

Temperature and depth profiles recorded during dives of elephant seals reflect distinct ocean environments

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Abstract

Foraging adult southern elephant seals, *Mirounga leonina*, from Península Valdés, Argentina, dive continuously while travelling across the continental shelf towards deep waters of the SW Atlantic. This study attempted to identify distinct ocean environments encountered by these seals during foraging migrations based on bathymetric and water temperature profiles, and to interpret these profiles in terms of mixing and systems of currents. Depth and water temperature were obtained with data loggers carried by 14 diving adult animals during spring (October–December) and summer (February–March) months. Dive depths allowed us to unmistakably differentiate extensive areas of the SW Atlantic: the Patagonian shelf, shelf slope and open waters of the Argentine Basin. Water temperature profiles added further details to the latter general oceanographic areas, and could be related to large-scale oceanographic processes that led to different water column structures. Temperature data reflected the mixing effects of winds and tides in coastal waters, the formation of a thermocline in mid-shelf areas, the northward flow of the sub-antarctic Malvinas Current at the edge of the shelf, and the effect of the subtropical Brazil Current further east over deep off-shelf waters. Some of these distinct areas are known for their enhanced primary production associated with frontal systems. The study shows that elephant seals could be useful, low-cost platforms to obtain oceanographic data. Studies that require extensive sampling of physical variables in large areas over long periods of time would benefit from this approach, pending on more precise and frequent locations of animals at sea. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Southern elephant seals, *Mirounga leonina*, from Península Valdés (PV), Argentina, forage in the

temperate waters of the SW Atlantic Ocean. Adult males and females move across the Patagonian continental shelf, shelf slope and open waters of the Argentine Basin, in the range of 36–55°S (Campagna et al., 1995, 1998, 1999). Some of these areas are known for their enhanced primary production associated with frontal systems, usually indicated by abrupt horizontal changes in water temperature (Brosin and Nehring, 1967; Carreto et al. 1972, 1995; Martos and Piccolo, 1988; Podestá, 1990). The aim of this study

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was to attempt to identify distinct ocean environments encountered by foraging seals based on dive-depth and water-temperature profiles. Samples were obtained with data loggers carried by seals during dives. The paper provides a description of depth-temperature gradients of generally identifiable places off the coast of eastern Argentina, interprets these gradients in relation to currents and frontal systems described for the SW Atlantic, and relates these distinct environments with areas of enhanced ocean productivity.

The annual cycle of adult elephant seals is divided in two terrestrial phases, devoted to breeding and moulting, and two pelagic foraging periods: post-breeding, lasting about 2–3 months, and post-moult, lasting 7 months (Le Boeuf and Laws, 1994). Southern elephant seals breed in the austral spring (early September to mid-November) and moult in summer (December–March) (Campagna et al., 1993). PV is one of the northernmost and temperate breeding colonies of a species that is mainly distributed around the Antarctic Polar Front (Campagna and Lewis,

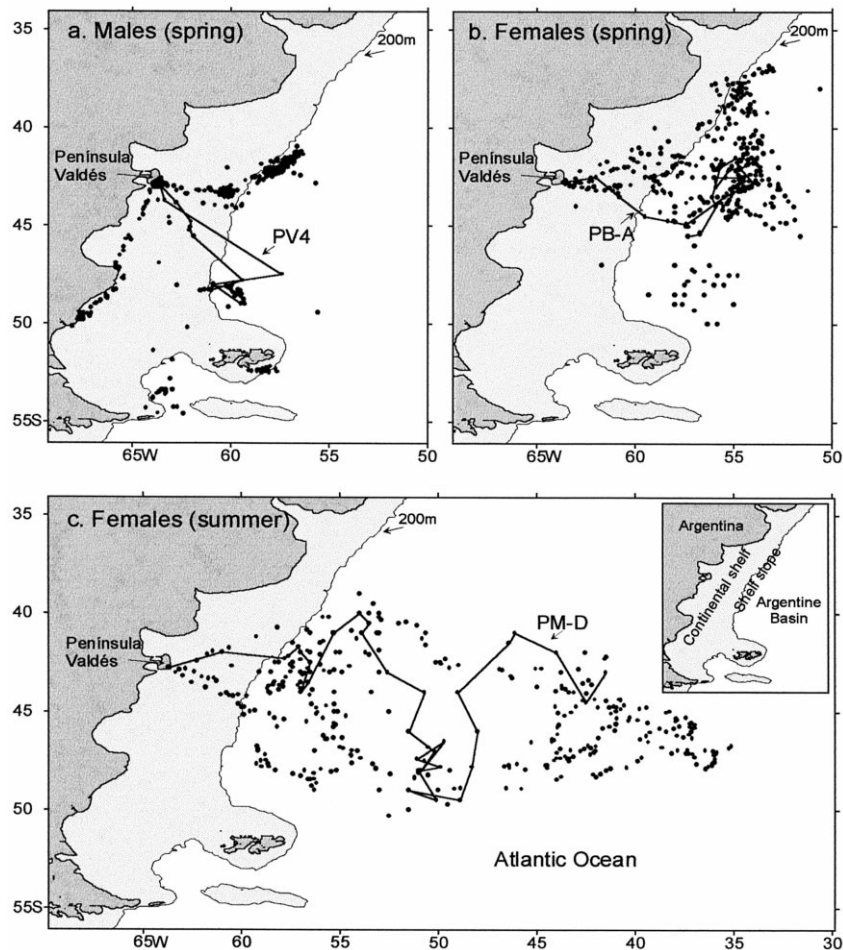


Fig. 1. General area of dispersion of southern elephant seals from Península Valdés determined with geolocation methods (Hill, 1994) and satellite telemetry ((a and b) seven males and six females during spring (post-breeding) pelagic trips, (c) five females during the summer part of the post-moult foraging trip; extracted from Campagna et al., 1998, 1999). Tracks illustrate movements at sea for one individual. The continental shelf (< 200 m) is shaded.

1992; Laws, 1994; Lewis et al., 1998). The colony faces an unusually broad continental shelf that stretches out 300–400 km to the east and that is less than 100 m deep in most of its extension (Parker et al., 1997). Ocean depths increase abruptly beyond the 200-m isobath, reaching more than 1000 m in 40–100 km.

Previous work described the general diving pattern and movements at sea of some of the animals included in this study (Campagna et al., 1995, 1998, 1999). Female migratory paths and location of potential foraging areas were first determined matching

light-level curves with sea surface temperature (SST), obtained with geographic-location time–depth recorders (De Long et al., 1992; Hill, 1994). As the method yields low resolution location estimates, more accurate tracks were later obtained from satellite relay data loggers using the Argos system (Argos, 1989; McConnell et al., 1992). Male movements were determined with satellite telemetry. Tracking results show that adult females disperse widely into the deep waters of the Argentine Basin (Fig. 1b–c; Campagna et al., 1995, 1998). Dives vary in depth following a diel pattern, being shallower at night.

Table 1

Length of the record, sample protocols for depth and temperature, number of dives recorded on and off the continental shelf and general statistics for nine post-breeding and six post-molt southern elephant seals (14 females and male PV-4) from Península Valdés, Argentina

Individual	Start sampling date	Days recorded		Sampling intervals (s)		Dives recorded	
		Total	On shelf ^a	Depth	Temperature	Total	On shelf ^a
<i>Spring trips (post-breeding)</i>							
PB-A	October 17, 1993	41.8	3.9	20	60	2543	275
PB-B ^b	November 7, 1993	58.0	3.3	20	60	3581	267
PB-C	October 11, 1994	41.2	3.4	30	–	2461	292
PB-D	October 24, 1994	68.5	7.0 (6.9)	30	^c	4168	599 (592)
PB-E	October 20, 1994	61.8	3.5 (2.6)	20	^c	3920	316 (261)
PB-I	October 6, 1997	12.1	12.1 ^d	5	5	1013	1013
PB-J	October 14, 1997	12.1	1.9 ^d	5	5	752	158
PB-K	October 9, 1998	12.1	5.6	5	5	852	460
PV-4 ^b	November 4, 1995	96.7	5.4 (6.4)	30	60	4756	403 (418)
Total post-breeding		404.3	46.1			24,046	3783
Mean		44.9	5.1			2672	420
S.D.		27.8	2.9			1444	242
<i>Summer trips (post-molt)</i>							
PM-A	January 24, 1994	23.3	3.0	30	180	1645	254
PM-B	February 3, 1992	69.7	2.2	30	600	3931	245
PM-C	February 14, 1992	67.1	2.4	30	600	4145	230
PM-D	February 12, 1992	63.4	2.7	30	600	4111	303
PM-E	February 6, 1992	68.2	2.5	30	600	3631	222
PM-F	February 9, 1994	4.0	2.6	30	180	392	289
Total post-molt		295.7	15.4			17,855	1543
Mean		49.3	2.6			2976	257
S.D.		25.9	0.2			1440	29
Grand total		700.0	61.5			41,901	5326
Mean		46.7	4.1			2793	355
S.D.		27.1	2.5			1450	204

^aData for the departure leg of foraging trips. In parentheses are the records for the returning leg of complete trips (not included in summary statistics).

^bDive depth was recorded up to 400 m due to failure in the sampling protocol.

^cSampling intervals depended on surface intervals between dives as only SST was recorded for this animal.

^dPartial record.

Some males remain on the shelf during extended periods, while others remain over the shelf slope during most of their time at sea (Fig. 1a).

2. Materials and methods

During the period 1992–1998, 23 adult seals (21 females, 2 males) were fitted with time–depth–temperature recorders (Wildlife Computers, Redmond, WA) at Punta Delgada, Península Valdés (42°45'S; 63°38'W). For a detailed description of instruments and sensors, see Le Boeuf (1994) and Le Boeuf et al. (1989). A detailed methodology regarding deployment techniques, analysis of diving data and location at sea of the animals of this study is provided in Fedak et al. (1983) and Campagna et al. (1995, 1998, 1999).

Recorders were programmed to collect data as soon as the animal entered the water following protocols described in Table 1. Sampling intervals for dive depth and water temperature varied according to the type of instrument (memory limitations) and to fit the needs of previous studies aimed at describing the diving pattern (e.g., Campagna et al., 1998). All protocols were designed to provide a high resolution profile of sea temperature and depth. Some instruments recorded only SST while others sampled temperature of the entire water column. Instruments were recovered 70–102 days after deployment, when post-breeding seals returned to moult, or about 7–8 months after deployment, when post-moult seals returned for breeding. As data loggers were filled with data after about 2 months at sea, the long, post-moult trip was sampled only during the first segment of migration. We will refer to pelagic phases as spring trips (post-breeding) and summer trips (first weeks of post-moult trips).

In an attempt to improve the clarity of the presentation of the physical data of this study, depth and temperature profiles will be related to locations at sea. Fig. 1 and insets in other figures illustrate the overall area where foraging animals disperse and show movements at sea determined by geolocation and satellite tracking methods reported in previous studies (Campagna et al. 1995, 1998, 1999).

3. Results

Sixteen of the 23 instruments were recovered: 14 sampled depth and water temperature at variable intervals, one recorded only dive depth and one failed to record data (Table 1). The 15 instruments that sampled depth (every 5–30 s) encompassed more than 40,000 dives and 700 days at sea. Water temperature was obtained for seven females and one male for spring trips, and six females for summer trips. Samples were taken at intervals of 5–600 s during 658 days at sea. The entire spring foraging trip was recorded for three animals (PB-D, PB-E and PV-4). The record for PV-4 covered 3 months at sea, but dive depth samples were restricted to 400 m due to a problem with the sampling protocol. Female records covered 12–70 days at sea.

3.1. Ocean environments reflected in dive depth profiles

Three distinct topographical areas of the SW Atlantic were unequivocally recognised based on dive depth data: the continental shelf, shelf slope, and deep waters beyond the continental slope (Fig. 1).

3.1.1. Continental shelf

More than 5300 on-shelf dives recorded for 15 seals yielded a mean depth at the bottom of the dive of 82 ± 25 m. Mean maximum dive depth at the bottom of the dives and the U-shape of most dives suggested that animals were diving to the bottom of the ocean. This was also supported by the fact that mean maximum dive depth increased slowly with time at sea (Fig. 2a, out). Records that covered the return leg of some trips (e.g., PB-D, PB-E and PV-4) showed a depth profile that confirmed results described for the outgoing part of the trip (Fig. 2a, in).

3.1.2. Continental slope

The shelf slope was evidenced by an abrupt increase in dive depth, from about 100 m to more than 400 m in 3–12 dives and 1–4 h (Fig. 2b). A concomitant change occurred in dive shape, from mostly flat-bottomed to V-shape dives that apparently did not reach the bottom of the ocean (Fig. 2b).

The most abrupt change in dive depths was found in the record of PM-C. She went from 50–100 m dives to more than 600 m dives in 3 h and nine dives.

3.1.3. Deep waters of the Argentine Basin

For female records, dives following the crossing of the shelf continued to be deeper than 200 m, until the return trip. Dive shape and a diel pattern of variation of depth (see non-shaded areas for dives of PB-A in Fig. 3 and PM-D in Fig. 4), indicated that dives were not to the bottom of the ocean, thus did not provide bathymetric cues to differentiate precise ocean areas. This is also suggested by the maximum depth attained in the total dive record, which showed that all seals spent time in waters deeper than 1000

m (Fig. 2c). A maximum dive depth of 1104 m was achieved by female PB-D (Fig. 2c).

Abrupt changes in dive depths that lasted hours suggested that male PV-4 spent some time near the shelf edge, moving in and out of the shelf. The continuous depth record, only partially shown in Fig. 5, showed a change in dive depth around January 7, that was preceded and followed by deeper (> 400 m) dives. Maximum dive depths for about 40 h was 190 ± 6 m, compatible with an on-shelf locations.

3.2. Ocean environments reflected in temperature gradients

Distinct areas identified based on the dive-depth pattern (continental shelf, shelf slope and Basin),

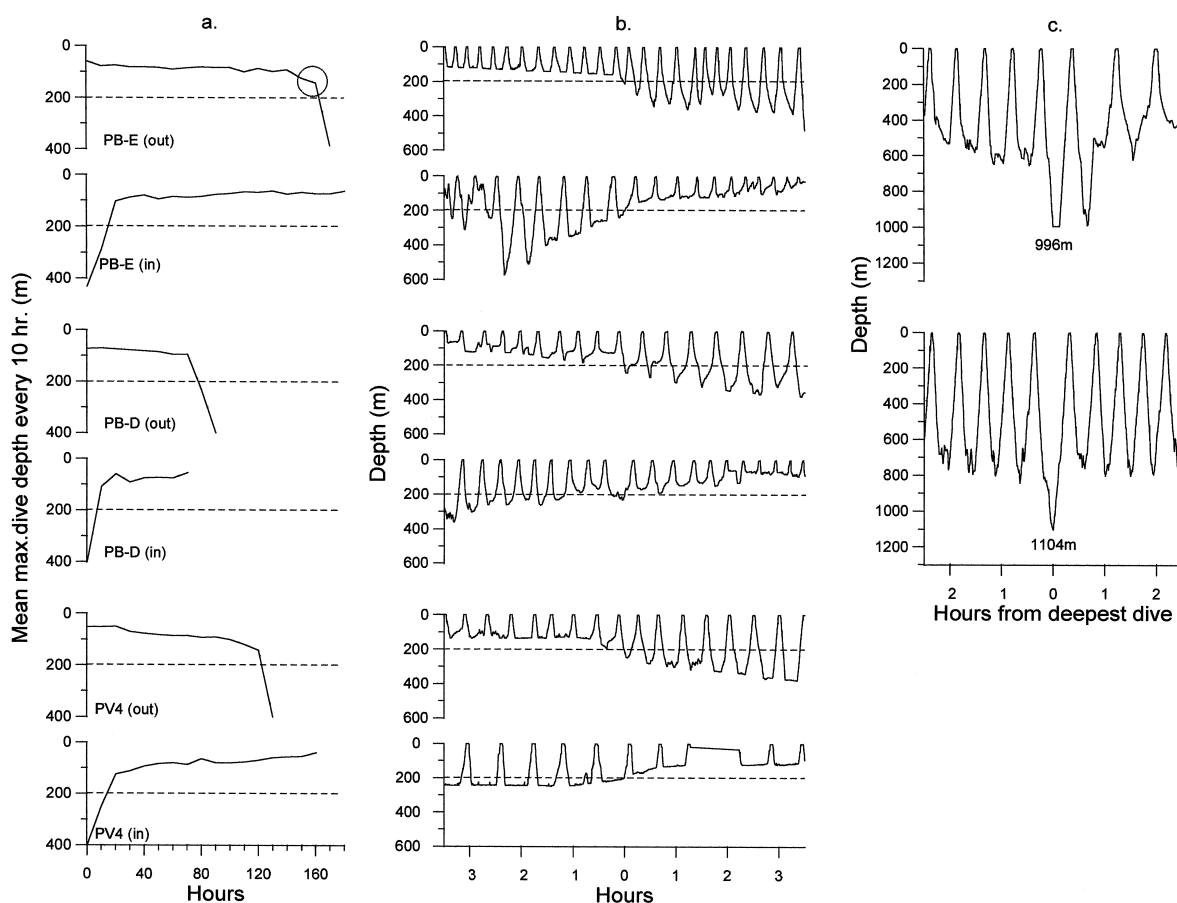


Fig. 2. Dive depth on the continental shelf for three individuals with a record that accounts the outgoing and incoming legs of the foraging trip. (a) Profile of mean maximum dive depths every 10 h. (b) Transition dives from the shelf to deep waters of the shelf slope and vice versa. The x-axis indicates hours before the first dive > 200 m for outgoing leg and before the first dive < 200 m for the incoming part. (c) Deepest dive of the record. Maximum dive depth for PV-4 was unknown due to a protocol failure beyond 400 m.

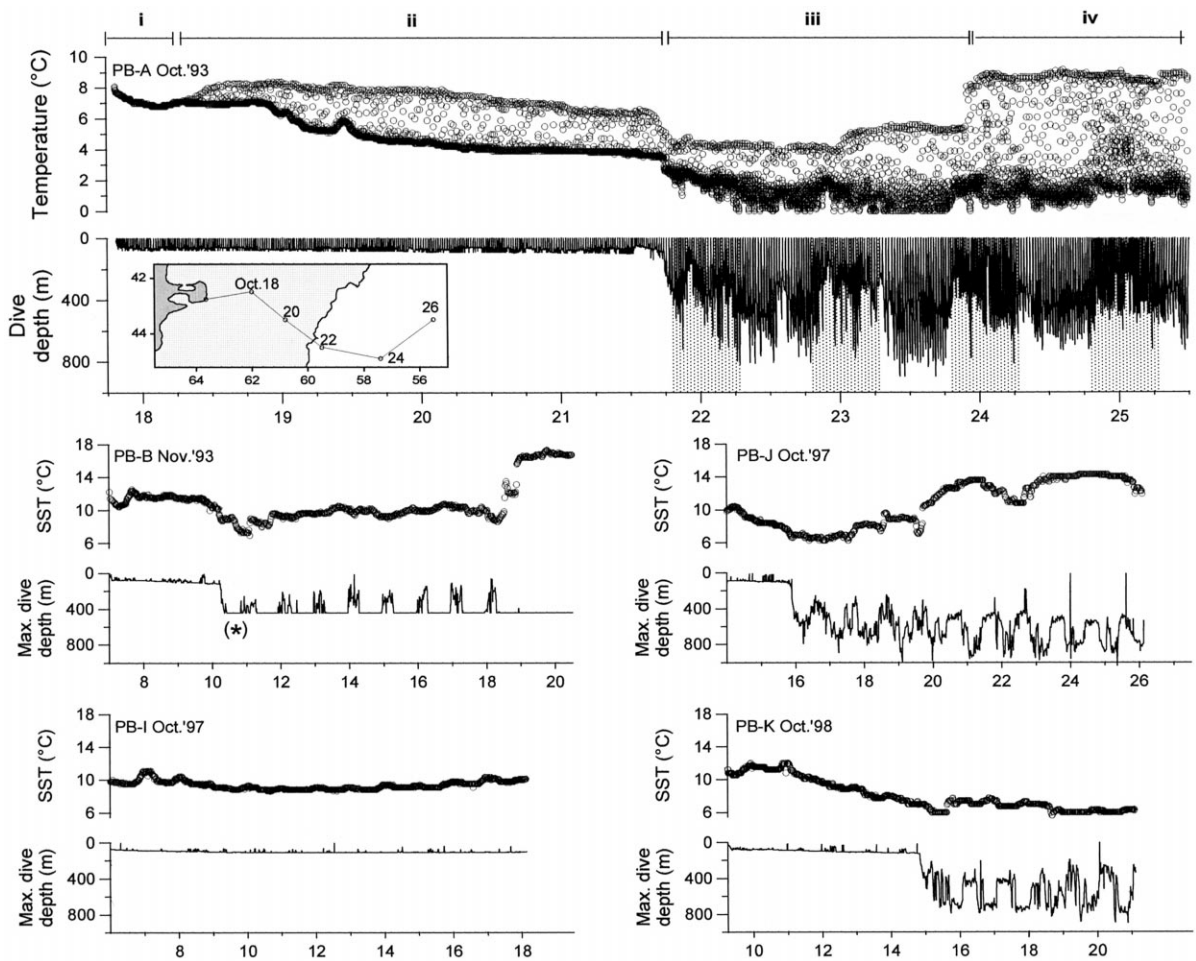


Fig. 3. Dive depth and water temperature records for spring trips. Data for PB-A are for the entire water column; SST is given for other individuals. Shaded, vertical bars indicate night time. (i) Mixed, coastal waters over the continental shelf. (ii) Offshore, stratified shelf waters with a thermocline. (iii) Edge of the continental shelf, with deeper dives and cold waters of the Falkland Current system. (iv) Warm waters over deep ocean. (*) Dive depth protocol failed to record beyond 400 m.

differed in their temperature profiles. As the thermal environment varied between the spring and summer trips, the record will be treated separately for each season.

3.2.1. Spring (post-breeding) trips

3.2.1.1. Continental shelf. Temperature profiles showed that: coastal waters were mixed and homogeneous in temperature, a thermocline developed in stratified, offshore waters, and SST decreased as animals travelled towards the shelf slope. The record

of female PB-A (Fig. 3) yielded a dive-temperature profile that best reflected relevant oceanographic phenomena for the identified areas of the SW Atlantic. The general dive-temperature profile of PB-A was similar to that of other females (e.g., PB-B and some features of PB-J and PB-K), with slight individual variations in temperature levels. PB-I remained on the shelf during the 12 days that lasted her record, showing constant depths and SST.

PB-A started her eastward trip at Punta Delgada on the night of October 17, 1993. She arrived to the edge of the shelf in 4 days and then continued

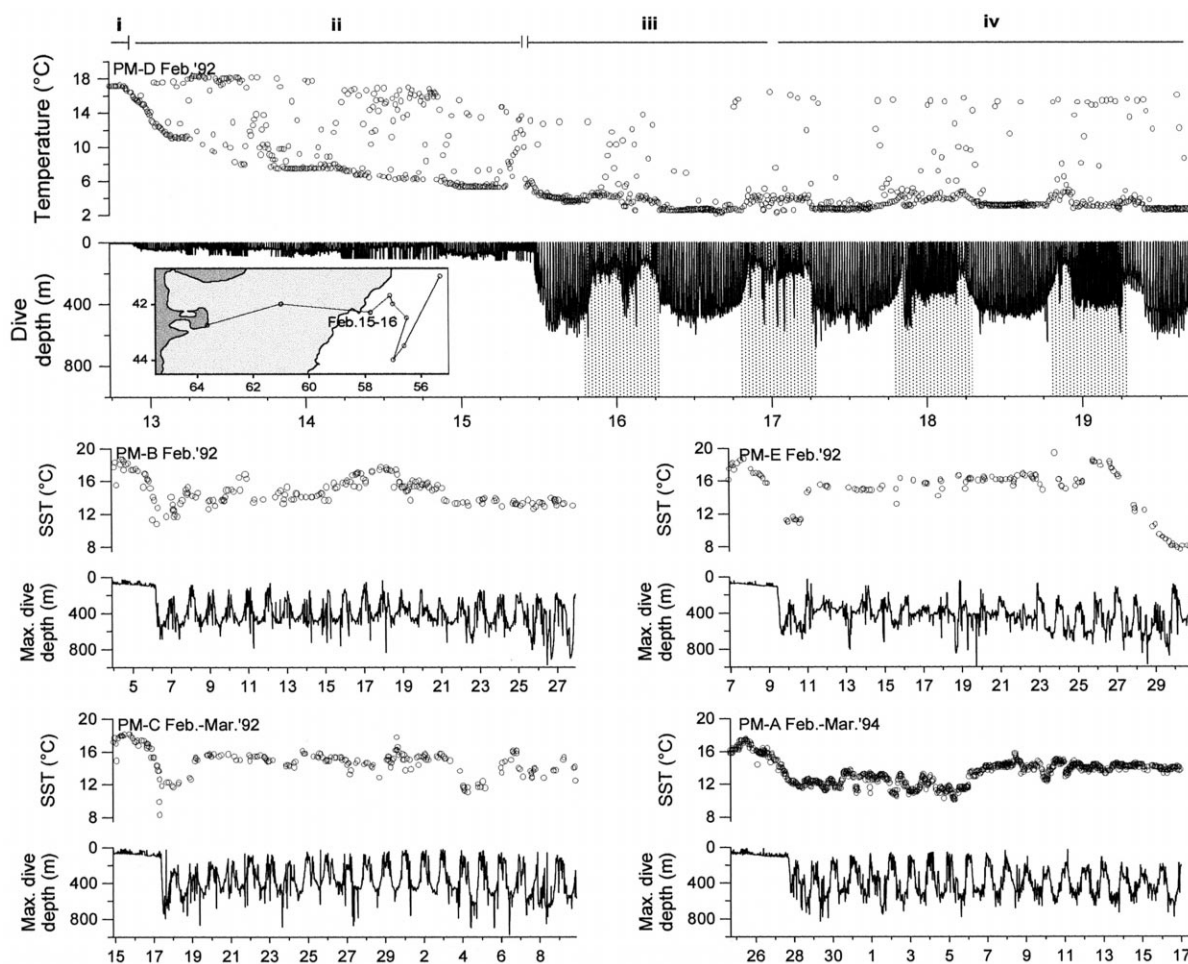


Fig. 4. Dive depth and water temperature records for the summer part of post-molt trips. PM-D temperature record is shown in detail. Only SST is given for all other females. Females differed in sampling frequency. Shaded, vertical bars indicate night time. (i–iv) Temperature and depth profiles for PM-D when she travelled from coastal shelf towards deep off-shelf waters.

towards deep Basin waters (Fig. 3). Coastal waters (mean maximum dive depth of 68 ± 11 m) were at 7°C from the surface to the bottom of the dive (Fig. 3i). After about 6–10 h at sea, a thermocline developed (Fig. 3ii), with a vertical gradient of about 3°C in less than 100 m of depth (SST = $7\text{--}8^{\circ}\text{C}$; bottom temperatures = $4\text{--}5^{\circ}\text{C}$). Dives were still limited by the depth of the shelf, and were not much deeper than coastal-water dives (mean maximum depth of 83 ± 15 m). SSTs decreased about 1°C from coast to the edge of the shelf.

Male PV-4 travelled to the SE of PV (Fig. 5), and encountered waters with different thermal characteristics than those sampled by most females. He left Punta Delgada later in the spring than females (November 4, 1995). Close to the coast, waters were mixed (Fig. 5a). The mid-shelf thermocline at departure had a vertical temperature difference of about $2\text{--}3^{\circ}\text{C}$ (Fig. 5b–d). The temperature gradient of stratified waters became more marked as the animal travelled further towards deep ocean. Coming back to the colony, he re-entered the continental shelf on

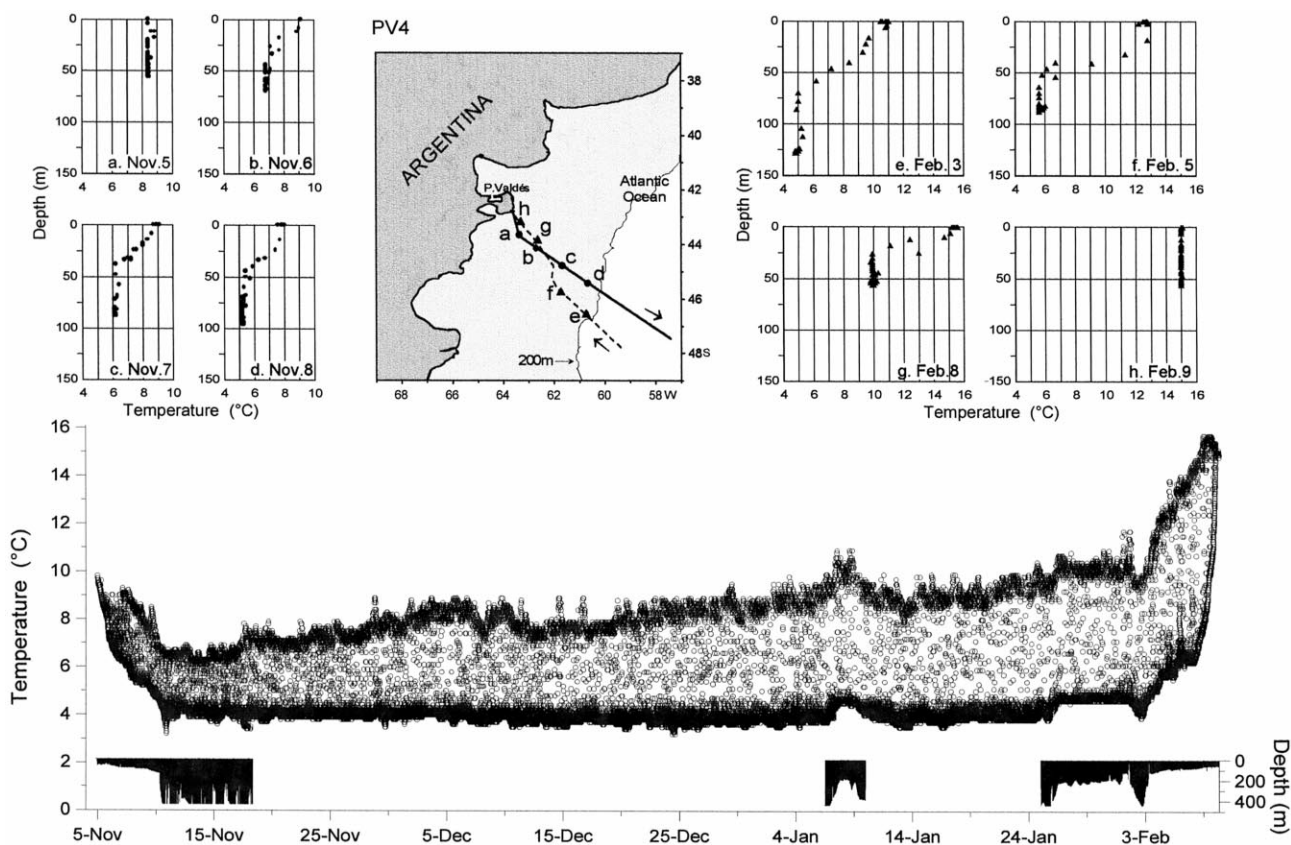


Fig. 5. Water temperature record for the complete trip of male PV-4. For clarity of the plot, only half of the total datapoints were represented. Sporadic samples that show as columns above SST reflect air temperature. Dives shown are restricted to the beginning and end of the record (shelf transition), and for a possible incursion over the shelf. Dive depth was recorded beyond 400 m due to a protocol failure. Eight detailed temperature–depth profiles (a–d for the departure, e–h for the return) represent 1 h samples on the shelf (about three dives). The map shows the general direction of the trip over the shelf and the estimated position of the animal for each example. The continental shelf (< 200 m) is shaded.

February 3, 1996. SST in mid-shelf waters was about 5°C higher than 3 months earlier (Fig. 5b–c vs. f–g). Approaching the coast, the thermocline broke down and waters were homogeneous and about 7°C warmer than in early November (Fig. 5h vs. a).

3.2.1.2. Continental slope. The arrival to the shelf slope was signalled in some females by a distinct decrease in SST that was maintained for 2–3 days. This was most evident in the record of PB-A and PB-B (Fig. 3). PB-A reached the shelf slope early in the evening of October 21 and travelled over the continental slope. Concomitant to a marked increase in maximum dive depth (from 70 m to more than 400 m in less than 1 h) occurred an abrupt decrease in SST of about 2°C (Fig. 3iii). She then moved further east, to the deep waters of the Argentine Basin. Satellite locations indicated that PV-4 left the shelf at about 46°S (Fig. 5, inset), where no abrupt decrease in water temperature was noticeable on the continental slope (Fig. 5).

3.2.1.3. Deep waters of the Argentine Basin. Females moved from cooler shelf and shelf-slope waters towards warmer off-shelf waters (e.g., PB-A, PB-B and PB-J, Fig. 3). No common pattern in SST emerged after seals had been over deep waters for a few days. After about 2 days of travel in cold waters, PB-A was exposed to an abrupt increase in water temperature, with SSTs of 9°C and a vertical difference of more than 8°C (Fig. 3iv). She remained in water masses with SST of 9–12°C during the remaining 35 days of her record (Fig. 6). PB-B also showed important fluctuations in SST over the deep ocean (Fig. 6).

SST for PV-4 was consistent with satellite-derived locations showing that he moved further south than the described range of latitudinal dispersal described for females (Figs. 1 and 5). He remained 80 days close to the shelf slope, in an area 250 km north of the Falkland (Malvinas) Islands. SST increased 3°C during the time spent over deep waters (Fig. 5).

3.2.2. Summer part of post-moult trips

The general temperature pattern described for spring trips applied to the summer part of the post-moult movements.

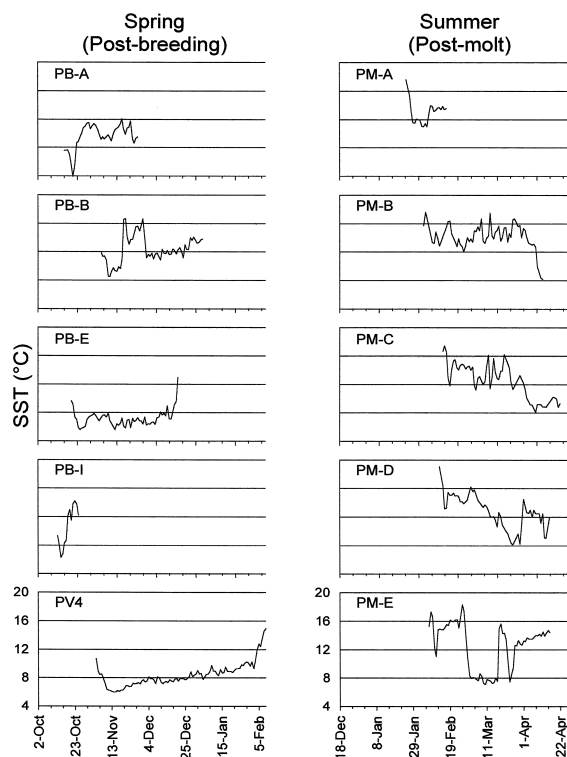


Fig. 6. Comparative profiles of mean daily SST (2–12 m) as a function of date at sea based on the total record obtained for most PB and PM animals (complete trips shown for PB-D and PV-4). A substantial variation in SST was evident in the middle of most female records (over deep waters). Data for PB-I were restricted to on-shelf samples.

3.2.2.1. Continental shelf. Most relevant results were: a marked increase in SST of 7–11°C over spring temperatures, and the broadening of the vertical thermal gradients to up to 8°C in less than 100 m (vs. 3–5°C for spring samples). Female PM-D yielded a typical temperature profile for this season (Fig. 4). She left Punta Delgada in the afternoon of February 12, 1992, and travelled for a short time through homogeneous waters of about 17°C (Fig. 4i). A thermocline quickly developed in off-shore waters, with vertical gradients of 7–10°C in a depth of less than 100 m (Fig. 4ii).

3.2.2.2. Continental slope and beyond. Females moved from warmer shelf waters to cooler, off-shelf waters (e.g., PM-A and other individuals in Fig. 4). An abrupt decrease in SST at the shelf slope of 3–4°C compared to middle-shelf waters was appar-

ent in PM-D (Fig. 4iii) and in other individuals (e.g., PM-B, PM-C and PM-E). After about 1–2 days, SST increased in all records (Fig. 4iv and others).

SST over Basin waters showed abrupt changes of about 8°C that lasted from a few hours to 1 or 2 weeks (Fig. 6). Female PM-E, for example, travelled about 2 weeks, from mid-February to early March, in waters with SST of about 15°C. She then encountered cooler waters (SST 7–8°C) where she remained for the next 2 weeks. In mid-March, PM-E travelled once again in warmer waters and then 2–3 days in cooler waters. The record ended with almost 3 weeks in waters of similar SST than those encountered in February. Other females (e.g., PM-B, PM-C and PM-D in Fig. 6) showed variations in SST.

4. Discussion

The study identified distinct ocean environments encountered by foraging seals, based on dive depth and water temperature profiles. Geolocation information and satellite derived locations (Campagna et al., 1998, 1999) confirm that animals travelled in the areas here characterised by depth and temperature patterns. Reports of the physical aspects of the continental shelf, shelf slope and deep Basin waters, based on traditional oceanographic methods (e.g. Parker et al., 1997), are consistent with depth–temperature profiles obtained by diving elephant seals, and help to interpret the data recorded by elephant seals used as sampling platforms. Oceanographic research that demand more frequent and precise locations of ocean samples would require satellite telemetry positioning (as for male PV-4 of this study). Physical data would then be useful for sampling large areas over long periods of time.

4.1. Physical oceanography of the SW Atlantic

Temperature records reflect four distinct physical systems described from hydrographic surveys and analysis of satellite images (Brosin and Nehring, 1967; Carretto et al., 1972, 1995; Legeckis and Gordon, 1982; Martos and Piccolo, 1988): (a) coastal, on-shelf waters, (b) offshore waters of the shelf, (c) sub-antarctic waters of the shelf slope, and (d) deep waters of the Argentine Basin. These systems have,

in turn, an ecological correlate in terms of productivity, availability and predictability of resources. We will first interpret results based on oceanographic phenomena and then describe productivity correlates.

4.2. Coastal water system

Seals leaving or arriving to the colony, both in spring and summer, show that coastal waters are vertically homogeneous. The shallow, near-shore waters of the shelf are mixed throughout the year through the effect of winds and tides (Glorioso, 1987). Atmospheric heat is therefore distributed in the entire water column, resulting in relatively cooler SST and warmer bottom temperatures than in more off-shore areas (Fig. 5a vs. b–d and h vs. e–g).

4.3. Offshore waters of the continental shelf

A system less affected by tidal movements, off-shore shelf waters are mixed only through the effect of winds. As a consequence, heat flow from the atmosphere affects a superficial layer of the water column and results in a seasonal thermocline that develops in late September and breaks off in mid-April (Rivas, 1993). Records from all studied seals cover the period of the year when the thermocline is established, and reflect its occurrence in off-shore, shelf waters (Figs. 3–5).

As animals move towards the continental slope or towards southern waters, SST of the shelf decreases. This is due to an increase in depth, to the influence of the sub-antarctic waters of the Malvinas Current and to the latitudinal attenuation of atmospheric heat flow. Female records reflect the former two phenomena while PV-4 record illustrates also the latitudinal attenuation of heat flow.

Atmosphere heat affects water temperature on the shelf more than in off-shelf areas. From the beginning to the end of PV-4 foraging trip (about 3 months), SST of the offshore waters of the continental shelf increased markedly due to a heating effect from the atmosphere. In coastal regions, where mixing overcomes stratification, the entire water column is affected by atmospheric heat. In offshore areas, where a thermocline inhibits vertical turbulent diffusion of heat, radiant energy is absorbed only by the superficial layer, broadening the vertical temperature gradient (Rivas, 1993).

4.4. Malvinas Current system

Along the shelf slope and the western boundary of the Argentine Basin circulates a northward flow of cold, sub-antarctic, low-salinity waters originated as a branch of the Antarctic Circumpolar Current (Roden, 1986; Peterson, 1992). This system is responsible for the abrupt decrease in water temperature when animals arrive to the border of the continental shelf. As PV-4 moved SE, he crossed the shelf-edge at lower latitudes than most females (Campagna et al., 1998). As a consequence, shelf waters were cooler than in northern latitudes and similar to the Malvinas Current system. Thus, no abrupt horizontal SST gradient was apparent for this animal (Fig. 5).

4.5. Deep waters of the argentine basin

Temperate, deep SW Atlantic waters are affected by the combined effect of the Malvinas and the warm, subtropical Brazil currents. The latter flows south-westward along the continental margin of South America to about 38°S. The location of the confluence of these currents varies seasonally between 33° and 40°S, being more northerly located in winter than in summer (Balech, 1949; Roden, 1986; Olson et al., 1988; Garzoli and Garraffo, 1989; Provost et al., 1992; Matano et al., 1993). It is characterised by intense horizontal temperature gradients (up to 1°C per km according to Legeckis and Gordon, 1982). After the confluence, the Brazil current turns SE, towards the Argentine Basin. This occurs in a series of large amplitude meanders and eddies that create SST anomalies (Roden, 1986).

At least two aspects of the temperature record may reflect the combined effects of these current systems: (a) the abrupt increase in water temperature, evident in female samples after animals had spent a few days under the effect of the Malvinas System (Figs. 3 and 4), and (b) the large SST gradients shown in the record of female PM-E, and other post-moult animals (Fig. 6). The record of PV-4 does not show an abrupt change in water temperature over deep, off-shelf waters probably because he remained at lower latitudes, less affected by the Brazil Current.

4.6. Productivity and frontal zones

Three thermal frontal zones are described for the areas that elephant seals encounter during foraging movements: (a) the transition between the homogeneous and stratified shelf waters (Glorioso, 1987; Glorioso and Flather, 1995), (b) the shelf-break system (Martos and Piccolo, 1988; Carreto et al., 1995) and (c) the Brazil–Malvinas (subtropical) confluence (Signorini, 1976; Roden, 1986; Gordon, 1989; Gordon and Greengrove, 1986). These three areas have been associated with high productivity and a rich fish and squid fauna that attracts top predators (Carreto et al., 1986; Csirke, 1987; Glorioso, 1987; Glorioso and Flather, 1995; Podestá, 1990, 1997; Prince et al., 1992, 1997; Olson et al., 1994; Croxall et al., 1999).

Magellanic penguins, *Spheniscus magellanicus*, and South American sea lions, *Otaria flavescens*, that reproduce along the coast of PV, forage in coastal and offshore waters of the continental shelf, apparently exploiting areas with enhanced productivity (Werner and Campagna, 1995; Wilson et al., 1995; Peters et al., 1998). Conversely, it is less clear the importance of shelf environments for foraging elephant seals. Females do not apparently exploit the productivity of the shelf (Campagna et al., 1998). PB-I was exceptional in the extent of time spent on shelf waters. Males may be more prone to remain in shallow waters. At least two of seven males carrying satellite tags remained on the continental shelf during the entire time tracked at sea (Campagna et al., 1999). One of male tracked for 66 days, concentrated his activity 6–10 km off the coast of Patagonia, in areas described for their potential high primary and secondary productivity (Glorioso and Flather, 1995).

The shelf-slope front occurs at the boundary between the shelf break and the Malvinas Current. Satellite images and in situ observations point out a sector of enhanced primary productivity over an area stretching from 37° to 50°S (Podestá, 1997). The northern part of the Malvinas Current serves as spawning grounds for the commercially important squid *Illex argentinus* (Rodhouse et al., 1995). Satellite tracked wandering albatrosses (*Diomedea exulans*) from South Georgia Island forage along the shelf slope (Prince et al., 1992; 1997). Five of seven PB, satellite-tracked southern elephant seal males

from PV (PV-4 was one of them) remained along the shelf margin, where travel rates decreased markedly, suggesting that they may have reached foraging grounds (Campagna et al., 1999).

The strongest thermohaline front for the SW Atlantic occurs at the subtropical confluence (Signorini, 1976; Gordon and Greengrove, 1986; Roden, 1986). The accumulation of plankton by the convergent flow and by high production supported by nutrient-rich waters of the Malvinas Current was documented by Gayoso and Podestá (1996) in the subtropical convergence area. Male and female elephant seals from PV tracked at sea with satellite telemetry (for which temperature data are not available) spent time near the southern range of this front (Campagna et al., 1998, 1999).

4.7. Physical cues and foraging areas

An implicit issue at the core of this study is related to the inconclusive attempts made to identify physical features of the marine environment that may signal foraging locations. Hindell et al. (1991) showed that locations at sea of foraging southern elephant seals from Macquarie Island are associated with distinct SST and depth profiles. McConnell et al. (1992) related geographical dispersal of elephant seals from South Georgia Island with particular physical and biological aspects of the oceanographic environment. Boyd and Arnborn (1991) went further to suggest that elephant seals may use temperature discontinuities between water masses to locate productive areas suitable for foraging. However, Hakoyama et al. (1994) concluded that the foraging environment of northern elephant seals, *M. angustirostris*, from Año Nuevo, CA, does not provide temperature discontinuities in the water column to serve as cues to locate prey.

This study concurs with Hindell et al. (1991) and McConnell et al. (1992) in providing evidence that elephant seals move across distinct ocean environments. The broad and shallow Patagonian shelf originate particular physical conditions, from which seals could profit to find a route or an area of enhanced productivity. A seal cueing on the depth of the bottom of the ocean and on abrupt changes in water temperature would be able to unmistakably locate

the transition between mixed coastal and stratified shelf waters, the edge of the shelf, the Malvinas current and the waters affected by the Brazil current. Moreover, previously described sex differences in location and movements at sea, suggest that males spend time at sea over potentially relocatable environments associated with predictable frontal zones, such as the shelf slope–Malvinas Current system. Females disperse over the Argentine Basin, where bathymetric cues may be less available but where localised variations in water temperatures, such as those of the subtropical convergence, may still guide their movements.

However, results from this study only point at the potential of distinguishing ocean environments; data do not show that physical features are indeed used by seals as cues to guide them to productive foraging areas. Conclusive results related to the hypothesis that animals profit from the distinctive characteristics of the water masses would have to wait for research that goes beyond the simple association of behavioural and physical records.

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