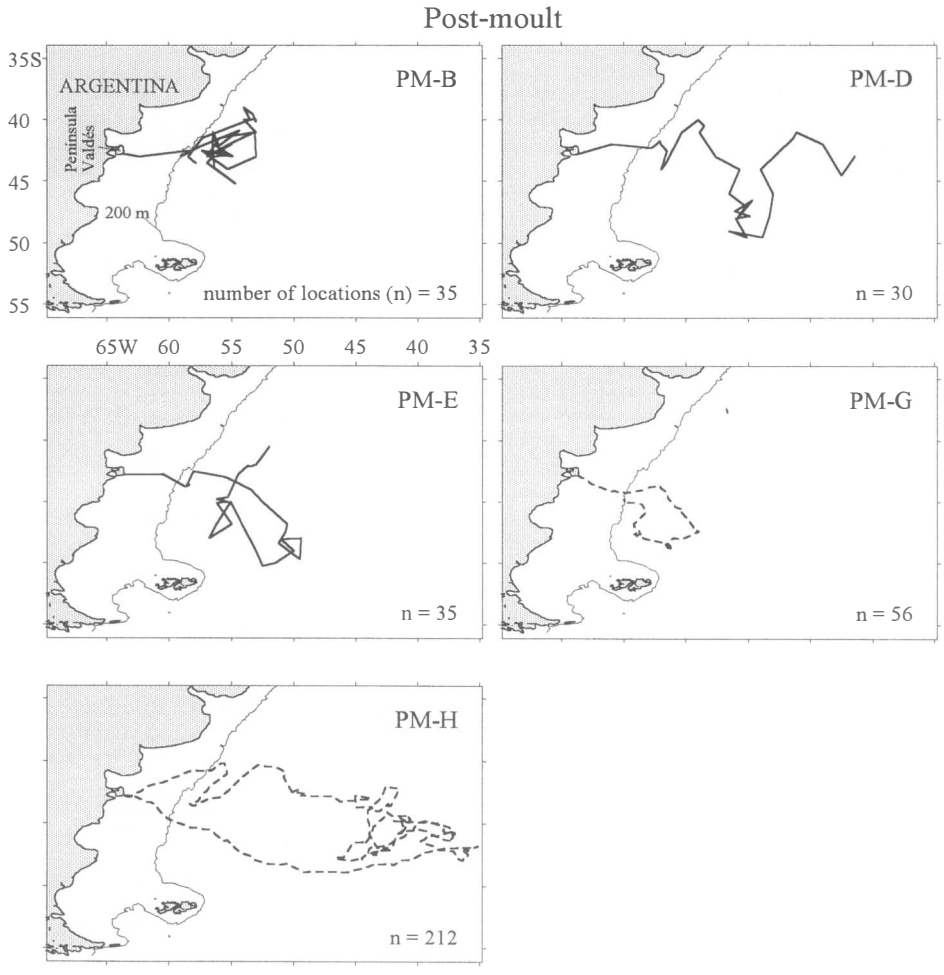

Figure 2(b).

Figure 2. Locations at sea of adult females after breeding at Punta Delgada, Península Valdés, Argentina, and after moulting in the same area. Two PB animals (PB-F and PB-G) and two PM individuals (PM-G and PM-H) carried satellite transmitters. Locations for other animals were estimated using geolocation time-depth recorders.

and are clearly mid-ocean searchers (e.g., PM-D and PM-H).

The margins of the Patagonian shelf are a reliable, highly productive and accessible foraging area located close to the breeding and moulting sites. The breeding sites at South Georgia and Macquarie Islands are often thousands of km away from the foraging places (McConnell *et al.*, 1992; Hindell *et al.*, 1991*b*). Individuals travel two to three weeks at a rate of 85 km/day to reach dependable foraging areas despite the energetic costs of long-distance transits (McConnell *et al.*, 1992; Fedak *et al.*, 1994). Seals from Patagonia may reach foraging grounds in about two days, dramatically decreasing commuting costs when compared to elephant seals from all other colonies. Therefore, overlooking the resources available to them on the continental shelf may not be, after all, too costly for these apparently obligated deep diving animals.

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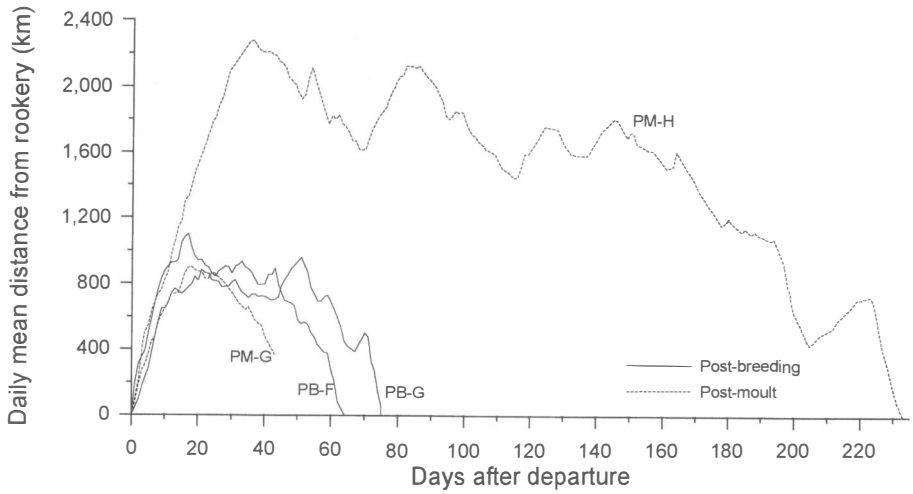

Figure 3. Mean daily distance away from the tagging site (Punta Delgada) at Península Valdés as a function of days after departure from the rookery for females studied during the post-breeding and post-moult pelagic phases of the annual cycle.

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