

Deep divers in shallow seas: Southern elephant seals on the Patagonian shelf

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Abstract

Elephant seals are wide-ranging, pelagic, deep-diving (average of 400–600 m) predators that typically travel to open waters and continental shelf edges thousands of kilometers from their land breeding colonies. We report a less common pattern of foraging in the shallow waters of a continental shelf. Southern elephant seals, *Mirounga leonina*, that breed at Península Valdés (Argentina), face an extended (~1,000,000 km²; 400–700 km-wide, depending on track), shallow (<150 m) and seasonally productive plateau, the Patagonian shelf. Adults of both sexes usually cross it in rapid transit to other potential foraging grounds on the shelf edge or in the Argentine Basin, but 2–4 year-old juveniles spread over the plateau and spent months in shallow waters. This behavior was recorded for 9 seals (5 males and 4 females) of 23 satellite-tracked juveniles (springs of 2004 and 2005) and for 2 subadult males studied in previous seasons. Trips included travel trajectories and time spent in areas where swim speed decreased, suggesting foraging. Preferred locations of juvenile females were in the proximity of the shelf break, where stratified waters had relatively high phytoplankton concentrations, but young and subadult males used the relatively cold (7–8 °C), low-salinity (~33.3) mid-shelf waters, with depths of 105–120 m and a poorly stratified water column. Three of the latter seals, instrumented with time–depth recorders, showed dives compatible with benthic feeding and no diel pattern of depths distribution. Regions of the mid-shelf were used in different seasons and were associated with low chlorophyll-*a* concentration at the time of the visit, suggesting that surface productivity does not overlap with putative quality habitat for benthic foragers. Benthic diving on the shallow mid-shelf would be a resource partitioning strategy advantageous for young males prior to greater energetic demands of a high growth rate and a large body size. Later in life, the more predictable, bathymetry-forced, shelf-break front may offer the food resources that explain the uninterrupted increase of this population over several decades.

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1. Introduction

Elephant seals forage exclusively at sea, where they typically engage in deep, long and continuous dives during distant trips from the land breeding and molting places (Hindell et al., 1991a; McConnell et al., 1992, 2002; Jonker and Bester, 1994; Campagna et al., 1998, 1999, 2006; Bornemann et al., 2000; Bradshaw et al., 2004b; see also contributions and references in Le Boeuf and Laws, 1994; Le Boeuf et al., 2000). The migration and foraging behavior relative to the physical environment has been intensively studied during the last decades and described for free-ranging animals of both the southern, *Mirounga leonina*, and northern, *Mirounga angustirostris*, species and for both sexes, different age categories and all major colonies in the world (e.g., Bester and Pasegrouw, 1992; Bailleul et al., 2007; DeLong and Stewart 1991; McConnell and Fedak, 1996; Hindell et al., 1991b, 1999; Bornemann et al., 2000; Campagna et al., 2000, 2006; Le Boeuf et al., 1988, 2000; Field et al., 2001, 2004, 2005; McConnell et al., 2002; van den Hoff et al., 2002). This paper reports a variant in the prevailing pattern: extensive periods spent on an extended and shallow continental shelf off the coast of Patagonia where seals are constrained to depth of about 100 m.

Southern elephant seals breed and molt on several oceanic islands and on the continent, at Península Valdés (Le Boeuf and Laws, 1994; McMahon et al., 2005a; Lewis M. et al., 2006; Fig. 1a). When seals from the Patagonian population leave the coast to embark on a foraging trip that may last 7 months, they face the extended Patagonian continental shelf, one of the largest (~1,000,000 km²), shallowest (<150 m) and most productive ocean plateaus in the world (e.g., color plates 1–4 in Longhurst, 1998; Croxall and Wood, 2002; Acha et al., 2004; Forero et al., 2004). The shelf is a broad, relatively smooth and irregularly shaped submarine platform that widens southward from about 170 km at 39°S to 850 km at 50°S and is bounded to the east by a sharp shelf break initiating near the 110–165-m isobaths (Fig. 1b; Parker et al., 1997). It supports a variety of species of top predators, including visitors from distant areas (Croxall and Wood, 2002). Therefore, seals that breed and molt at Península Valdés could save commuting energy by foraging on the shelf, as they would have to travel shorter distances, both in the horizontal and vertical dimensions, than seals exploiting deeper seas.

Despite expectations, data to date show that the shelf is no more than the required path to more distant foraging grounds. Adult, post-breeding and post-molt females move quickly over the shelf and do not appear to begin foraging until they reach depths exceeding 200 m (Campagna et al., 1995, 1998). Likewise, observations of adult males imply that they too cross the shelf towards putative foraging grounds located along the continental slope (Campagna et al., 1999).

Young elephant seals are as capable as adults of long-distance travel and deep diving (Hindell et al., 1999; McConnell et al., 2002; Field et al., 2005). Juvenile females from Península Valdés migrate far, even farther than adults, approaching South Georgia (~2300 km), the Antarctic Peninsula (~2100 km) or the South Pacific (~2200 km) (Campagna et al., 2006; www.sea-sky.org). However, contrasting with the dominant behavior of the species, some young seals remain in shallow waters for extended periods of their foraging phase. They offer a unique opportunity for intra-specific comparisons with the at-sea behavior of deep divers in distant waters. This paper describes the extensive use of shallow shelf habitats for the entire foraging period. Frontal 7 areas off the Patagonian coast are associated with bathymetric features; thus their locations are relatively stable from year to year (Romero et al., 2006). The diving behavior of shelf users is expected to be affected by the bathymetric profile, as dive depth will be limited by the topography.

2. Oceanographic background

The ocean circulation over the Patagonian continental shelf is dominated by tidal forcing and strong offshore winds and the Malvinas Current along its eastern margin. These forcings, combined with the irregularly shaped coast, the effects of bottom friction and solar radiation, determine the vertical stratification, the circulation and the seasonal variability of the shelf waters (see Rivas and Piola, 2002; Palma et al., 2004). The mean circulation is dominated by a weak northeastward flow of a few cm/s (e.g., Brandhorst and Castello, 1971; Forbes and Garraffo, 1988; Glorioso and Flather, 1995; Piola and Rivas, 1997; Palma et al., 2004).

The vertical salinity distribution generally presents weak gradients; therefore density stratification is mostly controlled by the temperature distribution. A seasonal thermocline develops in early October (Rivas and Piola, 2002). Vertical temperature

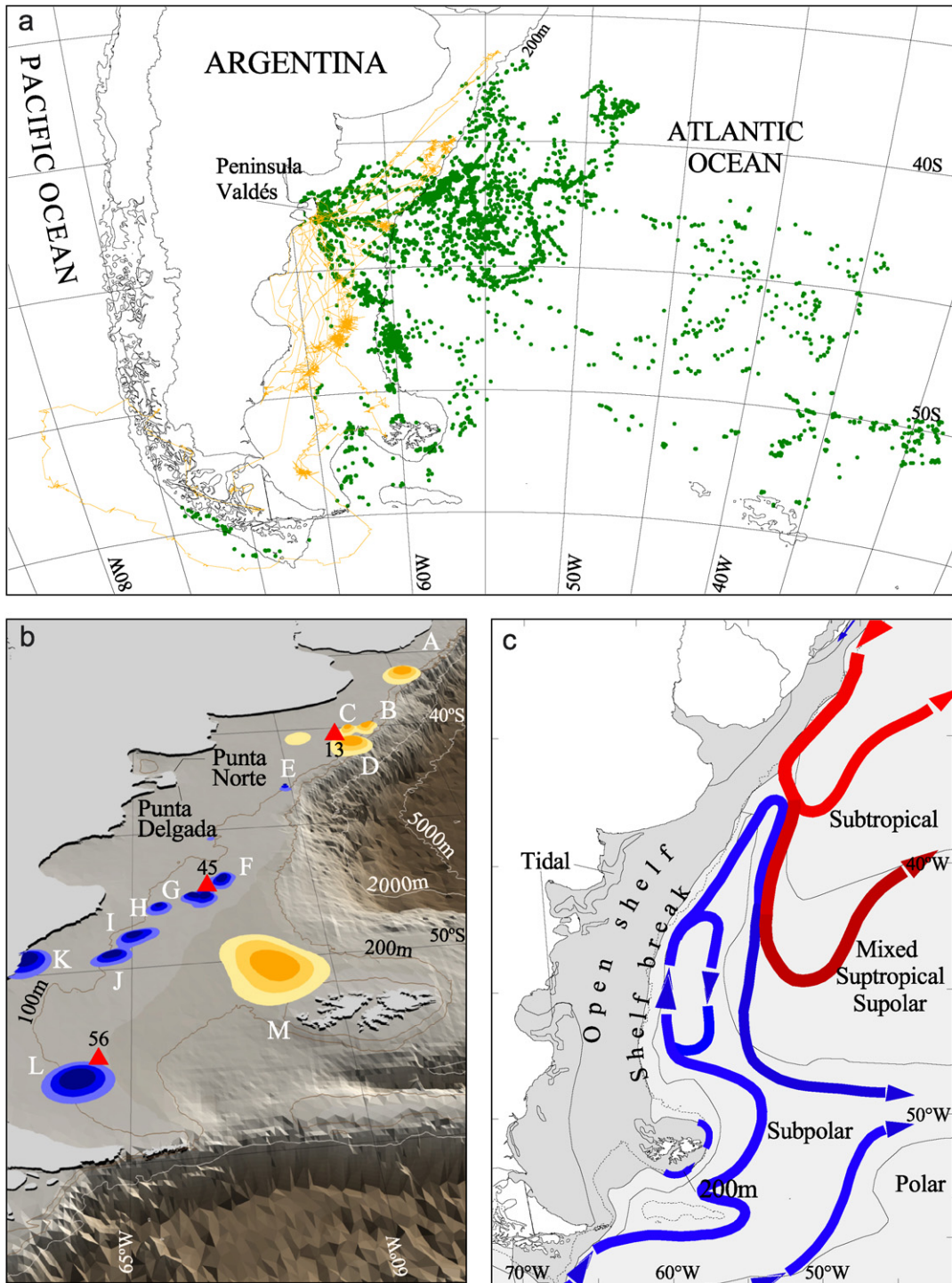


Fig. 1. (a) The Atlantic Ocean where satellite-tracked elephant seals from the Peninsula Valdés population dispersed. The 200-m isobath indicates the approximate offshore edge of the continental shelf. Orange trajectories are from 11 foraging animals (5 juvenile males, 4 juvenile females and 2 subadult males) that remain within the shelf area. For comparative purpose, green dots are satellite-determined locations of 12 additional juveniles, 4 adult females and 6 adult males that foraged in deeper waters. (b) Bathymetry and 75% focal bouts of shelf and shelf-break seals (blue: males, yellow: females). Red triangles indicate the positions of hydrographic stations referred to in the text. (c) Oceanographic regimes for the shelf (shaded in gray): tidal, open shelf and shelf break) and the Argentine Basin (subtropical, subpolar and mixed waters; see Piola and Matano, 2001). Blue arrows represent the circulation of Malvinas and Malvinas Return Currents. Red arrows indicate the flow of the Brazil Current (adapted from Piola and Matano, 2001).

stratification continues increasing until late January–early February, when the peak in SST is observed throughout most of the northern shelf (Podesta et al., 1991; Rivas and Piola, 2002). The vertical stratification begins weakening in early March and by late June the seasonal thermocline and pycnocline are eroded (Rivas and Piola, 2002).

Intense near-shore vertical mixing due to tidal current interaction with the bottom and against prominent coastal features prevents the formation of the seasonal thermocline even during the peak of the austral summer (Carreto et al., 1986; Glorioso, 1987; Glorioso and Simpson, 1994; Glorioso and Flather, 1995; Sabatini and Martos, 2002; Palma et al., 2004) and creates tidal fronts. The tidal fronts mark the inshore edge of the regions of high chlorophyll *a* (chl *a*) observed in summer, suggesting that tidal induced mixing plays a major role in the redistribution of nutrients and in maintaining the relatively high biological production associated with these sites (Romero et al., 2006). The tidal fronts are important for their influence on the distribution of species, ranging from phytoplankton, low-trophic-level invertebrates, commercial fisheries and top level predators (see Acha et al., 2004; Bogazzi et al., 2005, and references therein). The onset of vertical stratification is thought to trigger the spring phytoplankton blooms, which are most intense east of the tidal fronts and along the shelf break (e.g., Carreto et al., 1995; Romero et al., 2006; Signorini et al., 2006).

Background physical oceanography information on the other major ocean regimes and frontal zones illustrated in Fig. 1c and visited by the seals is discussed in Piola and Gordon (1989), Olson et al. (1988), Glorioso and Flather (1995), Goni and Wainer (2001) and Palma et al. (2004). For the shelf-break front see also Acha et al. (2004), Bogazzi et al. (2005) and Romero et al. (2006).

3. Data and methods

3.1. Study animals

This paper describes the at-sea behavior of satellite-tracked southern elephant seals from Península Valdés focusing on individuals that spent most or all of their foraging trips on the Patagonian continental shelf (Fig. 1b). Animals that crossed the shelf “in transit” to and from deep waters were not part of the analysis.

Data on shelf users are virtually restricted to 2–3 year-old, young juveniles. Age was estimated from body shape, length, girth and secondary sexual characteristics. Weight (Table 1) was estimated following Bell et al. (1997; body mass = $53.896 (\text{SLength}^{1.063}) (\text{Girth}^{1.697})$) for juveniles and Haley et al. (1991) for subadults ($M = 31.287 (L^{3.023})$). Satellite tags (SPOT4/SPOT5; Wildlife Computers, Redmond, WA; <http://www.wildlifecomputers.com>) were deployed on 28 (13 males, 15 females) 2–3 year-old juveniles in December 2003 (4), July 2004 (7) and July 2005 (7), at Punta Delgada (42°45'S; 63°38'W), and in December 2005 (10) at Punta Delgada and Punta Norte (42°4'S; 63°47'W; Fig. 1b). Two additional animals that, like juveniles, spent extended periods on the shelf were larger and older, subadult males (PLAST and LUCA; Fig. 2a and Table 1) instrumented for a previous study (Campagna et al., 1999). These seals were included in this paper as they also behaved as exclusive shelf users. Relevant methodological information and more detailed summary statistics on their behavior were reported in Campagna et al. (1999).

General procedures and anesthesia protocols to deploy and recover instruments for the study site were described in previous work (Campagna et al., 1995, 1998, 1999). Seals were anesthetized with tiletamine–zolazepam (Telazol[®], Fort Dodge Animal Health, Fort Dodge, IA 50501, USA) at doses of 1.2–1.6 mg/kg for juveniles and 0.5 mg/kg for subadults, administered by remote intramuscular injection in the gluteal region (Ryding, 1982; Baker et al., 1990). The drug is broadly used to immobilize elephant seals (e.g., McMahan et al., 2000). The procedure involved approaching a sleeping or resting seal, injecting the drug and retreating quickly, requiring less than 1 min to perform. The behavior of the subject was then observed at a distance to decrease disturbance during induction. Immobilizations were done at low tide as a safety measure to prevent seals from moving to the ocean during the induction phase. First evidence of immobilization occurred within 3–15 min after injection. Time between induction and recovery was sufficient to allow safe handling for approximately 40 min. Instruments (160 g of weight) were attached on the head with marine epoxy (Evercoat Ten-Set, Fibre-Evercoat Co., Cincinnati, OH) to facilitate transmission of location as the animal surfaced between dives. Immobilizations were smooth and uneventful; all animals behaved normally within 2 h of the injection.

Table 1
Descriptive data on the foraging trips of the 11 satellite-tracked animals included in this study

Seal	Departure			Arrival			Deployment date (dd/mm/yyyy)	Days at sea		Maximum distance from PV (km)	Travel distance (km)	Number of locations		Travel to focal bout		Focal bout on shelf		Return trip	
	Std. len. (m)	Girth (m)	Est. weight (kg)	Std. len. (m)	Girth (m)	Est. weight (kg)		Total	With location			Total	At sea	Days (%)	Mean (sd) swim speed (km/day)	Days (%)	Mean (sd) swim speed (km/day)	Days (%)	Mean (sd) swim speed (km/day)
<i>Subadult males</i>																			
PLAST	3.8		1701				23/10/1994	58	58	812	1845	420	202	34	51 (32)	59	43 (47)		
LUCA	4.1		2179				27/10/1995	94	64	337	2549	147	137	12	48 (26)	23	26 (34)		
Mean								76	61	575	2197			23	50	41	35		
Sd								26	4	336	498			15	3	25	12		
Total	(n = 2)							152	122			567	339						
<i>Juvenile males</i>																			
M54	2.0	1.6	251	2.2	1.8	363	12/07/2004	108	82	778	5574	432	395	5	85 (23)	48	63 (53)	14	70 (26)
M56	1.9	1.4	197	1.9	1.7	283	13/07/2004	107	88	694	6143	451	412	8	93 (37)	36	62 (49)	9	96 (47)
BK6	1.8	1.4	194	1.9	1.5	242	30/07/2005	98	95	1150	6996	624	582	30	85 (50)	48	72 (53)	15	102 (52)
SI4	1.8	1.5	171	2.0	1.6	224	30/07/2005	88	86	524	6245	460	421	28	75 (50)	39	71 (54)	12	94 (66)
SyS2	1.7	1.5	191	1.8	1.5	207	26/07/2005	90	77	579	5348	504	417	36	76 (58)	36	63 (49)	7	93 (39)
Mean								98	86	745	6061			22	83	41	66	12	91
Sd								9	7	247	644			14	8	6	5	3	12
Total	(n = 5)							491	428			2471	2227						
<i>Juvenile females</i>																			
HS2	1.8	1.4	186				24/07/2004	107	44	644	4266	126	126	40	98 (56)	35	58 (50)		
H58	1.8	1.5	210	1.9	1.7	283	24/07/2004	106	41	1058	3123	165	129	43	57 (45)	44	47 (44)	12	88 (57)
ACT3	1.7	1.4	160	1.8	1.6	225	30/07/2005	90	85	687	5636	577	547	21	71 (52)	47	68 (50)	8	108 (45)
FAR11	1.9	1.3	179	1.9	1.4	196	10/12/2005	218	90	1689	10,603	675	617	7	89 (44)	11	75 (60)	6	131 (42)
Mean								130	65	1020	5907			28	79	34	62	9	109
Sd								59	26	483	3295			17	19	17	12	3	22
Total	(n = 4)							521	260			1543	1419						
Mean								106		814	5303	416	362	24	75	39	59	10	98
Sd								40		370	2411	192	185	14	17	13	15	3	18
Total	(n = 11)							1164				4581	3985						

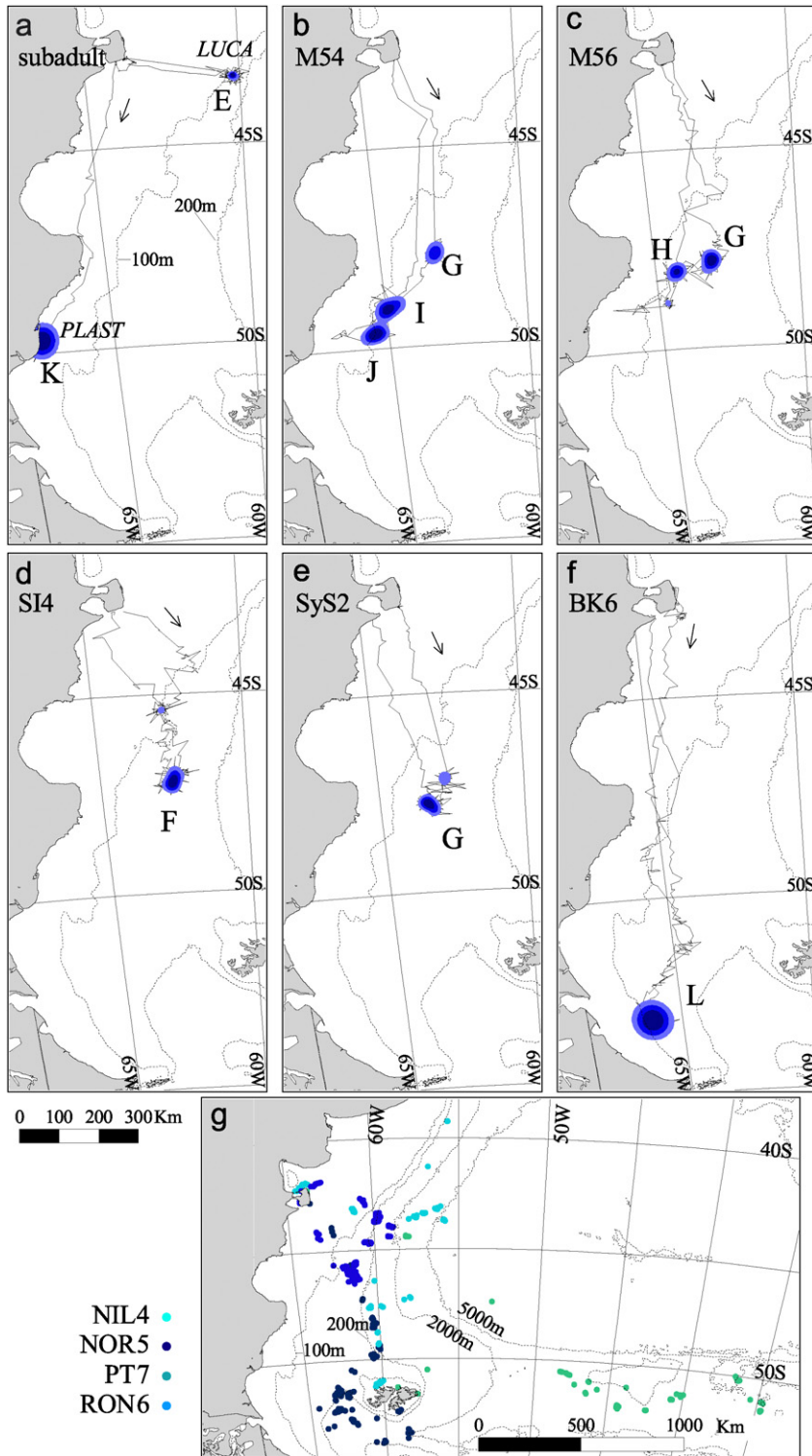


Fig. 2. Travel trajectories of male focal seals. All seals are juveniles, except for (a) (subadults instrumented in 1994 and 1995; see Data and methods). Density contours result from kernel estimation techniques; densities shown correspond to 75%, 50% and 25% kernels. Fig. 2g shows the locations of the 4 non-focal juvenile males.

Tags were configured to start sending information as soon as the animals entered the ocean. During the 2003–2005 seasons, the link with the satellite was active 24 h per day, with repetition rates of 457 6 s (2003 and 2004) and 407 6 s (2005). For the 2006 season, duty cycles were configured to operate 1 day on/1 off or 1 day on/2 days off, with a repetition rate of 407 6 s. Argos System (<http://www.cls.fr>) provides location data with an estimated accuracy of 150–1000 m, quoted in location classes 3, 2 and 1. Locations of estimated accuracy 4 1000 m (class 0) and with no estimate of their accuracy (classes A and B) are also provided. The iterative forward/backward averaging filter proposed by McConnell et al. (1992) was applied to reject records that would require an unrealistic travel rate greater than 2.8 m/s (10 km/h).

Assuming an elephant seal moves in a straight line at constant speed between two successive locations, each path was re-sampled at an interval of 1 h. Gaps of more than 24 h were not re-sampled (see BirdLife International, 2004, methods). Individual kernel density maps were obtained using the animal movement extension (<http://www.absc.usgs.gov/globa/gistools>) in ArcView GIS 3.3 with Spatial Analyst. Focal bouts are defined as relatively small areas of concentrated activity (high location rate) where seals spend weeks at a time and travel speeds decrease, compared to in-transit trajectories. Movements inside the bout are more erratic than during travel phases. Overall, a focal bout was assumed to be the area within the 50% kernel.

Travel time to putative foraging areas was estimated from departure to arrival at the edge of the 50% kernel curve. Female FAR11 (Fig. 3) spent part of her foraging time in the Pacific Ocean; this paper considered only the data that pertain to the Atlantic Ocean phase of her trip.

Three satellite-tracked juvenile males (M54, M56, BK6; Figs. 2b, c and f) were also instrumented with time–depth–temperature recorders manufactured by Driesen + Kern GmbH (www.driesen-kern.de). Additional diving information was available for the 2 subadult males referred to above and studied in previous seasons (Campagna et al. 1999). Dive depths were associated with locations within 7–30 min of available Argos positioning data and compared to bottom depths. Bottom depths were drawn from a 0.03° latitude \times 0.03° longitude continental shelf bathymetric data base (Palma et al., 2004). Bathymetric data for Fig. 1b were obtained from Palma et al. (2004) and the 2-min

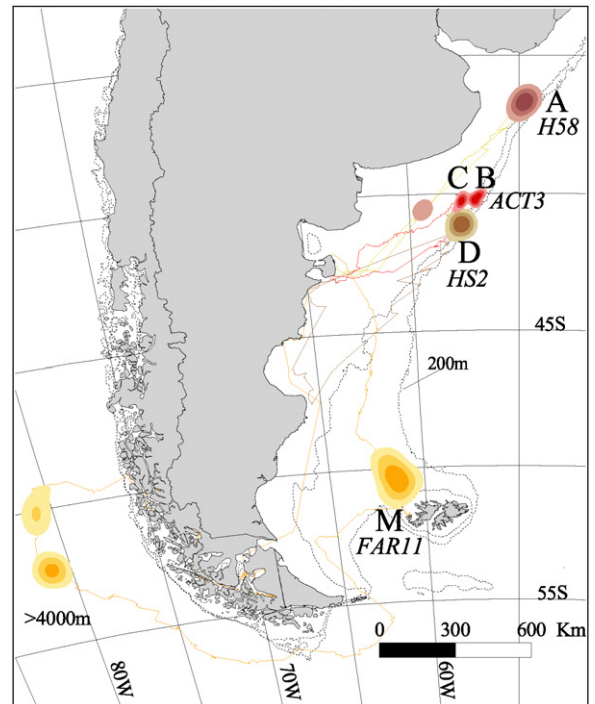


Fig. 3. Travel trajectories of juvenile female focal seals. Density contours result from kernel estimation techniques; densities shown correspond to 75%, 50% and 25% kernels.

gridded global relief data (ETOPO2v2), NOAA, National Geophysical Data Center, 2006 (<http://www.ngdc.noaa.gov/mgg/global/global.html>).

3.2. Hydrographic data

Concomitant to the satellite-tracking study, hydrographic data were collected in October 2005 along several cross-shelf and slope sections between 37°S and 55°S . At all stations a SeaBird Electronics model 911plus conductivity–temperature–depth (CTD) profiler fitted with a Seapoint chlorophyll fluorometer was used. Vertical CTD profiles were taken to within 5 m of the bottom. Stations were occupied at the approximate locations of elephant-seal concentrations at the shelf break near 41°S and in the mid-shelf regions near 48°S and 51°S and therefore provide information on the vertical water mass structure in these regions (Fig. 1b).

3.3. Satellite oceanographic data

Mean satellite-derived surface chl-*a* concentrations inside focal bouts were estimated using the weekly merged level-3 chlorophyll product derived

from SeaWiFS and MODIS/Aqua with 9-km resolution. Mean SST values were estimated from weekly level-3 SST derived from MODIS/Aqua with 4-km resolution. The original locations of the elephant seals prior to interpolation were used for both SST and chl-*a* estimations. Chl-*a* and SST data are available through NASA's Goddard Space Flight Center and the Physical Oceanography Distributed Active Archive Center at the Jet Propulsion Laboratory, respectively.

4. Results

Extended periods at sea, including 19 complete trips, were recorded for 23 of the 28 instrumented juvenile seals. Five seals (4 males) yielded sparse information or failed to transmit and were not included in the analysis. Twelve animals (2 males; Fig. 2g) used the shelf only in transit to non-shelf areas, or they spent on the shelf a small, non-representative proportion of their time at sea. In addition, as uplinks from 2 juvenile males, NIL4 and RON6, were received at a lower rate, these seals are not included in the analysis. Our core sample of continental shelf users was then composed of 11 seals, 9 juveniles (5 males; Table 1, Figs. 2b–f and 3) and 2 subadult males (Fig. 2a). Tables 1 and 2

summarize comparative tracking statistics for the 11 study animals, and Table 3 presents diving statistics for the 3 instrumented animals. Juveniles gained weight during their foraging trips (mean \pm standard deviation, s.d. = 1627 \pm 55 kg at departure and 2087 \pm 80 kg at arrival).

4.1. Travel pattern

Focal shelf users spread over the entire continental plateau, covering about 20° of latitude. The open-shelf areas are concentrated with more activity than coastal zones or tidal fronts (Fig. 1b). Males dominated the sample of shelf travelers (7 of the 11 focal shelf animals; Table 1). Individual male foraging trips are illustrated in Figs. 2a–f. Fig. 2g shows trajectories of the 4 additional satellite-tracked juvenile males that were not exclusive shelf users, or that traveled to distant locations. Four females were exclusive or important shelf users, the remaining seals spent their time at sea in deep waters of the Argentine Basin. Three of the focal shelf users (HS2, H58 and ACT3; Fig. 3) traveled close to the continental slope, but were included in the sample as their areas of concentrated activity occurred in waters shallower than 200 m, west of the continental slope. All of the shelf users presented

Table 2

Dimensions and major characteristics of areas of concentrated activity (4 50% kernels) for all animals located over the continental shelf and considered in the present study

Seal	Region (Figs. 1b, 2a–f and 3)	Mean depth in meters (sd)	Mean (sd) SST in °C	Mean (sd) chl <i>a</i> in mg/m ³	Bout area (km ²)	Initial date at bout (dd/mm/ yyyy)	Duration (days)
<i>Subadult males</i>							
PLAST	K	49 (20)	–	–	2620	08/12/1994	34
LUCA	E	101 (3)	–	–	240	14/11/1995	22
<i>Juvenile males</i>							
M54	G	117 (1)	6.9 (0.1)	0.3 (<0.1)	870	30/07/2004	9
	I	106 (1)	6.0 (0.8)	0.3 (<0.1)	1930	17/08/2004	24
	J	102 (4)	6.7 (0.3)	1.0 (1.3)	1810	15/09/2004	19
M56	H	106 (1)	6.7 (0.3)	0.4 (0.1)	920	25/07/2004	20
	G	118 (2)	7.2 (0.6)	1.5 (1.4)	1330	23/09/2004	18
BK6	L	108 (8)	5.6 (0.4)	0.4 (0.1)	5300	08/09/2005	47
SI4	F	116 (2)	6.5 (1.5)	0.5 (0.2)	1550	02/09/2005	34
SyS2	G	115 (3)	7.4 (0.7)	0.7 (0.5)	1310	17/09/2005	32
<i>Juvenile females</i>							
HS2	D	133 (58)	7.4 (0.6)	8.3 (11.8)	7230	02/09/2004	37
H58	A	80 (43)	11.3 (1.1)	1.8 (1.1)	8320	15/09/2004	47
ACT3	C	95 (1)	7.3 (0.7)	0.8 (0.7)	1580	24/08/2005	17
	B	102 (11)	8.3 (0.7)	2.3 (2.2)	2240	10/09/2005	25
FAR11	M	145 (26)	10.3 (0.7)	2.4 (0.8)	18,330	02/01/2003	23

Table 3

Diving profile for U-shaped, benthic, E dives (Crocker et al., 1994) recorded in the area of the 50% kernel for 3 young males instrumented with time–depth recorders

Seal	Total days recorded with dives % of days at sea (Table 1)	Dives recorded		Type E dives														
		Total	Type E dives			Duration (min)			Surface interval (min)			Dive depth (m)						
			Bout	Transit	Total	Bout	Transit	Total	Bout	Transit	Total	Day			Night			Total
		Bout										Transit	Total	Bout	Transit	Total		
M54	50 46%	3626	1191	995	2186	18	17	18	1.7	1.6	1.6	115	118	117	117	118	118	117
						(4)	(4)	(4)	(0.2)	(0.3)	(0.3)	(9)	(1)	(7)	(1)	(6)	(4)	(6)
						37	35	37	3.4	3.2	3.4	125	122	125	124	122	124	125
M56	68 64%	5530	957	3200	4157	17	16	16	1.7	1.6	1.6	113	116	113	116	113	114	114
						(4)	(4)	(4)	(0.3)	(0.3)	(0.3)	(7)	(2)	(7)	(2)	(6)	(5)	(6)
						34	41	41	3.6	3.9	3.9	123	122	123	123	123	123	123
BK6	64 65%	6492	1867	984	2851	12	12	12	1.5	1.4	1.5	117	115	116	115	118	116	116
						(3)	(3)	(3)	(0.3)	(0.3)	(0.3)	(20)	(5)	(13)	(5)	(20)	(12)	(12)
						29	28	29	10.0	7.3	10.0	157	127	157	124	159	159	159
Total	182 58%	15,648	4015	5179	9194	15	16	15	1.6	1.5	1.6	114	116	115	116	114	115	115
						(5)	(4)	(4)	(0.3)	(0.3)	(0.3)	(12)	(4)	(10)	(3)	(9)	(7)	(9)
						37	41	41	10.0	7.3	10.0	157	127	157	124	159	159	159

For every variable information provided corresponds to the mean (in bold), standard deviation (in parenthesis and italics) and max. value (regular type). Extended surface intervals (4–10 min) were not included in the analysis. The depth profile for daylight dives is based on 5581 E dives versus 3613 night dives.

the same travel pattern: fairly straight paths to focal areas and an erratic pattern inside the areas of concentrated activity.

Distance from the colony of male and female seals over the shelf were roughly 700 and 1000 km, respectively (Table 1). However, as focal seals dispersed widely, some animals (e.g., BK6, max. distance from Península Valdés = 1150 km; Fig. 2f) traveled similar distances or even longer than those located along the continental slope (e.g., PT7, max. distance from Valdés = 1025 km; Fig. 2g). Comparatively, animals dispersing in the deep ocean, or reaching the South Pacific (e.g., NOR5, Fig. 2g, and FAR11, Fig. 3, respectively; see also dispersion of recorded locations as green dots in Fig. 1a), showed maximum distances from the colony of 2500–3000 km. Mean travel time to putative foraging areas for juvenile shelf users (first bout of concentrated activity) was 25 days (s.d. = 14 days) and 16 days (s.d. = 6 days) for the sample that included subadult males.

Detailed trajectories recorded for some animals showed that a foraging trip included traveling and time spent in specific areas (focal bouts marked

with capital letters in Figs. 1b and 2–5). Swim speed tended to be 22% slower in areas of concentrated activity (Table 1). The trip of BK6 was the longest among males, with roughly 7000 km traveled in 3 months (Fig. 2f; Table 1). He swam directly southward, in a non-stop trip of 1 month at a mean travel speed of 85 km/day, to reach an area of concentrated activity (L in Fig. 2f) where he remained for 47 days. This focal area, located east of Tierra del Fuego, at 53°S, had about 5300 km² (Table 2). The animal traveled within its focal bout at a lower speed (~62 km/day; Table 1) than during the commuting phase. The return trip followed a path similar to the outgoing trajectory but lasted half the time (15 days).

A much more meandering trajectory characterized FAR11, the juvenile female with the longest trip, which included a crossing to the South Pacific through the Drake Passage and a return trip via the Magellan Strait. Three focal bouts were interspersed in a trip 218-day long: one on the Patagonian shelf, where FAR11 spent 23 days in an area 120–180 km wide (Fig. 3, bout M).

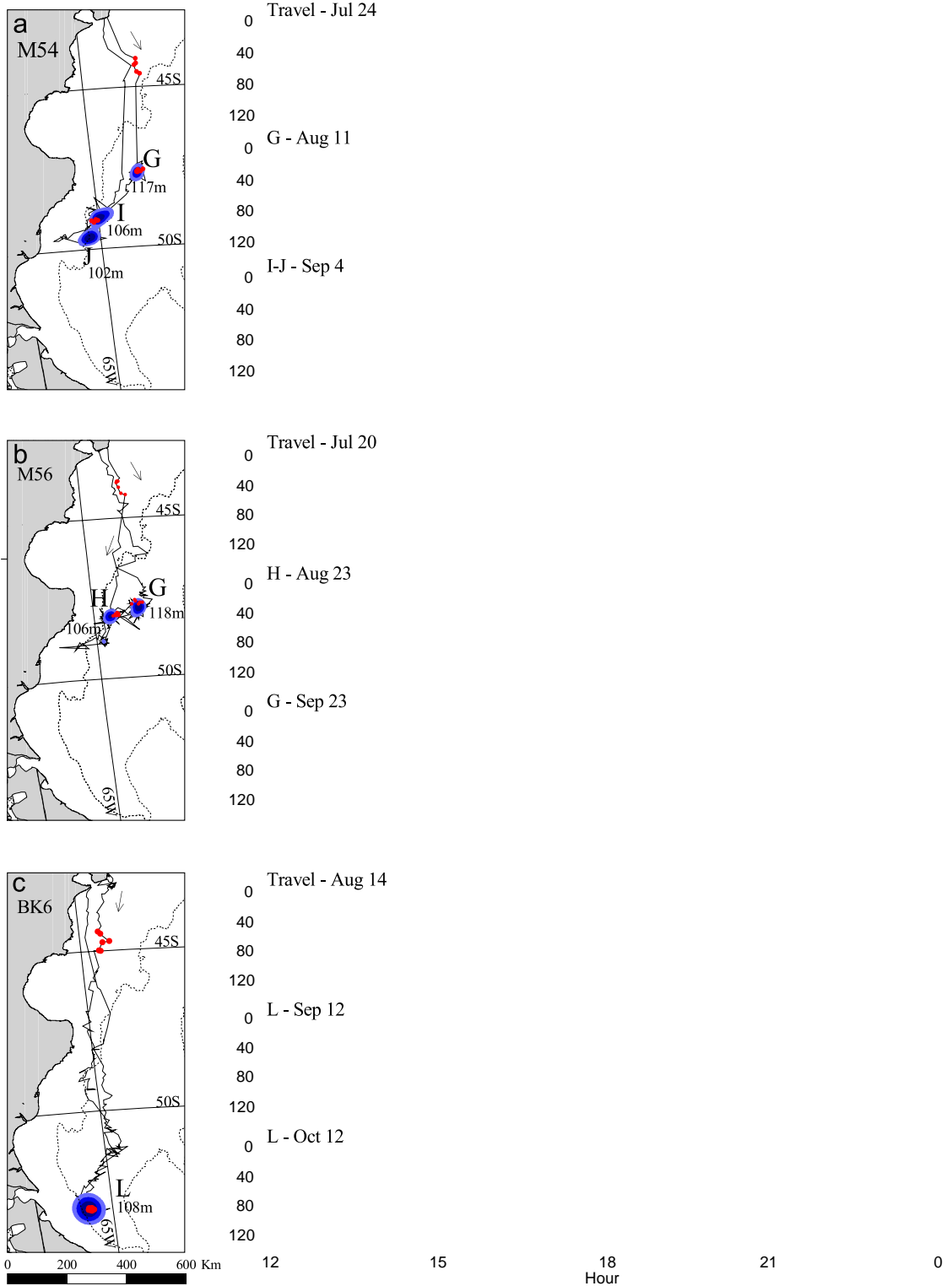


Fig. 4. Twelve-hour excerpts from the diving profiles of 3 satellite-tracked juvenile males that were also instrumented with time–depth recorders (right panels). Trajectories shown in the maps on the left (a–c) indicate the areas where dives occurred. Samples were taken from the areas shown as red dots.

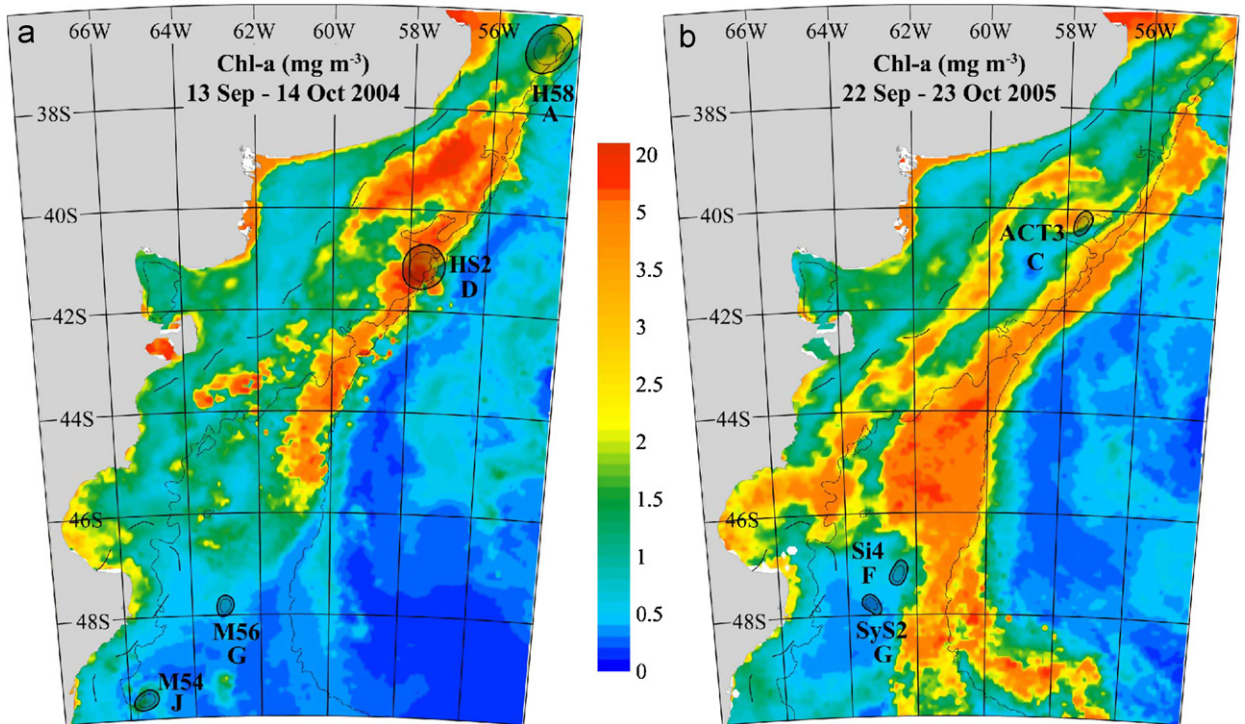


Fig. 5. Satellite-retrieved surface chlorophyll *a* from merged SeaWiFS–MODIS/Aqua averaged from 8-day binned, 9-km resolution data collected over the periods (a) 13 September–14 October 2004 and (b) 22 September–23 October 2005. Also, the areas of concentrated activity occupied by juvenile seals during each of these periods are shown.

4.2. Diving behavior on the shelf

The detailed dive record of 3 juvenile males (Fig. 4; Table 3) showed similar mean dive depths of 100–115 m, with relatively uniform dive durations that lasted 12–18 min (mean and s.d. of depth and duration for almost 16,000 dives = 1137 16 m and 157 5 min). The 2 subadult males for which some diving parameters were available also showed shallow dives, less than 60-m deep ($n = 1374$ dives). The similar trajectories and location of bouts of M54 and M56 and the different travel pattern of BK6 were reflected in the diving statistics. For example, the deepest dive was 185 m, BK6 immersion; M54 and M56 never dived deeper than 129 m. The duration of the dives of BK6 tended to be shorter than that of M54 and M56 (Table 3; 127 3 versus 16–187 4 min, respectively, $F_{2,9191} = 1557$, $p < 0.001$). The individual difference in duration was maintained when daylight dives were compared with night dives (BK6_{day} = 127 2 min; BK6_{night} = 137 4 versus M54–M56_{day} = 187 4 and M54–M56_{night} = 167 4 min).

The shape of ~60% of the dives indicated benthic swimming (type E dives according to Crocker et al.,

1994; see their Figure 18.1). No diel variation was found in depths for E dives (Table 3). The comparison of the diving depths with bottom depth further supports the inference that these seals dived benthically or to depths within a few meters from the bottom. Between 99 and 393 records of bottom depth were available (Palma et al., 2004) that correspond to the travel trajectory of the 5 seals for which diving data were recorded. Comparison of maximum depth per dive and bottom depth yielded that 4 seals (LUCA being the exception) dived a mean of 3–9 m deeper than the bathymetric records. When comparisons were restricted to focal bouts (75% kernels were used in this instance for comparative purposes) mean maximum dive depth for dives in the bout were within the range of the bottom depth 7 –20 to 1 m (negative = dive record deeper than bathymetric record). Dives attributed to traveling phases were similar in shape and profile to those occurring within focal bouts (Fig. 4; Table 3).

The second most common dive pattern after E dives were the D dives ($n = 1476$), with a ragged bottom, indicating depth changes within relatively small ranges. Type D dives were identical to E in

depth and duration, the only exception being dive depth of BK6 in transit between bouts (1187 19 m, $n = 317$ for daylight versus 1077 27 m, $n = 95$ for night dives; Mann–Whitney U test, $Z = -3.55$, $p < 0.001$). The rest of the sample ($n = 4478$) were dives of variable profiles (Le Boeuf and Laws, 1994) with no particular feature that differentiates them from the benthic immersions.

4.3. Physical oceanography

4.3.1. Surface temperature and productivity of putative foraging areas

Seasonal variability of SST and productivity patterns were similar between study years. Juvenile females located near the shelf break during the spring encountered waters of SST ranging between 7 and 11 °C (Table 2). By November, the cold water core of the Malvinas Current warmed to SST 4–10 °C and increased beyond 14 °C in early December. In September, SST in the region occupied by most male seals (~48°S) was ~7 °C, close to the lowest winter surface temperature. It began increasing in October and reached ~11 °C in late November. Further south, near the focal area of BK6, SST was 6 °C until late September, and increased to 8.5 °C in late November.

The chl-*a* distributions in early austral spring 2004 and 2005 illustrated the location of the most productive waters in terms of phytoplankton abundance during part of the foraging trips of the studied seals (Fig. 5). In September 2004, the chl-*a* blooms first developed in the mid-shelf and outer shelf regions north of 41°S (Fig. 5a). By October the shelf-break bloom extended southward from 40°S to 50°S, and bands of high chlorophyll developed in the mid-shelf region at that latitude. Both features persisted through November. In 2005 the spring bloom began over the shelf break from 37°S to 46°S and was particularly strong near 46°S, where it also occupied a wider region than in 2004 (Fig. 5). Elongated and patchy blooms, characteristic of the mid-shelf region, developed in October 2005 (Fig. 5b) and reached the southern shelf in November. By that time, north of about 42°S, only the shelf-break front remained highly productive.

4.3.2. Vertical hydrographic structure of putative foraging areas in October 2005

Preferred location of juvenile females at the shelf break, near 41°S (Fig. 1b), had a vertical structure characterized by a two-layer stratification: a shallow

(20 m), warm-fresh and high-fluorescence mixed layer, and a near-bottom layer (60 m to bottom), with an incipient thermocline, halocline and pycnocline in between (Fig. 6a). The high-fluorescence upper layer was associated with the high-chl-*a* waters revealed by the satellite image (Fig. 5b); both data sets suggested a relatively high phytoplankton concentration in the upper layer. The bottom layer was relatively cold-salty, suggesting the intrusion of slope water (Fig. 6a), and presented low fluorescence.

The mid-shelf vertical structure near 48°S, where males were concentrated (Fig. 1b), presented a quasi-homogeneous water column, with weak temperature and salinity stratification and moderate fluorescence in the upper 60 m of the water column. At that depth a slight salinity increase and fluorescence decrease are observed (Fig. 6b). The hydrographic data collected in October 2005 showed surface-to-bottom density differences $< 0.1 \text{ kg/m}^3$, associated with a temperature decrease of $< 0.4 \text{ °C}$ and salinity increase of ~ 0.04 (Fig. 6b). The quasi-homogeneity of the water column was typical of the late winter and early spring situation in the southern Patagonian continental shelf. Further south, near the region of concentrated activity of BK6, the water column was virtually homogeneous and of low fluorescence (Fig. 6c).

4.4. Seal trajectories associated with focal regimes

Fig. 5 integrates individual 50% kernels with the averaged chl-*a* concentration based on available 8-day binned data for 2004 and 2005. For each year, Fig. 5 displays seal positioning and chl-*a* data averaged over a 30-day period, selected to display as many kernels as possible and to highlight the mean chlorophyll distribution at that time.

4.4.1. Females

Three female seals spent most of their time at sea during the spring, near the productive shelf break (areas A–D in Figs. 1b and 3). Travel from the colony to these regions took about 21–40 days, at a mean speed of 757 21 km/day (Table 1). HS2 swam southward to a near-coastal region and then to the outer shelf, where she spent 37 days in an area ~100 km wide, located about 28 km inshore from the 200-m isobath (D in Fig. 3). The region was characterized by high levels of chl *a*, $\sim 8 \text{ mg/m}^3$ (Fig. 5a and Table 2). H58 also swam to the outer shelf, where she remained in a focal area

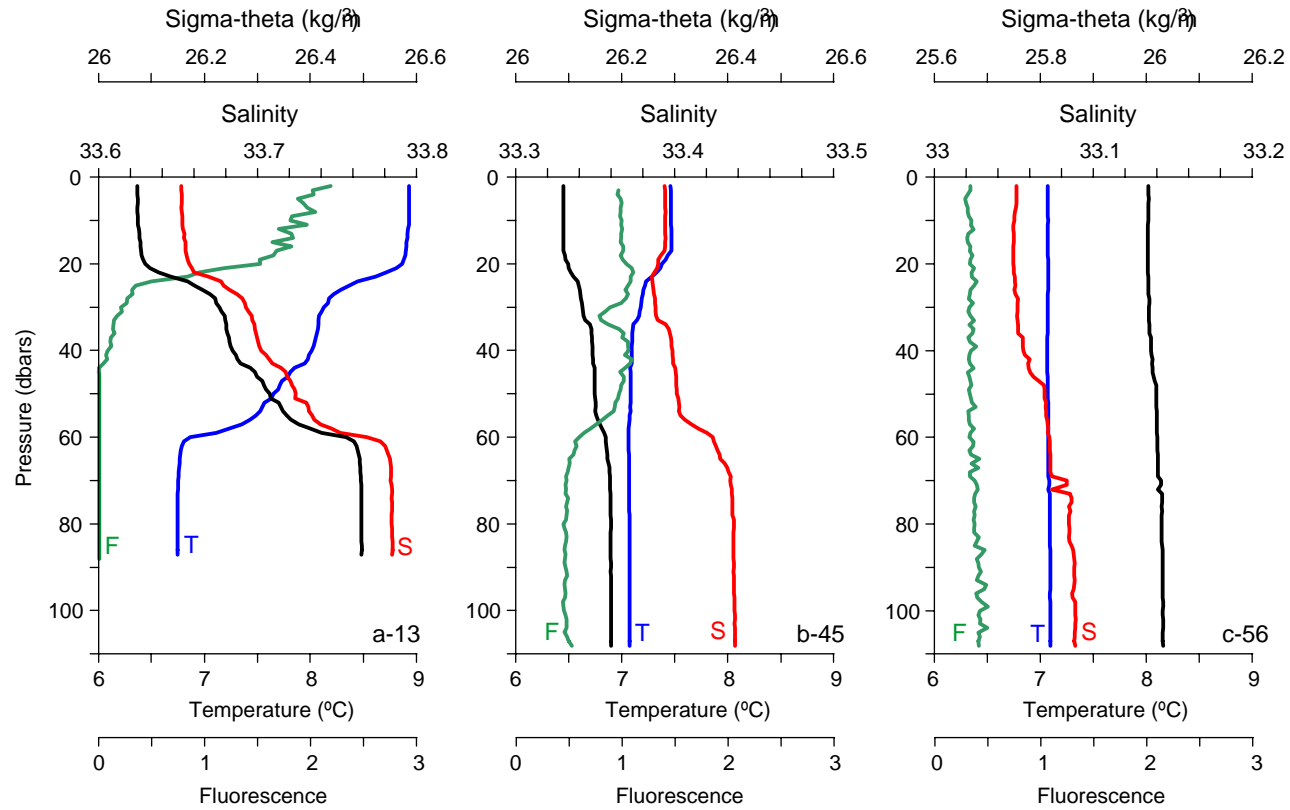


Fig. 6. Vertical profiles of temperature (T in $^{\circ}\text{C}$, blue), salinity (S , red), density anomaly (s in kg/m^3 , black) and fluorescence (F in arbitrary units, green) observed at stations (a) 13, (b) 45 and (c) 56 in October 2005. See Fig. 1b for station locations.

about 100 km wide located 40 km inshore from the shelf break (A in Fig. 3). H58 remained close to the 100-m isobath and the productive shelf-break waters, although in a relatively low-productivity area at the time of her trip ($<2 \text{ mg/m}^3$; Fig. 5a and Table 2). In late winter 2005, ACT3 swam north-eastward to the outer shelf, where she remained near 40°S , about 100 km north of the area occupied by HS2 in 2004 (areas C and B in Fig. 3). She stayed about 25 and 17 days in two focal areas (B and C) inshore from the 200-m isobath. Both regions contained relatively high chl-*a* and, presumably, high phytoplankton concentrations (Fig. 5b; Table 2). *In situ* fluorescence data collected in October 2005 also suggested that the productive waters in this outer shelf region extend throughout the mixed layer, to about 20 m, while deeper in the water column productivity decreased sharply (Fig. 6a).

4.4.2. Males

The region of highest male concentration, near $46\text{--}48^\circ\text{S}$ during the springs of 2004 and 2005, was characterized by bottom depths of 105–120 m (areas F–J in Figs. 1b and 2b–e) and relatively cold ($7\text{--}8^\circ\text{C}$; Table 2), low-salinity (~ 33.3) mid-shelf waters, with a poorly stratified water column (Fig. 6b). Some relatively well-defined regions were used by male seals in different seasons. In spring 2004, M56 occupied a small region of about 20-km radius in the mid-shelf near $47^\circ 40'\text{S}$ (area G, Figs. 2c and 5a). The same spot had also been occupied by M54 in early August 2004 (Fig. 2b) and was visited by SyS2 in spring 2005 (Figs. 2e and 5b). The combined region of six focal bouts F–J (Fig. 1b) occupied by juvenile males M54 and M56 in 2004 and S14 and SyS2 in 2005 forms a 390-km elongated strip located in the mid-shelf region (Fig. 1b). BK6 traveled further south than the rest of the males, reaching up to 53°S (area L in Fig. 2f). His core period at sea coincided with a spot of particularly low chl-*a* concentration ($\sim 0.4 \text{ mg/m}^3$) surrounded by slightly richer waters (chl *a* $\sim 0.6 \text{ mg/m}^3$, not shown). Only in November, when he began his return trip back to the colony, did BK6 encounter waters with abundant phytoplankton.

5. Discussion

The deepest diver among pinnipeds is capable of an alternative foraging behavior that contrasts in critical components with the typical pattern for the species. Young males, but also some subadult males

and juvenile females, spend months at sea over shallow ocean bottoms that force shallow, benthic dives, with no diel pattern. Animals spend weeks in localized patches often associated with specific physical features of the mid-shelf region, such as thermal fronts or seasonal changes in the patterns of vertical stratification. Travel rate decreases in these areas of concentrated activity (Le Boeuf et al., 2000). However, these regions of focal relevance may not be linked to high phytoplankton concentration at the time seals exploit them. This is despite the predictable location and seasonality of the shelf fronts and their associated productivity (see Romero et al., 2006). The link between productivity of the benthic community and chl *a* is poorly understood, and benthic feeding may decouple the seal distribution within the foraging area from surface productivity indicators at a coarse scale.

Because of the proximity of the shallow Patagonian shelf, elephant seals from Península Valdés offered the opportunity to test the prediction that, given productive foraging grounds close to a colony, animals will remain near the breeding and molting areas, despite the fact that coastal habitats may differ in physical profile from the more typical foraging areas of the species. However, instrumented adults from Valdés yielded a travel and diving pattern similar to animals from oceanic colonies surrounded by relatively narrow shelves (Campagna et al., 1998, 1999). Adults used the continental shelf only in transit to other habitats in deeper waters (green dots in Fig. 1a). Males tend to restrict their movements to the shelf-break front, while young and adult females are more distant travelers that spread in at least three ocean regimes, subtropical, mixed subtropical and subpolar. Regarding younger age categories, a small proportion of the population, perhaps restricted to juvenile females, may exploit ephemeral features on the offshore transitions, such as the eddies and meanders of the mixed waters of the Brazil–Malvinas Confluence, as observed by Campagna et al. (2006). In that study, a fine-scale association was found between the behavior of young females and the localized gradients in sea surface temperature, created at the convergence of the Brazil and Malvinas Currents and associated eddy fields (the semicircular patterns of green dots shown in Fig. 1a in the quadrant between 40°S and 45°S and 50°W and 55°W correspond to the latter animals).

In summary, prior to the results presented in this study, it seemed that the reliable bathymetric

features of one of the most extended and productive continental plateaus in the world were less attractive to foraging elephant seals than even ephemeral temperature fronts driven by the circulation. The latter generalization still holds for most of the population, but this study shows that at least a proportion of the juvenile classes, with a slight bias towards the young males, does use the shelf during all or most of their long foraging phases.

Some benefits derived from shelf foraging could be related to shorter travel distances and to food availability. Maximum distances from Península Valdés for seals that remain on the Patagonian shelf (excludes FAR11 in Table 1) range between 337 and 1150 km. Eight of 10 animals in the former group traveled ca. 800 km or less from the departing rookery, among the shortest recorded distances. Conversely, mean maximum distance for juveniles that associate to transient mesoscale features of the SW Atlantic is 1300 km (Campagna et al., 2006); it ranges between 600 and 1300 km for adult males that forage along the edge of the continental shelf, and 800 and 1800 km for adult females that travel to the Argentine Basin (Campagna et al., 1995, 1998). Maximum travel distances from the rookery of more than 2000 km are not unusual for 2–3 year-old juveniles (unpublished data; see: www.sea-sky.org). If shelf seals forage benthically, the vertical distance traveled to the bottom of each dive is much shorter than that for the average dive of a pelagic animal, thus shortening enormously the in-transit component of a foraging trip. These advantages should impact the energy expenditure while foraging, but we lack the data to test this hypothesis. All shelf seals gained mass during a trip at an estimated rate of 8–30% increase in their departure weight. The increase is, however, similar to non-shelf foragers and represents only a rough estimate based on length and girth.

Regarding availability of food, the shelf is a productive habitat that sustains other pinniped populations, such as the South American sea lion, *Otaria flavescens* (e.g., Koen Alonso et al., 2000; Campagna et al., 2001), many species of coastal and pelagic birds that reproduce locally (e.g., Yorio et al., 1998; Forero et al., 2002; Wilson et al., 2005) and pelagic bird and marine mammal visitors from distant places (Croxall and Wood, 2002). Likewise, commercial fisheries target several of the biomass-rich fish and cephalopod species of the shelf and slope (Bezzi et al., 2000; Rodhouse et al., 2001). The difference between elephant seals, other vertebrate

predators and most shelf fisheries is that seals typically forage deeper than the rest of the shelf users.

Continental shelf habitats are dependent on depth, tidal energy and winds and are highly seasonal in vertical stratification (e.g., Rivas and Piola, 2002). The shelf slopes gently towards deep waters, and bottoms are mostly gravel and sands (Parker et al., 1997). Therefore, the dominant habitats are the coastal waters, the benthic system, the seasonally stratified water column and the tidal fronts. Data suggest that although all these habitats are used by seals, the benthic habitats of the shelf may be the critical environments for shelf seal users.

5.1. Productivity and patches of concentrated activity

The distribution at sea of adult female elephant seals from Macquarie Island in relation to the physical profile at a broad scale of the surface waters may not capture the oceanographic pattern at depth, most relevant for a deep diver (Bradshaw et al., 2004a). This study provides a high-resolution profile of the physical oceanography of the water column for some of the critical areas of concentrated activity. However, our understanding of benefits from foraging on relatively exceptional habitats such as a shallow shelf is limited by the poorly known relationship between benthic and surface productivity.

The central and southern Patagonian continental shelf does not present sharp fronts in late winter and spring, when focal seals are in the area. The region is characterized by relatively cold, low-salinity waters, and even the subtle thermal fronts that develop near shore from late spring to late summer are not apparent earlier in the season. Males visiting this part of the shelf encounter rather homogeneous waters in the horizontal and also in the vertical. Despite that, the overall mid-shelf region visited by males in late winter and spring 2004 seems to closely match the region visited in 2005, suggesting that there might be semi-permanent features making the area attractive to them and suitable for foraging.

The mid-shelf sites where focal bouts occurred for M54 and M56 in spring 2004 overlapped with those for SI4 and SyS2 in 2005 (Fig. 5). These sites are located about 100–120 km east of a quasi-continuous tidal front that extends northeastward, towards the outer shelf (Bianchi et al., 2005). Although, as suggested by the chl-*a* distributions, these mid-shelf waters are very productive from late

austral spring to mid-summer (Romero et al., 2006), phytoplankton abundance was low in the early spring (Fig. 5). In October–November 2004, for instance, relatively productive waters are found east of the region of high male concentration, closer to the shelf-break front (Fig. 5a). Similarly, in early spring 2005, most locations fall outside of, but close to, regions of high satellite-derived surface chlorophyll (Fig. 5b). Only in November 2005 there seemed to be an association between male locations and regions of high chl *a* (not shown). At that time, SyS2 and SI4 were already traveling back northward on their way to the colony within regions of chl *a* 4–4 mg/m³, but their travel pattern did not reveal any change in behavior when traversing these productive regions.

The diving pattern was also similar during the relatively fast journey to and within the focal bouts, where seals spend weeks at a time. Comparison of maximum depth per dive and bottom depth (from Palma et al., 2004) for the entire trajectory and within areas of concentrated activity (bouts) for seals instrumented with a time–depth recorder indicates that the seals of this study dived to or within a few meters of the bottom. This observation confirms that, in this case, type E dives suggest bottom foraging. Reports of type E dives occurring in waters deeper than the diving capacity of a seal indicate that square-shaped dives could also represent feeding at a preferred depth rather than benthically (Stewart and DeLong, 1994; Bailleul et al., 2007). Conversely, diving versus bottom depth comparisons revealed that some dives are to depths several meters greater than the estimated mean bottom depth for the area. This apparent inconsistency may be due to errors in the pressure sensor, in the bathymetry data or in the location. Recorded depths vary considerably within focal bouts. For instance, bottom depth in area G varies between 95 and 138 m. Thus, it is also possible that seals are diving into relatively small-scale topographic depressions. As some of the selected sites were visited by more than one seal and in different years (Table 2), it may be possible that benthic bouts, at times perhaps within relative depressions, occur where prey might be more abundant.

5.2. Prey

Elephant seals are generalists that prey on different species of fish and squid and have a diet that may change seasonally (Daneri and Carlini,

2002; Bradshaw et al., 2003). Diet data of adult animals from Península Valdés based on stable C and N isotopes suggest sex differences, with female preying lower in the food web and foraging apparently on pelagic cephalopods (Lewis R et al., 2006). Cephalopod species known to be part of the diet of the elephant seals of South Georgia (Rodhouse et al., 1992a) are also present in the focal area in the Argentine Basin (Rodhouse et al., 1992b).

The shelf-slope and shelf-break fronts are areas rich in zooplankton, small pelagic fish and squid (see Acha et al., 2004). Juvenile females may then be feeding on species concentrating around these upper-ocean high-chlorophyll patches. Benthic species are also abundant around the shelf-break front (e.g., Lasta and Bremec, 1998; Bogazzi et al., 2005); thus females may also be taking advantage of patches of benthic organisms concentrating at the outer shelf.

Some of the mid-shelf sites where male elephant seals dive to the near-bottom layer are close to regions where the highest concentrations of scallop *Chlamys patagonica* have been reported (Waloszek and Waloszek, 1986). These same regions also present relatively abundant demersal species, which might be part of the seals' diet, such as king-clip (*Genypterus blacodes*; Cordo, 2004), skate (*Dipturus chilensis*; García de la Rosa et al., 2004) and hoki (*Macruronus magellanicus*; Giussi et al., 2004). Though at the times of seal occupation the mid-shelf focal bouts are not particularly productive in terms of chl *a* (Table 2), all the selected regions are highly productive later in the season (see Romero et al., 2006, their Figure 3). Significant phytoplankton abundance at other times may therefore sustain the benthic or demersal communities from which the elephant seals feed in late winter and early spring.

5.3. Comparative remarks

5.3.1. Users of the Patagonian shelf

The shelf is a biodiversity and biomass-rich ocean. Different oceanographic regimes (e.g., Guerrero and Piola 1997; Bianchi et al., 2005) create suitable and productive habitats that sustain a diverse community of pelagic, resident top predators, in addition to seasonal migrants coming from Antarctica, South Georgia and even New Zealand (Croxall and Wood, 2002). Magellanic penguins, *Spheniscus magellanicus*, are one of the most widely distributed species along coastal Patagonia and the

Malvinas (Falkland) Islands (Yorio et al., 1998; Gandini et al., 1994; Wilson et al., 2005). Tracked animals from different colonies along the Atlantic distribution range (e.g., Boersma et al., 2002; Pütz et al., 2002; Wilson et al., 2005), as well as stable-isotope analysis (Forero et al., 2002), indicate a strong dependency of the Magellanics on shelf resources, particularly anchovy, *Engraulis anchoita*, and sprat, *Sprattus fuegensis*. Other penguins are also shelf foragers, such as gentoos, *Pygoscelis papua*, rockhoppers, *Eudiptes chrysocome*, and kings, *Aptenodytes patagonicus* (Boersma et al., 2002; Pütz and Cherel, 2005; Pütz et al., 2006). At least three species of pinnipeds exploit the shelf, the South American sea lion, *O. flavescens* (e.g., Reyes et al., 1999; Koen Alonso et al., 2000; Campagna et al., 2001), the South American fur seal, *Arctocephalus australis*, and the Antarctic fur seal, *Arctocephalus gazella* (Stainland and Boyd, 2003). The first two species are local breeders and the Antarctic fur seal visits from South Georgia during the austral winter. Several coastal and pelagic cetaceans, some endemic to the Patagonian shelf and a few other places of the southern hemisphere oceans, depend on shelf resources (e.g., Schiavini et al., 1999; Croxall and Wood, 2002; Bastida and Rodriguez, 2005). Finally, at least six species of petrels and albatrosses are annual or seasonal users of shelf habitats (e.g., Nicholls et al., 2002; Quintana and Dell’Arciprete, 2002; BirdLife International, 2004). Besides birds and marine mammals, the biomass richness of the shelf in fish and cephalopod species (e.g., Figueroa et al., 1998; Cousseau and Perrota, 2000; Eder and Lewis, 2005) sustains large-scale, international, commercial fisheries (e.g., Bezzi et al., 2000; Rodhouse et al., 2001). These fisheries target species known to be prey items for many shelf top predators (e.g., Crespo et al., 1997). It is then possible that a relatively small population of a generalist, such as the elephant seals of Península Valdés (Lewis R et al., 2006), can be easily sustained by the resources of the shelf. However, shelf users will share foraging areas with many other species, some of which may be potential competitors. Conversely, the deep-diving seals, such as the adult females, that distribute in the high seas of the Argentine Basin foraging on mesopelagic, vertically migrating prey, or adult males that forage benthically, perhaps in the canyons of the shelf slope, are likely to deal with small number of other predators, and very likely with no important competitors.

5.3.2. Shelf users among elephant seals

Elephant-seal colonies rarely have extended and shallow (ca. 100 m) shelves in their vicinity. Northern elephant seals breeding along the coast of Baja and Central California face a narrow continental shelf, often ranging only a few km up to the 200-m isobath (~7 km for Isla Guadalupe; ~27 km for Año Nuevo). Deep waters surround all major sub-Antarctic islands where the largest colonies occur. The 200-m isobath, the approximate eastern limit of the Patagonian shelf, is located at 400–700 km off the coast of Patagonia, while it is only at 20–50 km off the coast of South Georgia, the largest population of the species in the world, and within 10–100 km for most other colonies (e.g., Kerguelen, Macquarie, King George, Nelson). The continental shelf of the Antarctic Peninsula is, after the Patagonian shelf, one of the most extensive within the range of distribution of the southern species, yet the 200-m isobath is only at 9–50 km from King George and Nelson Islands; the water then abruptly deepens to 1000 m or more.

It is therefore not surprising that reports of entire trips spent on shallow shelves are rare. Satellite-tracked seals from South Georgia, the largest of the southern elephant-seal population, show that adult females travel either to deep waters off the island or to the Antarctic continental shelf and slope (McConnell et al., 1992; Bennett et al., 2001). One satellite-tracked adult female traveled to the Patagonian shelf, to an area about 800 km southeast of Península Valdés, and then moved to the shelf of the Antarctic Peninsula. Her diving behavior reflected shallow-water feeding and epi-benthic dives affected by seafloor topography. The same female, however, also traveled and dived in deeper waters, along the margins and off the Antarctic Peninsula. Three post-breeding, adult females were likewise reported to visit the continental shelf of the Antarctic Peninsula, remaining close to the margin or diving to the sea bed of the shelf, usually deeper than 200 m (McConnell et al., 1992). Conversely, satellite-tracked adult males remained 5 months in shallow waters around South Georgia and over the shelf break (Bennett et al., 2001). Deep diving was common in all the animals visiting or spending part of their foraging trips on shelves. The use of the Antarctic continental shelf by adult males, and occasionally by females, was also reported for seals that belonged to the Macquarie (Hindell et al., 1991a, b) and Iles Kerguelen populations (Bailleul et al., 2007). The recent study of seals from

Kerguelen found that juvenile males travel to the Antarctic shelf and remain there during the winter, diving on the plateau to mean depths ranging between 311 and 434 m (Bailleul et al., 2007). Finally, one juvenile male from King George Island was last located on the Patagonian shelf, about 55°S (Bornemann et al., 2000), but this seems to be a rather unusual trip for juveniles from that colony.

5.3.3. Dive pattern

The topography of foraging areas affects the diving profile as well as the vertical distribution of prey (e.g., Bennett et al., 2001). When elephant seals travel over waters of thousands of meters, typical for adult females, foraging occurs in mid-water habitats, and the dive pattern is unlikely to be determined by the bottom of the ocean. But seals traveling on shelf areas have at least the vertical dimension of their dives limited by the bathymetry.

One aspect of diving behavior that integrates physical and biological variables is the diel pattern in dive depth and duration, associated with vertical migration of prey. A diel component of the diving behavior was reported for elephant seals and other seal species (e.g., references in Hindell et al., 1991a, 1999; Jonker and Bester, 1994; Le Boeuf et al., 2000; Bennett et al., 2001). A study of diurnal variation of dives for seals that foraged over the open ocean and shallow areas of the Antarctic shelf showed that mesopelagic foragers display greater daily changes in dive duration and depth than individuals diving on a shelf, with deeper and longer dives occurring during the daylight hours (Bennett et al., 2001). But seals diving over shallow waters are likely to be foraging benthically and thus would not follow prey vertical migrations.

Our results restricted to U-shaped dives from the 3 animals for which we have diving data do not support a well-defined, constant diel pattern. The 2 juvenile males that traveled to similar areas of the mid-shelf (M54 and M56; Figs. 2b–c and 4a–b) also share a diving pattern of mostly flat-bottomed dives of similar mean duration and depth (Table 3). The third male for which diving was recorded simultaneously with travel trajectories (BK6; Figs. 2f and 4c) moved further south to a different shelf area. It is clear from the diving statistics (Table 3 and descriptive data in Results) that the pattern of BK6 was slightly different in the duration of dives and depths, consistent with different trajectories and

location of bouts of activity. An interesting additional difference between these individuals occurred in the relative position of the body at the bottom of dives. The time–depth recorder of these seals had a sensor sensitive to relative body position referenced to the horizontal and vertical axes (pitch and roll; Campagna, Wilson and Dignani, unpublished data). Preliminary results based on body position indicate that M54 and M56 swam head down, at an angle of about -20° from an imaginary horizontal bottom. Conversely, BK6 remained almost horizontal. BK6 could have been searching for prey items that remained at or close to the bottom but that were movable rather than buried in soft sediment, while M54 and M56 may have actually been searching for sessile prey, compatible with the rich scallop communities reported for some of the shelf areas (Waloszek and Waloszek, 1986).

5.3.4. Site fidelity

Fidelity to foraging sites provides the opportunity of achieving longitudinal information on both oceanographic data that may otherwise not be accessible (e.g., McMahon et al., 2005b) and the correspondence of the hydrographic environment with animal behavior. The use of similar sites in consecutive years, as reported for M54, M56, S14 and SyS2 (Fig. 5), has been described for adult southern elephant-seal females from Macquarie Island (Bradshaw et al., 2004b) and, to a lesser extent, South Georgia (Bennett et al., 2001). Bradshaw et al. (2004b) argue that fidelity to a site may be beneficial if the productivity of the preferred areas remains differentially high and predictable over the life span of the individual. The constant location of topographically controlled fronts, such as the tidal and shelf-break fronts, would provide the required long-term predictability to sustain site fidelity behaviors, and adult males from Peninsula Valdés seem to benefit from that (Campagna et al., 1999). But understanding the benefits for seals using the same localized bottom area during consecutive seasons, even at times when surface productivity over these zones is low, must await further studies of the spatial correspondence between benthic productivity and ocean fronts (e.g., Bogazzi et al., 2005).

5.3.5. Resource partitioning

Temporal and spatial segregation of foraging areas by age and sex and sex-specific foraging strategies have been reported for both the northern elephant seal (e.g., Stewart and DeLong, 1994; Le

Boeuf et al., 2000) and its southern counterpart (e.g., Hindell et al., 1991b; Field et al., 2005; Lewis R et al., 2006). Temporal and spatial segregation related to age is already evident among the ages of 1–4 years, with younger seals remaining closer to the colony than older animals (Field et al., 2005). Sexual segregation of foraging areas has been reported for adults of both species (e.g., Hindell et al., 1991b; Campagna et al., 1998, 1999; Le Boeuf et al., 2000; Stewart and DeLong, 1994) and for juveniles as young as 2–4 years old (Stewart, 1997; Campagna et al., 2006, and unpublished data) but not for naïve pups (McConnell et al., 2002). Studies assessing diet based on C and N isotope ratios for the Patagonian population of seals suggest that males may differ from females in prey choice and trophic level, with males foraging in broader levels than females (Lewis R et al., 2006). This study also supports an age and sex difference in the foraging pattern, as at least a proportion of the young juvenile males differ from adults of both sexes and from juvenile females in the distribution at sea. This segregation is robust for the mid-shelf areas, as shelf-user females forage close to the continental slope, resembling adult males and some adult females. Sexual dimorphism at the early age of the focal juvenile seals of this study is barely apparent in length, girth and secondary sexual characters (Table 1), but sexual differentiation would soon start being more evident, with pubescent males depending on more energy to cope with differential growth rates. At this stage, the shelf does not seem to be as reliable as the slope to sustain energetic demands with enough food availability. Males would then tend to switch from shelf users to deep-water divers, although they may continue to be benthic foragers, as suggested by the diving record of adult individuals (Campagna et al., 1999).

In summary, foraging elephant seals from Península Valdés have several habitat choices, ranging, in the Atlantic, from the coastal waters to the shallow Patagonian shelf and the deep Argentine Basin. Adult and juvenile females tend to travel away from the colony into deep waters, to forage in the water column, and to exploit even ephemeral temperature fronts that depend on the major currents of the SW Atlantic. Others remain along the continental slope, and a few travel to the South Pacific, in both deep and more coastal waters. Males are less regional, travel shorter distances and remain on the shelf when young and along the margin when adults. Subadult males are a critical category in terms of

increase in energy demands due to differential growth. They are expected to act as indicators of the system that can cope with their food requirements. The productivity of the water masses under the influence of the shelf-break front would support differential growth better than other habitats. Larger energetic requirements per unit time would prevent mature and even pubescent males from the erratic and distant trips of some juveniles. The time to be explorers would be restricted to young age and in some degree to females. The distant travel of females would be explained by competition avoidance. It is unlikely that coastal environments will be of preference for any age or sex category, except perhaps for recently weaned pups in their first trip to sea. Their behavior is unknown for the Valdés population, but work from other places indicates that these very young age classes have physiological limitations, particularly during the first months at sea, that may restrict their feeding to depth of 100–300 m (Hindell et al., 1999). Therefore, behavioral choices linked to resource partitioning in a context of seasonal frontal systems that are strongly tied to bathymetry thus are predictable in place and time and would help explain why elephant seals from Península Valdés have been growing in numbers during several decades while other colonies were stable or decreasing.

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