POST-BREEDING DISTRIBUTION AND DIVING BEHAVIOR OF ADULT MALE SOUTHERN ELEPHANT SEALS FROM PATAGONIA

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Seven post-breeding adult male southern elephant seals, *Mirounga leonina,* were tracked using satellite-relay data loggers (SRDL) in 1994–1996. Two animals also were instrumented with a time depth recorder(TDR). Animals were monitored for 31–112 days at the end of the breeding season as they left Península Valdés, Argentina. Males traveled ≤1,300 km from the breeding rookery but remained in temperate waters of the SW Atlantic Ocean, between 42°S and 55°S. The maximum travel distance recorded for the entire trip for any one seal was >4,500 km. Five males swam across the continental shelf in 3–11 days and stayed along the shelf margin or break where travel rates decreased markedly and remained low, suggesting that they may have reached foraging grounds. The other two males remained on the continental shelf during the entire time that they were tracked at sea. One of them was tracked for 66 days and concentrated his activity only 6–10 km off the coast of Patagonia in two areas located 700–800 km S of Península Valdés. He never dived deeper than 94 m. The diving behavior sampled by one working TDR and several SRDL were similar. Dives over the continental shelf were mostly down to the seabed. Some dives over the shelf break were to the seabed (down to 1,500 m) but most were mid-water (300–600 m) and were deeper during the day. Previously studied post-breeding and post-molt adult females from the same colony spent virtually all their time over deep water off the shelf in the latitudinal range of 36–50°S. Their movements were less localized than those of males and dives did not take them to near the ocean bottom.

Key words: *Mirounga leonina,* southern elephant seal, diving behavior, foraging ecology, Patagonia

The southern elephant seal, *Mirounga leonina,* is a highly dimorphic species with adult males being up to 10 times larger than females. Both sexes use fat reserves to support breeding and molt (Le Boeuf and Laws, 1994), and both will often move large distances away from the breeding and molting colonies to feed (Campagna et al., 1995, 1998; De Long et al., 1992; Hindell et al., 1991*a*; Le Boeuf, 1994; McConnell and Fedak, 1996; McConnell et al., 1992; Stewart and DeLong,1994,1995).

The breeding colony of elephant seals at Península Valdés produces ca. 12,000 pups every breeding season (late August to early November), and pup production has increased by 3.4% annually since 1982 (Campagna and Lewis, 1992; Lewis et al., 1998). Contrary to all other colonies of southern elephant seals (Laws, 1994), Península Valdés is located on a continent rather than on an island and in temperate rather than Antarctic or subantarctic waters (Campagna and Lewis, 1992). The Patagonian shelf is one of the largest, most productive, and shallowest continental shelves in the world (Boschi, 1997; Podestá, 1989). At the latitude of Península Valdés, it extends 300–400 km E and is <100 m deep (Parker et al., 1997).

Despite the productivity of the continental shelf and the shelf break, foraging areas

TABLE 1.—*Basic methodological information, duration of the tracking period at sea, and maximum distance recorded from Punta Delgada (Peninsula Valdés, Argentina) for seven male southern elephant seals (NR = not recovered).*

Male	Instrument deployed[a]	Date of deployment	Date of recovery	Number of locations	Days recorded: On shelf	Days recorded: Off shelf	Days recorded: Total	Max. distance (km)	Traveled distance from rookery (km)
PV1	SRDL	23 Oct 1994	NR	259	66	0	66	882	2,083
PV2	SRDL	24 Oct 1994	23 Feb 1995	217	8	104	112	622	4,608
PV3	SRDL	27 Oct 1995	3 Feb 1996	136	94	0	94	331	2,269
PV4	SRDL/TDR	31 Oct 1995	10 Feb 1996	28	17	80	97	772	2,452
PV5	SRDL/TDR	2 Nov 1995	NR	12	11	52	63	650	1,521
PV6	SRDL	30 Oct 1995	NR	36	44	13	57	1,167	2,195
PV7	SRDL	5 Nov 1996	NR	29	13	18	31	1,316	1,998
Total	—	—	—	717	253	267	520	—	—

[a] SRDL = satellite-relay data logger; TDR = time-depth recorder.

of post-breeding and post-molt adult female elephant seals from Península Valdés are located in the open temperate waters of the SW Atlantic, in the range of 36–50°S. Females are pelagic mid-water feeders and their dives to the seabed are infrequent (Campagna et al., 1995, 1998). Foraging movements of adult males from the same colony have not been studied.

We describe movements and diving behavior of adult male southern elephant seals from Patagonia during post-breeding foraging using a combination of satellite relay data loggers (SRDL) and time-depth recorders (TDR). Sex differences in foraging behavior are expected due to differences in energy stores and requirements associated with sexual dimorphism in body mass and composition. The greater daily intake requirements of males, which may be more than three times those of females (Boyd et al., 1994; Le Boeuf et al., 1993), may mean that they forage in areas with higher prey availability and they also may be able to handle larger prey than females. Studies conducted elsewhere have shown that males can perform deep oceanic diving behavior similar to that displayed by females, and they have suggested that males may go to different locations and use different parts of the water column (De Long and Stewart, 1991; De Long et al., 1992; Hindell et al., 1991*a*, 1991*b*; Le Boeuf, 1994; Le Boeuf et al., 1993; McConnell and Fedak, 1996; Slip et al., 1994; Stewart and DeLong, 1995).

Knowledge of movements and diving patterns of both sexes from the Patagonian colony of elephant seals is necessary to adequately describe foraging behavior. This information may help explain why this population is growing, while others are stable or declining (Le Boeuf and Laws, 1994; Scientific Committee for Antarctic Research—SCAR, 1991).

MATERIALS AND METHODS

Seven adult males (standard length 3.8–4.8 m) were captured on the breeding beaches at Punta Delgada (Península Valdés, Argentina, 42°46′33″S, 63°39′11″W) during the last week of October 1994 (n = 2), 1995 (n = 4), and 1996 (n = 1) and tracked during the post-breeding pelagic phase of their annual cycle (November–February; Table 1). During the breeding season, four of the males had been peripheral to large harems, and three were harem masters (PV4, PV5, and PV7).

Males were anesthetized with an intra-muscular injection (ca. 0.5 mg/kg) of Telazol (Elkins-Sinn, Inc., Cherry Hill, NJ; Baker et al., 1990) and fitted with SRDL attached to the fur of the top of the head with rapid setting marine

epoxy (Evercoat Ten-set, Fibre-Evercoat Company, Cincinnati, OH; Fedak et al., 1983). The SRDL were built by the Sea Mammal Research Unit (SMRU, Gatty Marine Laboratory, University of St. Andrews, Fife, Scotland) and described in detail in McConnell et al. (1992, 1994). They consisted of a data logger and a control unit interfaced with a transmitter enclosed in a pressure resistant housing. Data from pressure, wet-dry, and swim-speed sensors were collected every 4 s. That information was used to create dive records that included duration and maximum depth of a dive and subsequent surface duration. Each dive also was divided into five segments of equal time, and depths at the end of each segment and mean swim speeds during each segment also were transmitted. Data on percentage of time spent in a dive, at or near the surface, and hauled out also were summarized over 6-h intervals and transmitted. Sets of dive and summary records were transmitted to the Argos satellite system (Service Argos, Inc., Toulouse, France; Argos, 1989) on a preset schedule when animals surfaced, if it was ≥45 s since the previous transmission.

Two males (PV4 and PV5; Table 1) also were instrumented with time-depth recorders (TDR; Wildlife Computers, Redmond, WA; DeLong and Stewart, 1991; DeLong et al., 1992) to have a more detailed profile of depths and duration of dives. The TDR were attached with marine epoxy on the dorsal midline above the shoulders (Le Boeuf et al., 1988) and were programmed to collect data as soon as the animal entered the water, recording dive depth every 30 s.

Data from SRDL were examined using a visualization system specially designed for the analysis of movement and diving behavior of marine mammals (Fedak et al., 1996). Locational data were filtered by the algorithm described by McConnell et al. (1992) using a maximum mean velocity parameter of 2.0 m/s. Locations with a running mean velocity greater than that value were rejected. Mean daily locations were calculated from filtered data; these were used to estimate distance away from Península Valdés and total distance traveled.

Results

We obtained 717 filtered locations and 4,542 dives from 7 seals with SRDL over 520 seal days ($\bar{X}$ = 1.38 locations/day; Tables 1 and 2, Fig. 1). Percentage of each Argos location quality category after filtering (Argos, 1989) was: classes 2 and 3 = 7%, class 1 = 15%, and class 0 = 78%. The mean tracking period was 74 days, and three seals (PV2, PV3, and PV4) were studied over their entire period at sea between breeding and molting (Table 1). The other four packages stopped transmitting when seals were still at sea. We recovered one of the two TDR (on PV4), but the recording protocol failed and dive depths were recorded only ≤455 m. The instrument yielded the duration of >4,700 consecutive dives and depths of 1,100 dives on the continental shelf (Table 2).

The following generalizations could be made. There was great individual variability in the direction that males took from the rookery; three males traveled east while four traveled south >1,000 km from Punta Delgada (Table 1, Fig. 1). Five of seven males had a final destination on the continental shelf break; two males never got off the continental shelf; none of the males went into areas over abyssal depths. There was great variability in distance traveled, with some traveling four times as far as others. All males remained within the temperate waters of the SW Atlantic Ocean between 40°S and 55°S. For all individuals, dives recorded while in transit over shallow shelf areas were to the same depth as the seabed and were flat-bottomed, suggesting that the animals were diving along the bottom. While not in transit, mid-water dives were deeper during the day, whereas dives near to the seabed showed little diurnal variability.

Of the three males for which we had records spanning the entire post-breeding trip (PV2, PV3, and PV4; mean trip duration = 101 days), only one (PV3) yielded locations restricted to the continental shelf (Fig. 1), but no locations were received between 11 January and 4 February, when he returned to Península Valdés. Two other males (PV1 and PV6) that were tracked at sea for 66 and 57 days also remained over the shallow waters of the shelf (Fig. 1; Table 1), al-

TABLE 2.—*Summary dive statistics (± SE) from post-breeding male southern elephant seals, grouped into the time when a seal was on the continental shelf edge of when it was close to the shelf break. Errors in locations may have caused misclassification near the boundary. All data are from satellite-relay data loggers (SRDL), with the exception of seal PV4 for which time-depth recorder (TDR) information is also shown (PV4b). The TDR data are not included in the total values. Mean surface intervals exclude surface intervals > 10 min.*

	On shelf						Off shelf					
Male no.	No. dives	Depth (m) Mean	Depth (m) Max.	Duration (min) Mean	Duration (min) Max.	Mean surface interval (min)	No. dives	Depth (m) Mean	Depth (m) Max.	Duration (min) Mean	Duration (min) Max.	Mean surface interval (min)
PV1	1,341	57 ± 0.33	94	14.0 ± 0.15	29.0	3.3 ± 0.04						
PV2	120	67 ± 2.25	102	15.0 ± 0.81	32.2	5.2 ± 0.21	748	479 ± 16.19	1,468	21.8 ± 0.50	57.8	4.8 ± 0.09
PV3	145	68 ± 1.71	200	20.8 ± 0.77	40.8	4.0 ± 0.16						
PV4a	245	86 ± 1.25	118	16.0 ± 0.31	31.1	2.1 ± 0.05	865	463 ± 4.28	612	27.0 ± 0.19	52.5	3.3 ± 0.03
PV4b	1,100	91 ± 1.24	200	18.5 ± 0.18	45.6	3.0 ± 0.02	3,655			27.6 ± 0.11	96.6	3.6 ± 0.01
PV5	38	71 ± 4.32	109	20.7 ± 1.17	26.6	3.0 ± 0.34	164	477 ± 8.33	646	27.1 ± 0.58	47.4	3.8 ± 0.08
PV6	69	134 ± 12.86	532	13.5 ± 1.10	29.0	2.4 ± 0.27	273	171 ± 2.04	285	14.0 ± 0.28	32.2	2.1 ± 0.03
PV7	222	105 ± 4.91	305	16.3 ± 0.64	40.5	2.6 ± 0.12	312	319 ± 10.50	595	21.8 ± 0.80	60.0	3.2 ± 0.08
Total	2,180						2,362					
Mean		69	209	15.1	32.7	3.2		416	721	23.1	50.0	3.6

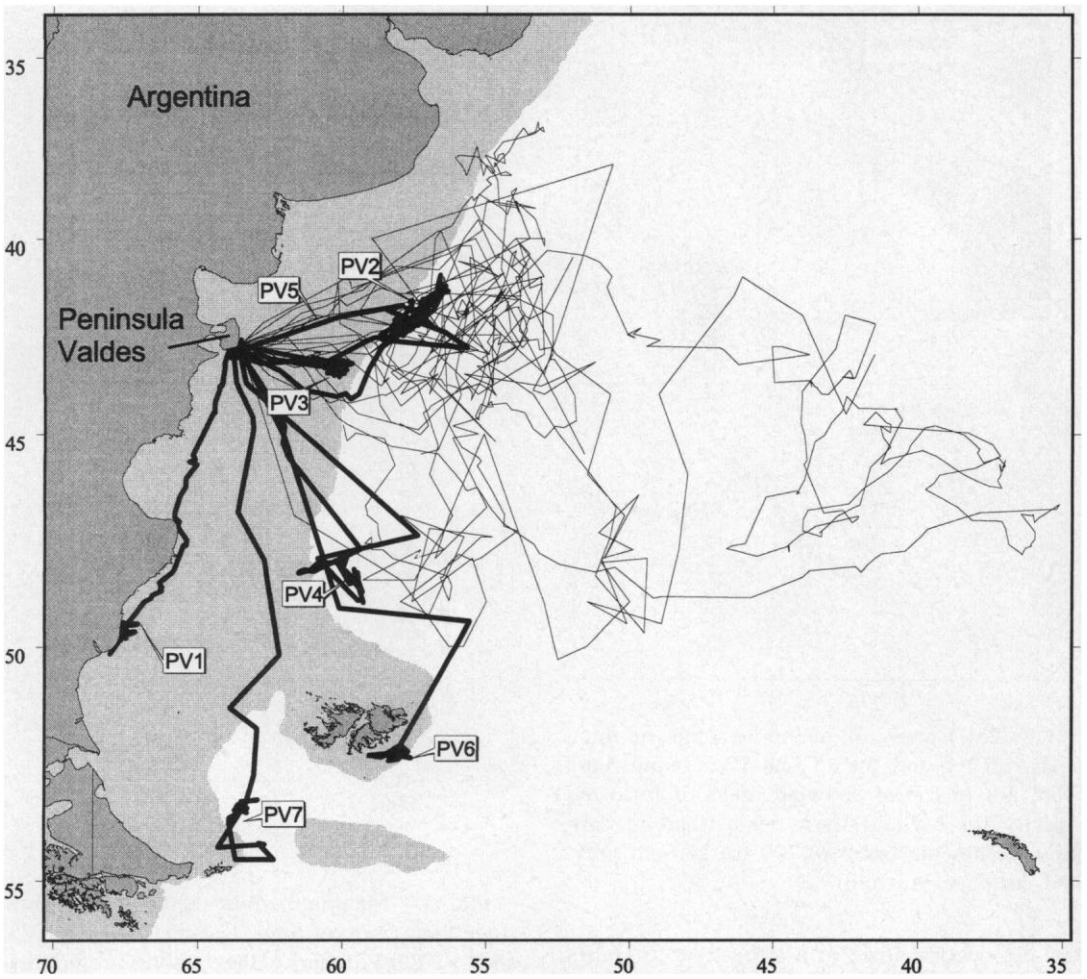

FIG. 1.—Movements of seven male southern elephant seals fitted with satellite relay data loggers (thick lines) after breeding at Punta Delgada, Península Valdés, Argentina. Movements of females from another study (Campagna et al., 1995, 1998) are shown by thin lines. The continental shelf (<200 m deep) is shaded.

though they may have gone elsewhere during the times that they were not tracked. One location for PV6 was off the shelf but was of the lowest Argos quality, and all other locations were on the shelf. The other four males (PV2, PV4, PV5 and PV7) were tracked to the continental shelf break during part of their foraging trip, and all made occasional dives to >600 m.

On-shelf behavior.—Three males spent their entire tracking period in shallow water on the continental shelf where their dives were shorter than those for males that traveled off shelf (on-shelf versus off-shelf duration of dives, $t = -29.5$; Table 2). Seal PV1 spent all of his tracking period in water 100 m deep and within a few kilometers from the coast (Fig. 1; Table 2). After leaving Punta Delgada in mid-November, he spent 66 days at sea interrupted by 5 short haul-out periods. He spent 1 week at sea in an area close to Península Valdés and returned to the Península to haul out for 5 days. He then traveled southward, crossing the productive and intensively fished San Jorge Gulf in ca. 1 week, and moved to land

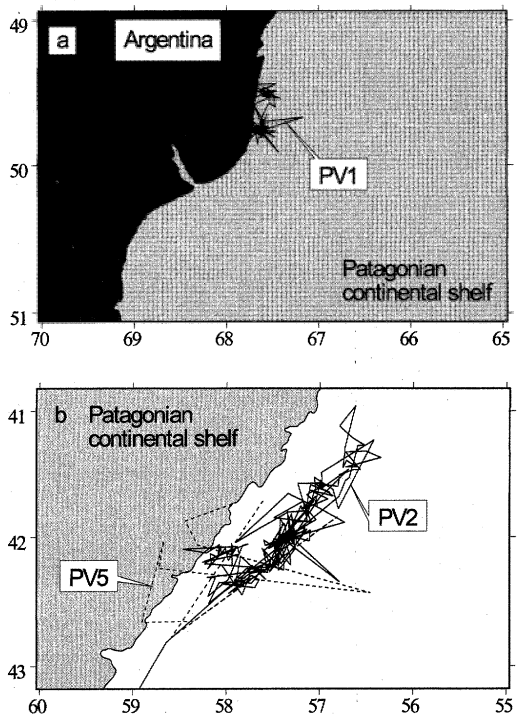

FIG. 2.—Details of the movements of three seals: a)PV1 and b)PV5 and PV2, while they were not in transit showing areas of localized activity for each of these seals (land in dark gray, continental shelf (<200 m) in light grey, and deep sea in white).

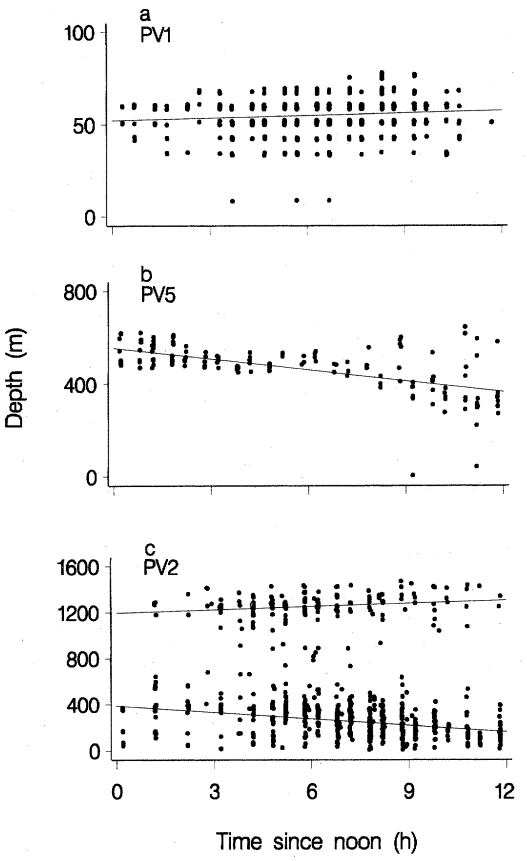

FIG. 3.—Maximum dive depth against time since local noon of three seals: a) PV1, b) PV5, and c) PV2. For clarity, the symbols are jittered. Seal PV1 was tracked only up on the shelf and all dives were near to the sea bed. The dives of seal PV2 showed a bimodal depth distribution and were split into those shallower or deeper than 800 m. Dive depth was regressed against time since noon. Although all regression lines had a slope significantly different from zero ($P < 0.05$) the slopes of the lines were small in seal PV1 (0.4 m/h), and the deep dives of seal PV2 (9.1 m/h).

for the second time at a site close to Bahía Sanguineto (47°08′53″S; 65°49′30″W), where a small group of ca. 12 elephant seals were found regularly among one of the largest colony of juvenile South American sea lions (*Otaria flavescens*) on the Patagonian coast. He stayed ashore for <1 day and continued to move south arriving, on 8 December, at the first of two discrete locations, diving there for ca. 2 weeks. He then moved further south to a second area for 1 month. He combined diving in these locations with three 0.5–2.5-day haulouts that took place over 42 days. These areas of concentrated activity were located 700–800 km from Punta Delgada and only 6–10 km off the coast of Patagonia (Fig. 2a). At both of these sites, all recorded dives were 40–70 m deep, which was the range of water depths in the area. The depth of the dives of PV1 was ≤100 m and remained similar during day and night (Fig. 3). When dive depth was regressed against time since noon, all regression lines had a slope significantly different from zero ($P < 0.05$; Fig. 3) because of the large sample sizes. The slopes of the line for seal PV1 was small (0.4 m/h).

Mean duration of his dives (14 min) was 31% shorter than the deep water dives of PV4 and 54% shorter than those of PV2, a male that spent most of his time over deep water and dived more deeply (Table 2) than other males.

Seal PV3 was the second of the seven animals for which all 136 locations at sea recorded during the entire trip occurred on the continental shelf, but no locations were obtained for 24 days before his return to Península Valdés. He traveled east to around 59°W, remaining within the latitude of Península Valdés and a maximum distance of 331 km from Punta Delgada. Despite remaining close to the rookery, the estimated total distance traveled by that male exceeded 2,200 km.

Seal PV6 traveled to 53°S, 1,200 km from Punta Delgada and 30 km S of the Falkland Islands, arriving on 22 November. At that point, the shelf break was within ca. 80 km of the Falkland Islands. He remained in that area until 1 January when contact was lost. Total travel distance for this male exceeded 2,000 km. Most of his dives were between 150–200 m depth, or the approximate sea bed depth. Only 17 of 342 dives recorded were deeper than 200 m.

Shelf break behavior.—The other four animals spent at least some time over the continental shelf break in restricted patches, as indicated by Argos locations and dive depths (Fig. 1; Tables 1 and 2). Two of them (PV2 and PV5) traveled directly eastward toward deep water and crossed the continental shelf in <1 week. Afterwards, they spent the rest of the recorded time in relatively deep water at the shelf break (Fig. 1). Of those two males, only PV2 dived to depths >1,000 m (Table 2).

Seal PV2 left Península Valdés on 30 October and traveled eastward, crossing the shelf at one of its narrowest points in 4 days (Fig. 1). He then traveled north, along the continental shelf break (Fig. 2a). On 8 November, he arrived at an area where he remained for >3 months. The area was ca. 600 km from Punta Delgada at its furthest point along the 1,000–1,400 m contours and was ca. 200 km long and 80 km wide. After he reached that area, his travel rate decreased markedly and remained low for several weeks. He spent ca. 100 of the 115 days that his trip lasted at almost a constant distance from the colony (ca. 500 km). On 15 February 1995, he traveled westward, crossing the shelf in 5 days, back to a spot in Península Valdés 2 km N from the departure point. He spent 112 days at sea (7% on the continental shelf) with no haulout periods. While over the shelf break, seal PV2 had a bimodal pattern of dives, the deeper dives descending nearer to the sea bed (ca. 1,200 m) and another mode in the upper 300–500 m of the water column. The shallower dives showed a marked diel change with the deeper dives occurring during daylight hours (Fig. 3). For the deep dives of seal PV2, the slope of dive depth regressed against time since noon was significant but small (9.1 m/h).

Seal PV5 went to the continental shelf break to an area 600 km from the rookery just east of the area used by PV2 the previous year. Locations from this animal were relatively infrequent and were received only from this area from 20 November through 11 January when contact was lost. Most dives were ca. 450–600 m, probably to the sea bed (Table 2). That animal showed a marked diurnal variation in the maximum depth of dives with deeper dives occurring during mid-day (Fig. 3).

The remaining three males departed to the south or southeast and reached positions near the shelf break south of Península Valdés. Dives of all three while in transit over the shelf were to the seabed. The tracking record of PV4 covered his entire feeding trip (97 days). He crossed the continental shelf in 5.3 days traveling south and reaching 49°S (Fig. 1). The maximum distance recorded from Península Valdés was 772 km, and the total travel distance exceeded 2,400 km (Table 1). After at the shelf break, he remained in an area 250 km N of the Falkland (Malvinas) Islands for ca. 80 days.

It took him 6.2 days to travel back to Punta Delgada to molt. Dive duration for that individual varied according to his location at sea. While on the shelf, he dived continuously to a mean depth of ca. 90 m and for a mean duration of 18.5 min (Table 2). After he left the shelf, he dived to >400 m and duration of dives increased to a mean of 27.6 min (Table 2). Dives tended to be longer and shallower in the early morning, averaging 225 m during 0300–0500 and >400 m the remainder of the day. Dive depth and duration during the return trip were similar to those of the outgoing trip.

Seal PV7 reached the southernmost latitude (54°34′S) and traveled further from Punta Delgada than any other male (1,316 km). During his trip south, he remained on the shelf for ca. 11 days. He spent the remainder of the time usually diving to the sea bed at depth of ca. 500 m.

Discussion

Male southern elephant seals breeding at Península Valdés preferred areas located either on the shallow Patagonian continental shelf, where they were probably feeding at or close to the bottom, or along the shelf break. Dive behavior of the males in the study varied markedly, depending on where the animals spent their time at sea. In general, shallow epi-benthic dives by all animals displayed no diurnal pattern while mid-water dives did, with deeper dives occurring during the day. This variability may offer clues to types of prey taken. Dives on the shelf were necessarily shallower, often shorter than those along the shelf break and usually descended to near the seabed. Seal PV1 remained in very shallow water; dives were consistently near the bottom, and there was no diurnal variation in diving depth. Animals such as PV2 and PV5 both spent time in deeper areas and displayed variations in diving depth with time of day.

Seal PV2 performed a bimodal combination of deep epi-benthic dives and mid-water dives. Only the mid-water dives displayed a diurnal variation with deeper dives during daylight hours. Seal PV5 consistently displayed diurnal variation in diving depth, with deeper dives occurring during the day. Similar patterns were displayed by the other seals in the study. These data suggest that males prey on both epi-benthic and diurnally migrating mid-water prey.

This distribution and behavior differed markedly from that of adult females from the same colony that moved off the shelf and wandered over the deep Argentinean basin, diving only to mid-water (Campagna et al., 1995, 1998; Fig. 1). These differences may be related both to ecological features of the shelf and shelf break and to the extreme sexual dimorphism of the species, but the explanation for differences between sexes remains unclear.

Foraging behavior and sexual dimorphism.—A complete record of the diving behavior of one male (PV4) and the SRDL-derived diving data for six other individuals suggest that, like adult females, males show the typical pattern of continuous bouts of long dives with short surface intervals described for both the northern species (*Mirounga angustirostris*) and southern species of elephant seals (De Long and Stewart, 1991; Hindell et al., 1991*a*, 1991*b*; Le Boeuf et al., 1988, 1989; McConnell and Fedak, 1996). The position of dives in the water column varied among individuals. Males diving along the shelf break dived both to the bottom and also in mid-water to depths that often showed diel variation with the shallower dives during darkness or early morning (Campagna et al., 1995, 1998). The pattern of coastal foraging and shallow, short, mostly benthic dives of male PV1 previously have not been described for an elephant seal.

Females that previously have been studied crossed the continental shelf in <1 week and spent virtually all of their time at sea in deep open water where they dived in the upper 1,000 m of the water column far from the bottom (Campagna et al., 1995, 1998; Fig. 1). Most dives of post-breeding and post-molt females beyond the continen-

tal shelf had the time-depth profile and diel variability in depth assumed to represent pelagic foraging (Campagna et al., 1998). Although the latitudinal range of female foraging areas (36°–50°S) overlapped with that of males (ca. 41–55°S), females undertook long meandering migrations to the open SW Atlantic (Fig. 1), rarely demonstrating extended localized activity (Campagna et al., 1995, 1998).

Sex differences in the locations at sea were first described for the northern elephant seal. Males of this species had a shallower dive pattern than females (Le Boeuf et al., 1993). Benthic dives also were more common in males, and migrations often occurred along the continental margins. Males remained on the continental shelf or along the shelf break where they tended to forage in localized areas (De Long and Stewart, 1991; Le Boeuf, 1994; Le Boeuf et al., 1993; Steward and DeLong, 1994, 1995).

Similar sex differences were described for the southern species of elephant seals (Hindell et al., 1991*b*; McConnell and Fedak, 1996). On South Georgia, McConnell and Fedak (1996) observed that all study females traveled far into the open ocean, but the two adult males spent nearly all of their time on the continental shelf or shelf break 20–60 km from South Georgia. One of these females traveled north up to the latitude of Península Valdés (42°S). However, two females crossed the shelf or shelf break to areas far from the island, and one of them reached the continental shelf west of the Falkland Islands, an area that was only 200 km from locations of one male from Península Valdés.

Southern elephant seals from colonies in the Southern Indian Ocean have been shown to spread widely to Antarctic and subantarctic waters or remain along the Antarctic Polar Front (APF). Males from Macquarie Island (around which there is no shelf area) have tended to go south to the distant continental shelf break along the Antarctic continent, but females from this colony have shown the pelagic meandering typical of females elsewhere. A few females also have moved to distant shelf areas along the Antarctic continental margin (Hindell et al., 1991*a*). Females from Marion Island have traveled up to 1,460 km (post-breeding) or 3,133 km (post-molt) from their breeding island and seem to feed in deep water on vertically migrating prey along frontal zones over wide areas (Jonker and Bester, 1998).

Male and female elephant seals display morphological dimorphisms greater than any other species of seal. Indeed, they are more disparate than many species. In view of these, it is not surprising that differences in foraging distribution and behavior occur. But our understanding of causes and functional consequences of sexual differences in foraging behavior of elephant seals remains incomplete. Females could exploit the same foraging areas as males, but sexes from any one breeding site do not often overlap in foraging distribution. Reasons for the differences remain obscure and warrant further study.

The Patagonian shelf and its relation to foraging behavior.—The Patagonian shelf break creates a frontal system associated with the cold and productive Falkland Current (Carreto et al., 1995; Martos and Piccolo, 1988). This system has a rich fish and squid fauna (Podestá, 1989; Rodhouse et al., 1992) that attracts other top predators besides elephant seals. Wandering albatrosses (*Diomedea exulans*) from the Island of South Georgia tracked by satellite telemetry during the reproductive season have been shown to forage along the shelf break (Prince et al. 1992, 1997). Indeed, the foraging patch of one of these birds coincided almost perfectly with the foraging location of male PV2 (Fig. 1, Prince et al., 1992, 1997). The productivity of the shelf and shelf break seems to have a greater influence on males than it does on the females of Península Valdés (Campagna et al., 1998).

The status of the Península Valdés colony is unique among populations of southern el-

ephant seals because it is the only one in the world that has been growing steadily for several decades (Campagna and Lewis, 1992; Lewis et al., 1998). In contrast, the population of elephant seals on South Georgia, the largest in the world, with a production of ca. 100,000 pups/year, seems to be stable (Boyd et al., 1996), while populations of the Southern Pacific and Indian Oceans are declining, apparently due to factors affecting survival while at sea rather than on land at the breeding beaches (Hindell et al., 1994; Scientific Committee for Antarctic Research—SCAR, 1991). Seals from South Georgia, Macquarie, and Marion islands are major components of the Antarctic and sub-Antarctic food webs (Clarke and MacLeod, 1982; Green and Burton, 1993; Rodhouse et al., 1992) and forage adjacent to or south of the Antarctic Polar Front or on the Antarctic continental shelf (Bester and Pansegrouw, 1992; Boyd and Arnbom, 1991; Hindell et al., 1991*a*; McConnell et al., 1992). However, some individuals of these three sites forage north of the APF (Jonker and Bester, 1998) or, in the case of South Georgia seals, even visit locations that overlap with the foraging sites of some seals from Península Valdés.

While several general hypotheses have been suggested to explain the decline in the southern Indian Ocean populations of elephant seals on Macquarie, Kerguelen, Marion, and Herd islands (Hindell et al., 1994), there is little information on which to construct convincing detailed hypotheses or to test them. Productivity of Patagonian shelf and proximity of rich shelf-break areas surrounding the colony could play a role in the success of the population on the Península Valdés. The paradox is that the females, whose foraging success is likely to be more important in influencing population growth rates, do not seem to use these areas to a large extent. Instead, they forage in deep open waters (Campagna et al., 1995, 1998; Fig. 1). It is possible that the shallow Patagonian shelf and shelf break could provide foraging opportunities for young animals with limited diving capabilities and this may increase juvenile survivorship. Information on the foraging distribution of young animals could then provide valuable information in this regard.

There is an expanding high-sea fisheries on and along the shelf supported by the Falkland Current and the upwelling along the margins of the Patagonian shelf. If the increasing population trend of the Patagonian seals is related to the better foraging areas provided by this shelf area and current system, the present status of the population may be vulnerable to the impact of this development. Continued population monitoring and examination of foraging movements, particularly of young animals, will be necessary to determine if exploitation has adverse consequences on Patagonian elephant seals.

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Literature Cited

Argos, 1989. Guide to the Argos System. Argos CLS, Toulouse, France.

Baker, J. R., M. A. Fedak, S. S. Anderson, T. A. Arnbom, and R. Baker. 1990. Use of tiletamine-zolazepam mixture to immobilise wild grey seals and southern elephant seals. Veterinary Record, 126: 75–77.

Bester, M. N., and H. M. Pasegrouw. 1992. Ranging behaviour of southern elephant seal cows from Marion Island. South African Journal of Science, 88: 574–575.

Boschi, E. E. (ed.) 1997. El Mar Argentino y sus re-

cursos pesqueros. Antecedentes históricos de las exploraciones en el mar y las características ambientales. Contribución del Instituto Nacional de Investigación y Desarrollo Pesquero de la Argentina No. 817, Mar del Plata, Argentina.

BOYD, I. L., AND T. ARNBOM. 1991. Diving behaviour in relation to water temperature in the southern elephant seal: foraging implications. Polar Biology, 11:59–266.

BOYD, I. L., T. A. ARNBOM, AND M. A. FEDAK. 1994. Biomass and energy consumption of the South Georgia population of southern elephant seals. Pp. 98–117, *in* Elephant seals: population ecology, behavior and physiology (B. J. Le Boeuf and R. M. Laws, eds.). University of California Press, Los Angeles.

BOYD, I. L., T. R WALKER, AND J. PONCET. 1996. Status of southern elephant seals in South Georgia. Antarctic Science, 8:237–244.

CAMPAGNA, C., AND M. LEWIS. 1992. Distribution and growth of an elephant seal colony. Marine Mammal Science, 8:387–396.

CAMPAGNA, C., B. J. LE BOEUF, S. B. BLACKWELL, D. E. CROCKER, AND F. QUINTANA. 1995. Diving behaviour and foraging location of females southern elephant seals from Patagonia. Journal of Zoology (London), 236:55–71.

CAMPAGNA, C., F. QUINTANA, B. J. LE BOEUF, S. BLACKWELL, AND D. CROCKER. 1998. Diving behaviour and foraging ecology of female southern elephant seals from Patagonia. Aquatic Mammals, 4(1): 1–11.

CARRETO, J. I., V. A. LUTZ, M. O. CARIGNAN, A. D. CUCCHI COLLEONI, AND S. G. DE MARCO. 1995. Hydrography and chlorophyll *a* in a transect from the coast to the shelf–break in the Argentinean Sea. Continental Shelf Research, 15:315–336.

CLARKE, M. R., AND N. MACLEOD. 1982. Cephalopods in the diet of elephant seals at Signy Island, South Orkney Islands. British Antarctic Survey Bulletin, 57:27–31.

CSIRKE, J. 1987. Los recursos pesqueros patagónicos y las pesquerías de altura en el Atlántico Sud-occidental. FAO Documentos Técnicos Pesca, 286:1–78.

DE LONG, R. L., AND B. S. STEWART. 1991. Diving patterns of northern elephant seal bulls. Marine Mammal Science, 7:369–384.

DE LONG, R. L., B. S. STEWART, AND R. D. HILL. 1992. Documenting migrations of northern elephant seals using day length. Marine Mammal Science, 8:155–159.

FEDAK, M. A., S. S. ANDERSON, AND M. G. CURRY. 1983. Attachment of a radio tag to the fur of seals. Journal of Zoology (London), 200:298–300.

FEDAK, M. A., P. LOVELL, AND B. J. MCCONNELL. 1996. MAMVIS: a marine mammal visualization system. Journal of Visualization and Computer Animation, 7:141–147.

GREEN, K., AND H. R. BURTON. 1993. Comparison of the stomach contents of southern elephant seals, *Mirounga leonina,* at Macquarie and Heard Islands. Marine Mammal Science, 9:10–22.

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

———. 1994. Possible causes of the decline of southern elephant seal populations in the Southern Pacific and Southern Indian Oceans. Pp. 66–84, *in* Elephant seals: population ecology, behavior and physiology. (B. J. Le Boeuf and R. M. Laws, eds.). University of California Press, Los Angeles.

JONKER, F. C., AND M. N. BESTER. 1998. Seasonal movements and foraging areas of adult southern elephant seals, *Mirounga leonina,* from Marion Island. Antarctic Science, 10:21–30.

LAWS, R. M., 1994. History and present status of southern elephant seal populations. Pp. 49–65, *in* Elephant seals: population ecology, behavior and physiology (B. J. Le Boeuf, and R. M. Laws, eds.). University of California Press, Los Angeles.

LEWIS, M., C. CAMPAGNA, F. QUINTANA, AND V. FALABELLA. 1998. Estado actual y distribución de la población del elefante marino del sur en la Península Valdés, Argentina. Mastozoología Neotropical, 5(1): 5–12.

LE BOEUF, B. J. 1994. Variation in the diving pattern of northern elephant seals with age, mass, sex and reproductive condition. Pp. 237–252, *in* Elephant seals: population ecology, behavior and physiology (B. J. Le Boeuf, and R. M. Laws, eds.). University of California Press, Los Angeles.

LE BOEUF, B. J., AND R. M. LAWS. 1994. Elephant seals: an introduction to the genus. Pp. 1–26, *in* Elephant seals: population ecology, behavior and physiology (B. J. Le Boeuf, and R. M. Laws, eds.). University of California Press, Los Angeles.

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

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

LE BOEUF, B. J., D. E. CROCKER, S. B. BLACKWELL, P. A. MORRIS, AND P. H. THORSON. 1993. Sex differences in diving and foraging behaviour of northern elephant seals. Symposia of the Zoological Society of London (London), 66:49–178.

MARTOS, P., AND M. C. PICCOLO. 1988. Hydrography of the Argentine continental shelf between 38° and 42°S. Continental Shelf Research, 8:043–1056.

MCCONNELL, B. J., AND M. A. FEDAK. 1996. Movements of southern elephant seals. Canadian Journal of Zoology, 74:485–1496.

MCCONNELL, B. J., C. CHAMBERS, AND M. A. FEDAK. 1992. Foraging ecology of southern elephant seals in relation to bathymetry and productivity of the Southern Ocean. Antarctic Science, 4:93–398.

MCCONNELL, B. J., O. P. COX, AND M. A. FEDAK. 1994. Satellite observations on free living seals. Report to United Nations Environment Program, Project FP/

5103-85-05, Sea Mammal Research Unit, Cambridge, United Kingdom.

PARKER, G., M. C. PATERLINI, AND R. A. VIOLANTE. 1997. El fondo marino. Pp. 65–87, *in* El Mar Argentino y sus recursos pesqueros (E. E. Boschi, ed.). Contribución del Instituto Nacional de Investigación y Desarrollo Pesquero de la Argentina, 817(1):5–87.

PODESTÁ, G. P. 1989. Migratory pattern of Argentine hake "*Merluccius hubbsi*" and oceanic processes in the Southwestern Atlantic Ocean. Fishery Bulletin, United States, 88:67–177.

PRINCE, P. A., A. G. WOOD, T. BARTON, AND J. P. CROXALL. 1992. Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. Antarctic Science, 4:1–36.

PRINCE, P. A., J. P. CROXALL, P. N. TRATHEN, AND A. J. WOOD. 1997. The pelagic distribution of South Georgia albatrosses and relationship with fisheries. Pp. 137–167, *in* Albatros biology (G. Robertson and R. Gayles, eds.). Surrey Beaty & Sons, Chipping-Norton, Australia.

RODHOUSE, P. G., T. R. ARNBORN, M. A. FEDAK, J. YEATMAN, AND A. W. A. MURRAY. 1992. Cephalopod prey of the southern elephant seal, *Mirounga leonina* L. Canadian Journal of Zoology, 70:1007–1015.

SCIENTIFIC COMMITTEE FOR ANTARCTIC RESEARCH (SCAR). 1991. Report of the workshop on southern elephant seals, Monterey, California, May 22–23, 1991.

SLIP, D. J., M. A. HINDELL, AND H. R. BURTON. 1994. Diving behavior of southern elephant seals from Macquarie Island: an overview. Pp. 253–270, *in* Elephant seals: population ecology, behavior and physiology (B. J. Le Boeuf and R. M. Laws, eds.). University of California Press, Los Angeles.

STEWART, B. S., AND R. L. DE LONG. 1994. Postbreeding foraging migrations of northern elephant seals. Pp. 290–309, *in* Elephant seals: population ecology, behavior and physiology (B. J. Le Boeuf and R. M. Laws, eds.). University of California Press, Los Angeles.

———. 1995. Double migrations of the northern elephant seal, *Mirounga angustirostris*. Journal of Mammalogy, 76:96–205.

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