

Southern elephant seal trajectories, fronts and eddies in the Brazil/Malvinas Confluence

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Abstract

This study describes the association between transient, mesoscale hydrographic features along the axis of the Brazil–Malvinas Confluence, in the SW Atlantic, and the foraging behavior of 2–3-year-old (focal) juvenile southern elephant seals, *Mirounga leonina*, from Península Valdés, Argentina. Departing from the dominant pattern of foraging on predictable bathymetric fronts on the Patagonian shelf and slope, three females out of 12 satellite-tracked juveniles remained at the edge of young warm-core eddies and near the outer core of cold-core eddies, coinciding with the most productive areas of these temperature fronts. Seal trajectories along high-temperature gradients were always consistent with the speed and direction of surface currents inferred from the temperature distribution and confirmed by surface drifters. Movements of foraging seals were compared with those of surface drifters, coinciding in time and space and yielding independent and consistent data on regional water circulation parameters. The diving pattern recorded for one focal seal yielded shallower dives and a loose diel pattern in the eddy, and a marked diurnal cycle compatible with foraging on vertically migrating prey in the cold waters of the Malvinas Current. Pre-reproductive females that use the mesoscale fronts of the Argentine Basin as an alternative foraging area would benefit from lower competition with more experienced seals and with other top predators that reproduce along the coast of Patagonia.

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1. Introduction

Behavioral studies of marine vertebrates that combine satellite tracking techniques, samplers of environmental and physiological parameters and satellite remote sensing have revolutionized our view of the ocean and unraveled intricate

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associations between the physical environment, productivity and the foraging ecology and energetics of diving and migrating top predators (e.g., Bost et al., 1997; Le Boeuf et al., 2000; Boehlert et al., 2001; Field et al., 2001; Polovina et al., 2004; Wilson et al., 2002). Large ocean areas have been probed in situ using as cost-effective sampler stations several species of pelagic predators such as giant blue fin tuna (Block et al., 2001, 2005), several species of penguins (e.g., Charrassin et al., 2002; Wilson et al., 2005; Sokolov et al., 2006), sea turtles (e.g., Polovina et al., 2004) and marine mammals (e.g., Boehlert et al., 2001; Davis et al., 2002; Fadely et al., 2005). Results range from detailed ocean temperature profiles at depth (e.g., Campagna et al., 2000; Boehlert et al., 2001; Boyd et al., 2001; Charrassin et al., 2002) to characterization of mesoscale features, such as eddies and meanders (e.g., Sokolov et al., 2006).

From the wide range of species involved, foraging elephant seals combine exceptionally deep diving with long-distance traveling, covering millions of square kilometers while traversing a wide range of oceanographic regions during up to 7 months at sea (e.g., Le Boeuf et al., 2000; Field et al., 2001, 2004; McConnell et al., 2002; Bradshaw et al., 2004a, b). Seals spend differential time in particular water masses that include frontal systems, currents and shifting marginal ice-edge zones (Hindell et al., 1991; McConnell et al., 1992; van den Hoff et al., 2002; Field et al., 2005). These are areas of high productivity that could attract and guide not only migrating seals, but also birds, turtles and fish (e.g., Hindell et al., 2003; Polovina et al., 2004; Sokolov et al., 2006). However, studies of foraging locations relative to frontal zones, bathymetry and ocean surface properties (sea-ice concentration, sea surface temperature (SST)) indicate that oceanographic profiles defined at coarse scales are poor predictors of elephant seal behavior (e.g., Field et al., 2001; Bradshaw et al., 2004b).

We describe a fine scale association between the distribution of near-surface water masses and the behavior of juvenile southern elephant seals, *Mirounga leonina*, from the Patagonian colony of Península Valdés, Argentina. Previous studies of this population report the typical deep and continuous diving pattern during extended trips to the edge of the Patagonian shelf (adult males) and to the Argentine Basin (adult females) in the SW Atlantic (Campagna et al., 1995, 1998, 1999, 2000). This paper focuses on the unusual finding of

juvenile seals that remained in close association with transient oceanographic features, such as warm-core and cold-core eddies, created at the convergence of the Malvinas and Brazil currents. Juvenile females may find in the mesoscale temperature fronts of the Argentine Basin alternative foraging areas where competition for food within the population and with other species of diving birds and marine mammals is reduced.

2. Methods

Satellite tags (SPOT4/SPOT5; Wildlife Computers, Redmond, Washington; instrument description at: <http://www.wildlifecomputers.com>.) were deployed with 14 pre-reproductive, 2–3-year-old juveniles during winter haul out in August 2004 and 2005 at Punta Delgada (42°45'S; 63°38'W), the southeastern tip of Península Valdés (Fig. 1; Table 1). One individual (Bon5) was also instrumented with a 16 Mbyte time–temperature–depth recorder (Driesen + Kern GmbH, www.driesen-kern.de). Samples were taken every 5 s. Mar3 was instrumented with a Light-Temperature Logger (Platypus Engineering, Australia). Because of the relatively long time response of the temperature sensors (~4.5 min) SST recorded during active diving periods in regions of strong vertical temperature gradient are generally lower than satellite-derived surface temperatures. The age of the seals was estimated based on body shape, length and secondary sexual characteristics.

Tags were configured to send information as soon as the animals entered the water, 24 h per day with repetition rates of 45 ± 6 s in 2004 and 40 ± 6 s in 2005. The estimated accuracy of each location was provided by the Argos System (<http://www.cls.fr>). The behavior of elephant seals at sea and their short surface intervals precludes high accuracy with position fixes and introduces errors in the linear interpolation between fixes (Boehlert et al., 2001; Vincent et al., 2002; Hays et al., 2001). The iterative forward/backward averaging filter proposed by McConnell et al. (1992) was applied to reject uplinks that would require an unrealistic travel rate greater than 2.8 m/s (10 km/h). To fill location gaps, the position data were then fitted with a cubic smoothing spline (de Boor, 2001). Curvilinear interpolations generally produce more realistic tracks than linear interpolation (Tremblay et al., 2006). To avoid unrealistic track overshoots in poorly sampled regions, when raw position data

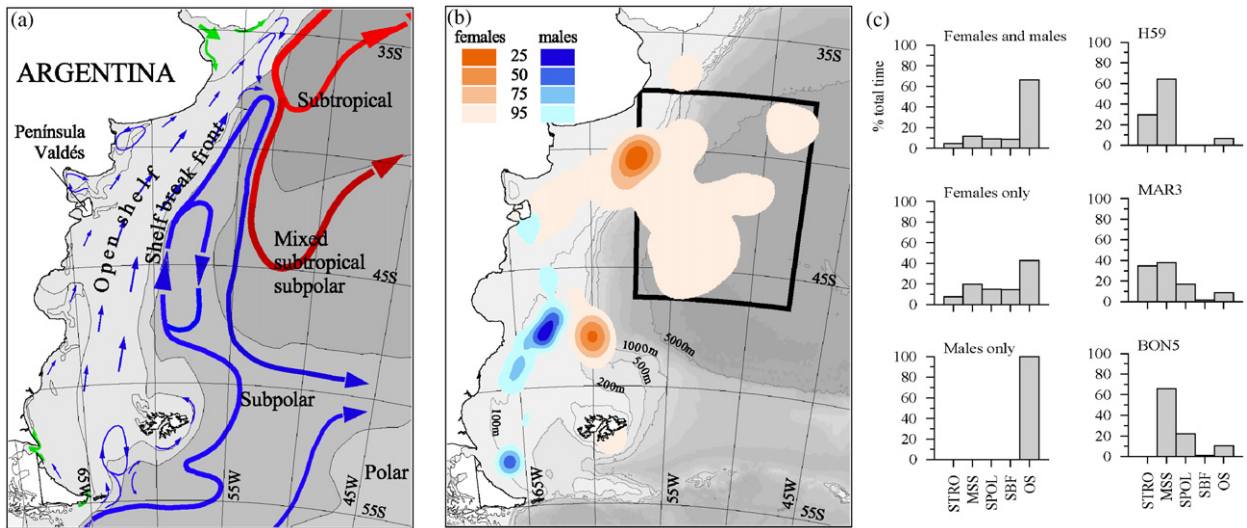


Fig. 1. (a) Major oceanographic features of the southwest Atlantic Ocean where juvenile elephant seals from Peninsula Valdés forage in late winter and spring (August–November). The 200 m isobath indicates the approximate offshore edge of the continental shelf. Shaded in gray are the relevant oceanographic regimes for the region (see description in Methods): subtropical, subpolar, open shelf, shelf break front, subtropical and mixed subtropical–subpolar (adapted from Piola and Matano, 2001; see also Rodhouse et al., 1992). 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). (b) Kernel polygons representing 25–95% of the filtered elephant seal uplinks by sex. The rectangle indicates an area within the mixed Subtropical–sub Antarctic regime that involves about 90% of the locations of focal seals and where their trajectories presumably follow the surface circulation. (c) Percent time spent in the oceanographic regime areas represented in a. STRO: subtropical, MSS: mixed subtropical subpolar, SPOL: subpolar, SBF: shelf break front, OS: open shelf.

were unavailable for periods longer than 24 h the data were discarded from the analysis. The smoothed tracks were re-sampled at 6-h intervals. No significant differences were observed between tracks interpolated based on different cubic schemes. The mean and standard deviation of the distance between ARGOS locations and closest interpolated data is 5.1 ± 4.0 km. To test if seals moving within or in the vicinity of fronts and eddies were drifting passively or were actively swimming, trajectories done at speeds lower than 1 m/s (86 km/day) were discriminated from faster ones.

Instruments were glued directly on the fur of the head using a 10-min setting epoxy resin (Campagna et al., 1999). The aerial was at a 45° angle from the longitudinal dimension of the instrument and pointed forward to allow a transmission when the animal emerged to the surface. Anesthesia protocols to deploy and recover instruments were described in Campagna et al. (1995, 1998, 1999). Seals were anesthetized with tiletamine–zolazepam (Telazol[®], Fort Dodge Animal Health, Fort Dodge, Iowa 50501, USA) administered by hand as a deep intramuscular injection in the gluteal region.

Description of the foraging trips followed previous work in grouping movements into three phases: Phase-1: dispersal, Phase-2: locations related to putative foraging areas, Phase-3: return to the colony (e.g., McConnell et al., 2002). Travel patterns were coupled with water mass distributions as reflected in satellite-derived SST maps (Sumner et al., 2003). The Austral winter is characterized by intense cloudiness that prevents SST detection of high spatial resolution. Therefore, we present 8-day, 4-km resolution SST composites from the moderate-resolution imaging spectroradiometer (MODIS) Aqua. A similar procedure (8-day, 4 km resolution MODIS data from the Aqua satellite) was adopted with near-surface phytoplankton abundance, indicated by the distribution of satellite-retrieved chlorophyll-*a* (chl-*a*) from mid-September 2005.

To refer and ease description of the ocean area where focal seals (H59, Mar3 and Bon5; Table 1) spent most of their foraging time, we selected a rectangular space of ca. 780,000 km² (Basin focal area; Fig. 1 and Fig. 2) that encompasses all the uplinks of focal animals in the Argentine Basin, together with relevant mesoscale features.

Table 1
Descriptive data of the foraging trips of three focal animals (H59, MAR3 and BON5) compared to the rest of the sampled juveniles ($n = 9$)

Season	Individual	Date deployment	Days recorded at sea	Mx distance from PV (km)	Estimated total travel distance (km)	Number of uplinks		Travel to Basin focal area		Within Basin focal area		Duration of return phase (days)	
						Total	At sea	Days	Mean (sd) swim speed (km/day)	Dates in focal area	Days (% of total trip)		Mean (sd) swim speed (km/day)
2004/2005	(n = 9) Mean Std		104.4 17.4	802 768	5748 1280	436 170	400 164						
		H59 MAR3	24-Jul 27-Jul	49 111.1	1342 1462	3780 7999	124 521	122 488	3.1 4.8	115.5 (56.5) 99.5 (42.3)	3-Aug/11-Sep 9-Aug/10-Nov	45.8 (93.7) 99.7 (89.8)	92.8 (50.5) 83.7 (52.6)
2005	BON5 Mean Std		100.4 86.8 33.2	1084 1296 193	7760 6513 2370	532 392 232	518 376 220	5.6 4.5 1.3	117.0 (75.2) 110.7 9.7	8-Aug/2-Nov	87.8 (87.5) 77.8 28.3	83.8 (51.7) 86.8 5.2	6.9 6.7 0.3
		Total	(n = 12) Mean Std	100.0 22.0	925 313	5939 1527	425 177	394 169					

Total number of animals instrumented = 14 (7 males, 7 females). Two instruments did not transmit.

A kernel technique was employed to estimate the foraging ranges of males and females separately. The ArcView GIS software with the Animal Movement extension (Alaska Science Center website: http://www.absc.usgs.gov/glba/gistools/animal_mvmt.htm) was used as the tool to obtain the 95%, 75%, 50% and 25% probability contours shown in Fig. 1.

To determine the extent to which the focal seals are drifting passively or swimming we compare some basic path statistics with those of drogued surface drifters, which have been designed to follow the upper layer currents to within ± 0.013 m/s in 10 m/s winds (see Niiler et al., 1995). The original position data have been quality controlled and optimally interpolated to uniform 6-h interval trajectories following standard procedures for surface drifter positioning (Hansen and Poulain, 1996). The data are available at NOAA's Atlantic Oceanographic and Meteorological Laboratory (AOML, <http://www.aoml.noaa.gov/phod/index.php>).

3. Oceanographic background

Focal seals traversed or used five major oceanographic regimes of the SW Atlantic (Fig. 1a). Open continental shelf waters (OS) are of subantarctic origin (Guerrero and Piola, 1997). During the spring, SST off northern Patagonia range between 6 and 10 °C. The shelf break front (SBF) is a narrow transition region between subpolar and shelf waters characterized by a moderate SST front (Saraceno et al., 2004) and frequent chl-*a* maxima in summer, resulting from the upwelling created by the Malvinas Current interaction with the bottom topography (Saraceno et al., 2005; Romero et al., 2006). Along the western boundary of the Argentine Basin the warm-salty subtropical waters (SPTRO) carried by the Brazil Current (BC) collide with the cold-fresh subpolar waters (SPOL) of the Malvinas Current near 38°S (Gordon and Greengrove, 1986). The area downstream from the separation of the western boundary currents from the continental shelf break is characterized by intense surface temperature gradients (e.g. Roden, 1986; Gordon and Greengrove, 1986; Saraceno et al., 2004), referred to as the Brazil/Malvinas Confluence (BMC).

Further downstream the BMC describes a sharp anticyclonic loop (seen near 44°S in Fig. 4a), and the flow continues northward. Hereafter we will refer to this feature as the BMC loop. Water following surface drifters reveal strong currents

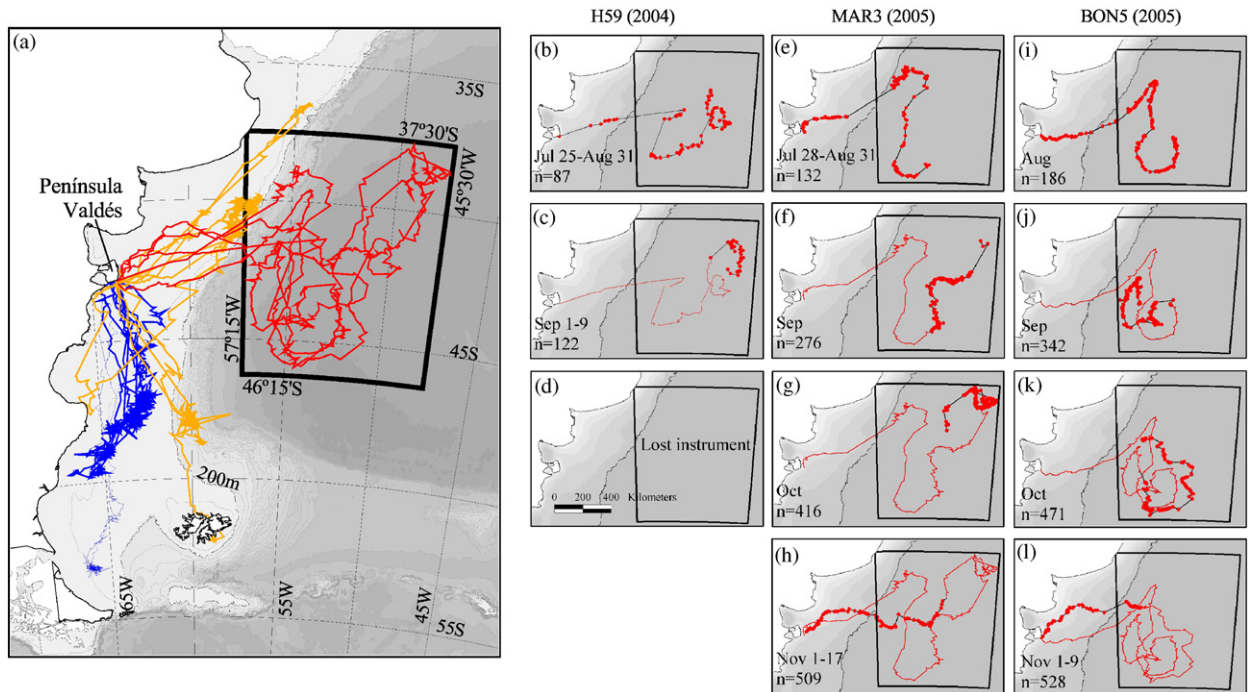


Fig. 2. (a) Travel trajectories of 12 juvenile southern elephant seals instrumented with satellite transmitters. The rectangle indicates the Basin focal area described in Fig. 1b. Blue lines are juvenile males, orange lines are non-focal juvenile females, and red lines are focal females. (b) Extracts of the foraging trips of focal individuals. The series illustrate the progression of travel in subsequent phases up to 1 month long. Red dots are uplinks for the period. Black lines indicate trajectories where location coverage was poor. Red lines are trajectories for the previous period. H59 ended transmission on 9 September, giving an incomplete record.

(> 1 m/s) along the Confluence axis (Peterson et al., 1996). The region is also associated with intense eddy activity (Gordon, 1989; Chelton et al., 1990) characterized by mixed subtropical-subpolar waters (MSS). Warm-core eddies arising from instabilities of the BC are associated with anticyclonic (anticlockwise (ACW)) rotation and cold-core eddies, associated with intrusions of subpolar waters into the subtropical domain, present cyclonic (clockwise (CW)) rotations. The eddies in the western Argentine Basin have diameters ranging from 50 to 350 km, and average around 150 km (Legeckis and Gordon, 1982; Lentini et al., 2002).

4. Results

Table 1 presents summary statistics for the three focal seals compared with the rest of the satellite tracked juveniles. Position fixes were obtained from 12 of the 14 animals (7 females, 5 males). Uplinks for the three focal animals ($n = 1177$) represented 23% of the total satellite locations ($n_{\text{tot}} = 5098$ uplinks). Focal animals had a similar distribution of ARGOS categories compared to the rest of the

sample. Classes A and B represented for the total 83% of the entire record. Fig. 1b shows the most important areas of concentrated activity compared to the major oceanographic regimes and upper layer circulation of the SW Atlantic (Fig. 1a). Fig. 2 discriminates trajectories of males and females and provides details of the behavior of the focal seals. Locations represent one foraging trip per animal, except for one individual (H59-2004) that returned to land for a few days and departed on a second trip. H59 stopped transmission after 49 days at sea, before her trip was over. Mar3 and Bon5 were tracked for their entire foraging excursion, lasting 111 and 110 days, respectively (Table 1). Fig. 3 presents satellite-derived SST-time series at the locations of each individual, which suggest that most seals were exposed to relatively homogeneous regimes compared to the focal animals.

4.1. The physical environment at the time of foraging

4.1.1. SST

Fig. 4a–c depicts the thermal fields around the BMC, where the three focal seals spent 90% of their

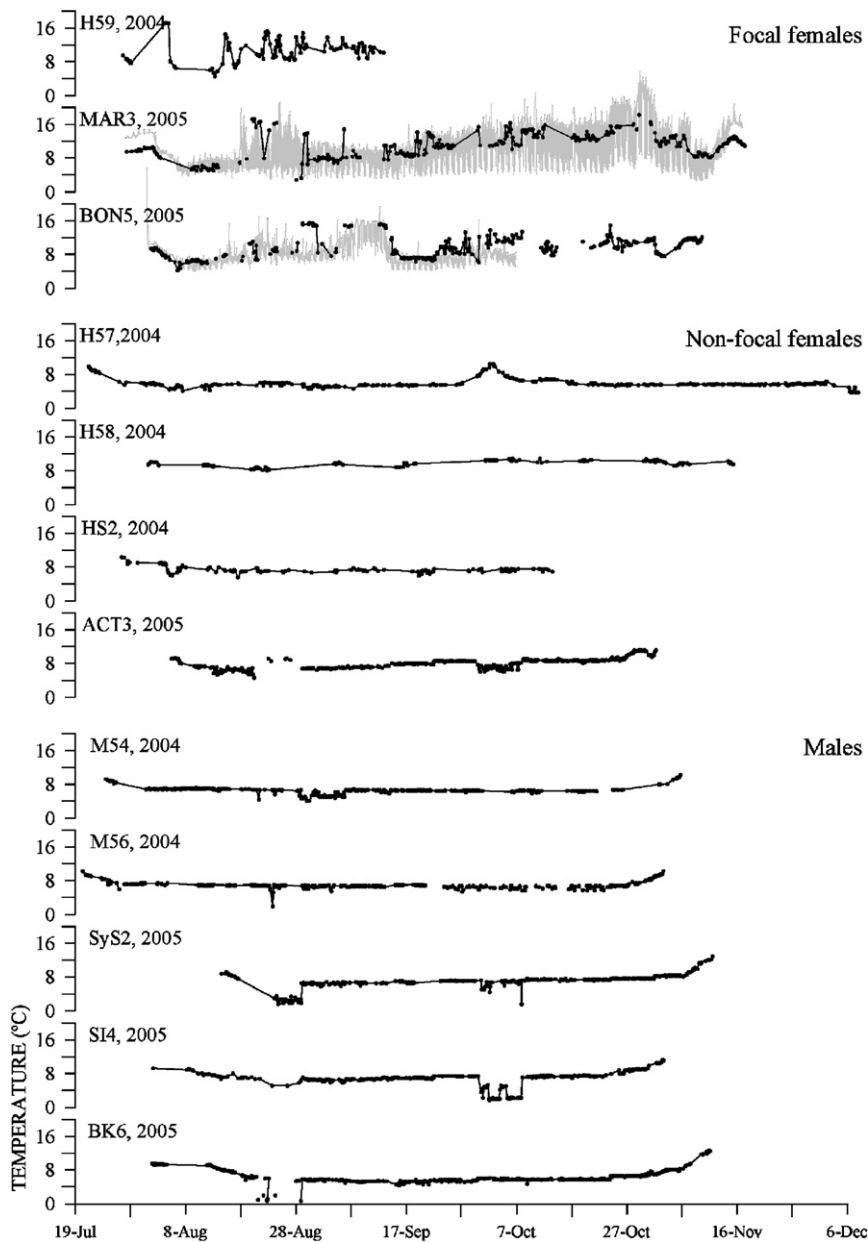
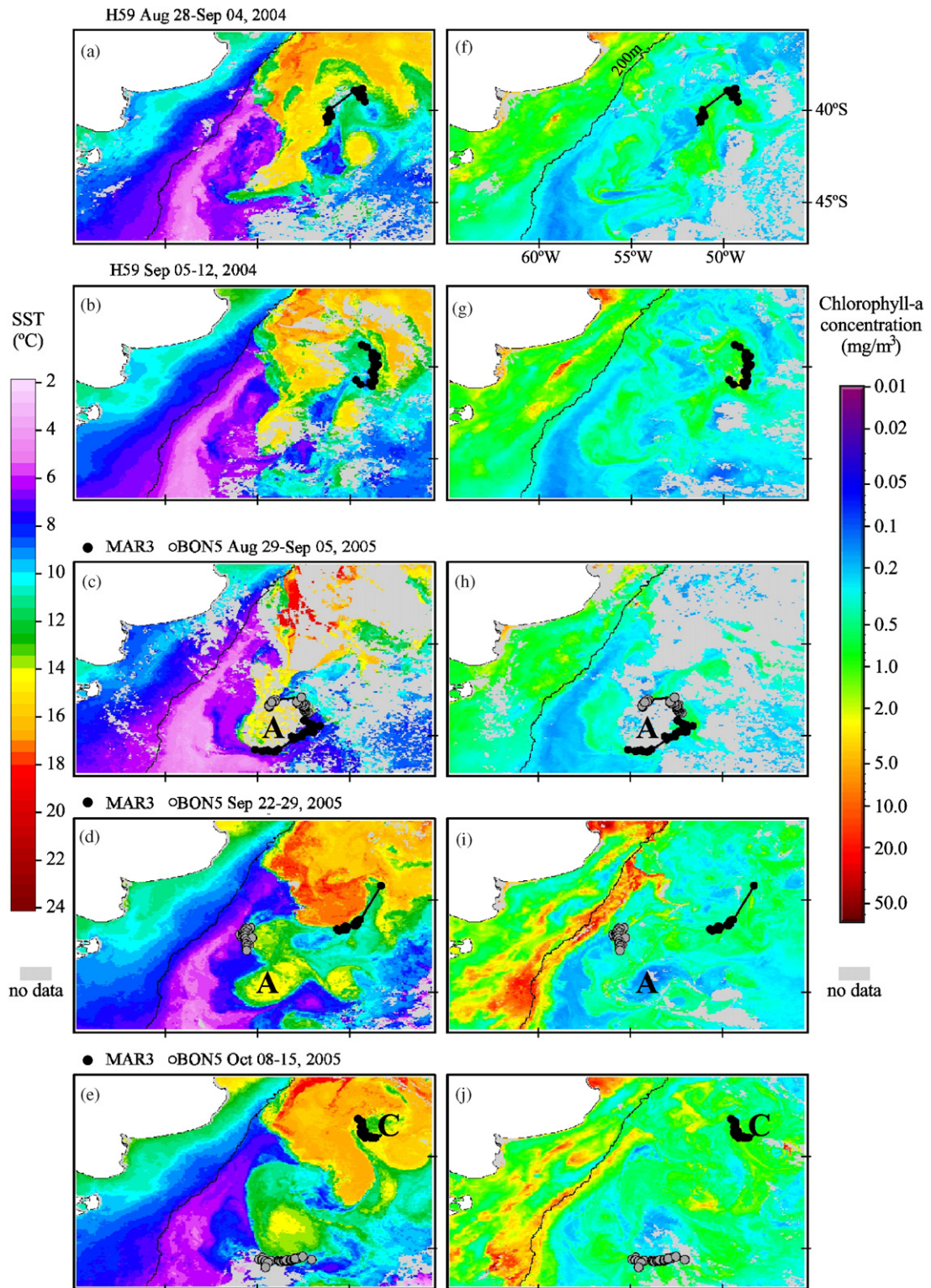


Fig. 3. Satellite-derived SST ($^{\circ}\text{C}$) time series along trajectories of focal (upper panel) and non-focal (middle panel) females and males (lower panel). Each line represents one individual. In situ temperature measurements recorded by Bon5 and Mar3 throughout their diving cycles are shown in gray (upper panel). See Figs. 1b and 2a to correlate these time series with oceanographic regimes and locations.

Fig. 4. (a–e) Satellite-derived sea surface temperature distribution. Each image represents 8-day, 4-km resolution SST composites from the moderate-resolution imaging spectroradiometer (MODIS) Aqua. Dates are shown in each composite. Dots indicate the seal trajectories: H59 and Mar3 (black) and Bon5 (gray). The 200 m isobath (black line) marks the outer edge of the continental shelf. Data show that after reaching the Basin focal area elephant seals are located along the Brazil/Malvinas Confluence and at the periphery of warm core eddies. Color scale is shown at left. (f–j) Satellite retrieved chlorophyll-*a* for the same periods as the SST images. Composites represent 8-day, 4 km resolution MODIS data from the Aqua satellite. A (C) indicates the location of a warm-core (cold-core), eddy. Color scale is shown at right.



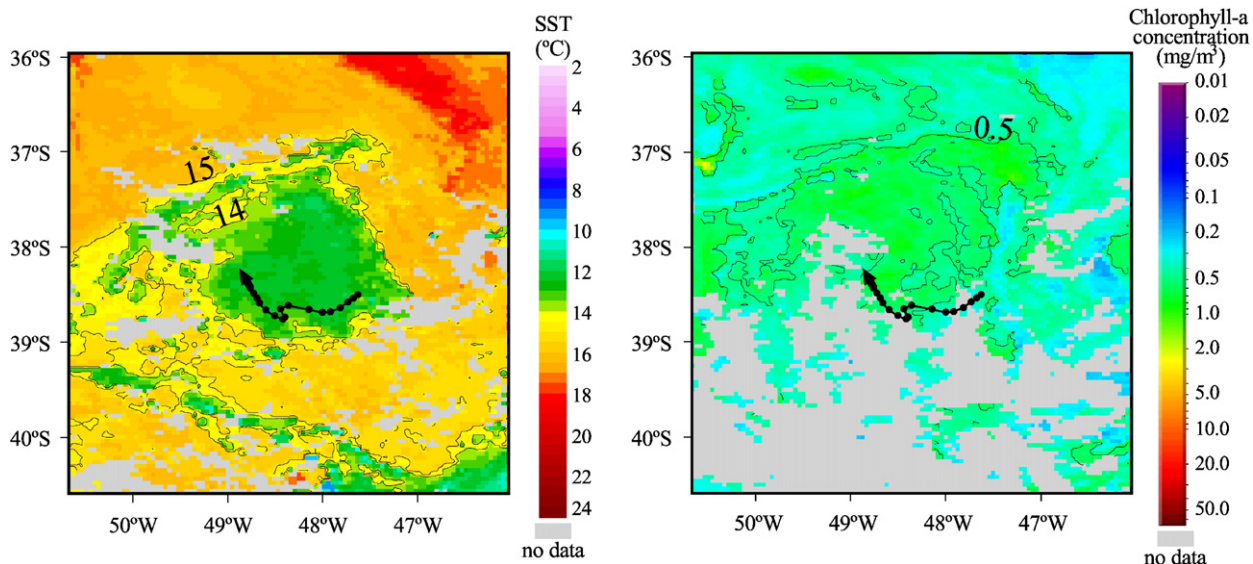


Fig. 5. (a) Sea surface temperature distribution depicting the cold core eddy observed on the week beginning 16 October 2005 overlapped with the 6-h smoothed trajectory of Mar3 from 17–21 October (black line). Also shown are the 25 valid raw positions received during this period (black dots). The arrow indicates travel direction. (b) As in (a), for chlorophyll-*a* distribution.

foraging time. In late August-early September 2004, the MC and BC collide at the shelf break near 39°S and the BMC extends southward to 45°S (Fig. 4a). The BMC presents a large meander which by mid-September is about to produce a warm-core eddy (SST > 14°C, Fig. 4b). East of the BMC (50°W) a warm-core eddy and a cold-core eddy are observed (Fig. 4a and b). In early August 2005, at ~34°S the BC was characterized by surface waters warmer than 18°C. At 37°S the BC was separated from the shelf break by a wedge of relatively cold surface water (SST < 6°C) derived from the MC (Fig. 4c). The warm BC continued its southward path east of the MC, with SST reaching 16°C at 40°S. Relatively warm surface waters (SST > 14°C) extended yet further south to about 45°S, creating a sharp transition with the cool waters from the MC. This southward extension of warm-salty subtropical waters, similar to the observation in early September 2004 (Fig. 4a), presumably is correlated with enhancements of BC transport (Goni and Wainer, 2001) and is a precursor of the large eddies which detach from the BMC extension. By mid-September 2005, the core of warmer surface waters was confined to north of 41°S and a large eddy (eddy A in Fig. 4d), completely detached from the BC. The eddy core presented surface temperatures warmer than 14°C, covering an area of ca. 36,000 km². The surface temperature gradient reached 9°C/10 km across the Confluence and

about 3°C/10 km around the eddy edges. In early October 2005 eddy A remains at about the same location (Fig. 4e).

4.1.2. Sea surface chlorophyll

Satellite-derived surface chlorophyll images (Fig. 4f–j) reveal intense blooms over the shelf and shelf break. Further offshore regions of relatively high chl-*a* concentration (>1 mg/m³) are found along narrow bands and streaks. In late September 2005, the most noticeable of these features, presenting chl-*a* > 4 mg/m³, extends from the shelf-break maximum near 39°S, closely following the edge of warm waters where the Confluence originates (Fig. 4i). Additional offshore regions of moderate chl-*a* (~1 mg/m³ Fig. 4f–j) closely follow the transition between subtropical and subantarctic waters along the edges of eddies and meanders. Chl-*a* images suggest that the center of the relatively young warm-core eddy “A” (chl-*a* < 0.2 mg/m³, Fig. 4i–j). In contrast, cold-core eddies present relatively high chl-*a* interiors (chl-*a* > 0.9 mg/m³) compared to the surroundings (chl-*a* = 0.2 mg/m³, Fig. 5).

4.2. Description of the travel patterns

Seals traveled to localized areas on the Patagonian shelf (males; Fig. 1b and 2a-blue), shelf break

(some females, Fig. 1b and 2a-orange), or Argentine Basin (focal females, Fig. 1b and 2a-red). Fig. 2(b–l) illustrates the trajectories of the three focal seals in phases, from dispersion after leaving the colony, travel in the Basin focal area, and finally back to land (see also Table 1). Depth range in the Basin area varied from 200 m at the edge of the shelf up to 6000 m.

4.2.1. *Travel to the basin*

The focal females swam eastward to the shelf break at speeds varying between 1.15 and 1.35 m/s (ca 100 km/day, Fig. 2 and Table 1). In 3–5.5 days they reached waters deeper than 200 m.

4.2.2. *Travel inside the basin focal area*

Focal animals spent in this area about 90% of their time at sea. They had a meandering trajectory with changes in speed and direction, reflected as several CW and ACW paths lasting 2–3 weeks each (Fig. 2b–l, see also Fig. 7a–d). H59 (2004) encountered a narrow band of warm waters (SST > 16 °C) from the BMC, surrounded by cold sub Antarctic waters (SST < 10 °C; Fig. 4a). The seal first followed the BMC and looped ACW along the southernmost Confluence extension (Fig. 2b). She then began describing a closed CW loop encircling cold waters (Fig. 2b–c and Fig. 4a). This path continued until data reception was interrupted (Fig. 4b). Mar3 and Bon5 (2005) showed similar trajectories with similar physical backgrounds. Starting at about 37–40°S, both turned abruptly southward on a trip of 700–1000 km at an average speed of 100 km/day for both animals (Fig. 2e and i).

These southward journeys closely followed the edge of the warm surface waters (high-temperature gradient region) associated with the BMC at a time when a large warm-core eddy was about to detach (Fig. 4c–e). The ACW loop of Bon5 (Fig. 2i–j) took 2 weeks of travel around the warm-core anticyclonic eddy A (Fig. 4c). She then swam away from the eddy into the sub Antarctic waters of the Malvinas Return Current and back northward within cold surface waters (SST ~7 °C; Fig. 6c). At 75 km/day this part of the journey, against the southward mean flow, was consistently slower than the earlier part of the trip. Finally, Bon5 re-joined the rim of warm-core eddy A and described yet another large ACW loop, closely following its edge until reaching 41°S, near the Confluence (Fig. 2k).

Mar3 also described a large ACW loop similar to Bon 5 (Fig. 2e–f). Further into the season, this

female did two complete cyclonic (CW) turns around a relatively small cold-core eddy (C) centered at 38°16'S–48°48'W (Fig. 4e and Fig. 5). These cyclonic rotations were carried out at a mean speed of 70 km/day. In late October, she swam across the warm BC waters, reached the Confluence, drifted briefly along the northward edge of the warm-core eddy, and crossed the MC to head back to Península Valdés (Figs. 2g–h).

4.2.3. *Return to the coast*

The signal from H59 was lost after 49 days at sea. Bon5 approached land along a more northerly path than she used at departure (Fig. 2(l), while Mar3 followed a path similar to that taken out (Fig. 2(h). The shelf was crossed in about 7 days at a speed of 100–124 km/day (Table 1).

4.3. *Description of the dive pattern for Bon5*

The dive pattern of Bon5 varied according to her location (Fig. 6). A regular diel pattern coincided with satellite fixes in the cold waters of the MC (Fig. 6g–i). Dives during this phase of the trip were more than three times deeper during daylight hours than at night (mean dive depth = 553 ± 110 m, $n = 294$ dives vs. 159 ± 76 m, $n = 428$). No diel pattern occurred while Bon5 was at the edge of eddy A (Fig. 6a–c; 237 ± 129 vs. 233 ± 93 m, for 394 and 407 dives, respectively). When the seal was inside eddy A, deep dives were dominant during the day and often also at night (Fig. 6d–f; daylight: 534 ± 134 ; night = 324 ± 187 m; $n = 268$ and 289 dives, respectively). The vertical temperature profile indicated that during early September Bon5 remained in the colder side of eddy A, where there is weak temperature stratification (Fig. 6c), and then moved into more stratified waters at the core of the warm eddy (Fig. 6f). MC waters presented a weak temperature stratification ranging 4–6 °C, characteristic of sub Antarctic waters (Fig. 6i).

4.4. *Differential use of large-scale oceanographic regimes*

Focal and non-focal seals spent differential time in particular oceanographic regimes (Fig. 1c; see Section 2 for background). Some traveled on the open continental shelf (OS) on their way to or returning from presumed foraging areas elsewhere (Fig. 2), while others, particularly juvenile males, remained on the shelf all their time at sea (Figs. 1

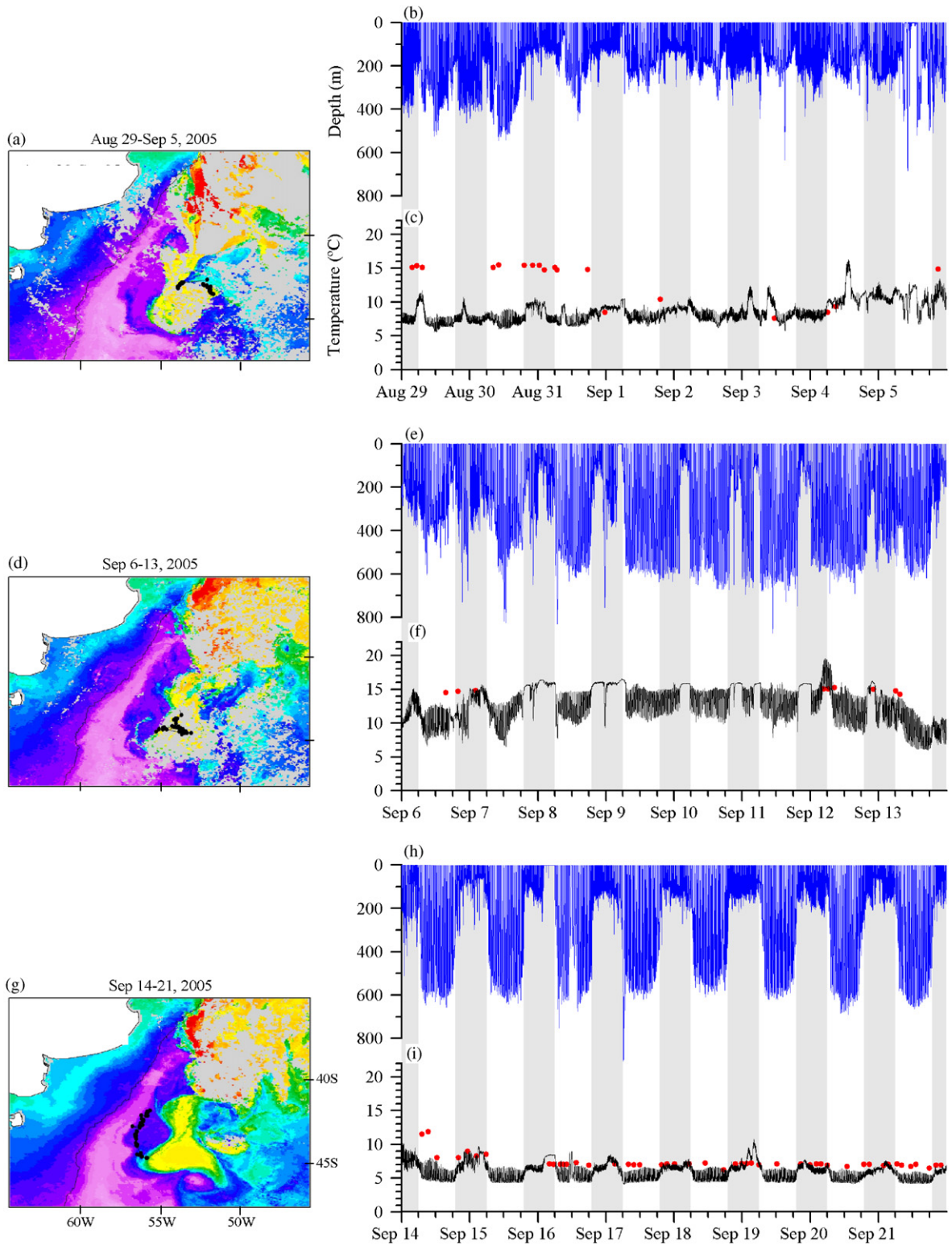


Fig. 6. Extracts from the diving pattern of Bon5 spanning three weeks of her foraging trip. (a, d and g): sea surface temperature with track (color scale in Fig. 4); (b,e and h): depth vs. time; (c, f and i): temperature vs. time. Each diving profile covers eight days: upper panel 29 August–5 September 2005, middle panel: 6–13 September 2005, lower panel: 14–21 September 2005. Background shadings in time series indicate nighttime. Red dots on top of temperature profiles are estimated SSTs from satellite imagery.

and 2). Females traveled through oceanographic regimes different than males. The Basin focal area is within the subtropical and mixed subtropical–subpolar waters. Two of the focal seals were the only individuals using the subtropical area.

The SST-time series for non-focal females (Fig. 3) showed small fluctuations (generally $<1^{\circ}\text{C}$) except when they were departing from and returning to land, when they traversed warmer waters. In early October, H59 returned to land, shown in the figure as an increase in SST of 2°C , immediately followed by a second trip to sea. Males also remained in relatively isothermal waters. In contrast, focal seals traversed areas of highly variable SST, ranging from 4 to 16°C within a few days. These SST changes are compatible with frontal structures associated with the BMC, meanders and eddies (Fig. 4a–e).

Locations within the Basin focal area suggest that individuals selected regions in the proximity of high SST gradient, such as the axis of the BMC and the edges of warm and cold eddies. For example, Bon5 spent 20 days (from 24 August to 10 September) at the edge of a warm-core eddy (Fig. 4c). She then left the eddy for about 2 weeks and reoccupied the edge of the same eddy for another 18 days (from 26 September to 13 October, Fig. 4c).

4.5. Drifting and swimming

Elephant seal tracks closely followed high SST gradients (Fig. 4), suggesting they also stayed in regions of high surface current velocity. To determine if seal tracks follow surface currents, we compared them with surface drifter trajectories. Observations support a strong coupling between the swimming dynamics of seals and ocean currents in the Basin focal area.

Most surface drifters entered the western Argentine Basin carried by the BC and MC. After separating from the continental margin the surface drifters follow the axis of the BMC (Fig. 7e–f). Once they reached the southernmost extent of the Confluence, drifters entered the region dominated by eddies and meanders (Fig. 7e; see also Piola et al., 1987; Olson et al., 1988). For instance, after arriving at the southernmost reach of the Confluence, drifters described an anticyclonic loop and then either re-circulated back northward or were trapped by eddies (Fig. 7e–f). Drifter 17459 (orange trace in Fig. 7e) described eight anticyclonic loops around a BC eddy during about ten weeks (25

December 2001 to 10 March 2002), before it re-circulated back northward. Drifter 34012 (yellow trace in Fig. 7e) made one complete loop at the southernmost extent of the BMC and then continued eastward near 45°S . Finally, drifter 31551, which was almost simultaneous with the focal seals, moved south along the Confluence axis and, after reaching the BMC loop, turned around the warm-core eddy (Fig. 4f) and later drifted southeastward (not shown in the figure). These drifter trajectories in the BMC and the warm-core eddy closely coincided with seal tracks (Fig. 7).

Within four distinct physical environments, BMC, BMC loop, warm-core and cold-core eddies, elephant seal travel speeds were similar to those of surface drifters (Tables 2 and 3). Only drifter 31551 was simultaneous (within a few days) with the elephant seals transit in the Basin focal area (see also Fig. 7f). Speeds of both seals and drifters were highest at the BMC and BMC loop. Seals traveled around eddies at velocities similar the mean surface currents (Table 3). The lowest surface currents and travel velocities within eddies were also comparably low (a few cm/s). In addition, drifter and seal velocities around warm-core eddies were higher than around cold-core eddies (Table 3).

The variability of the drifter velocity data is inherent to the turbulent nature of the Confluence and the associated eddy field. Both surface drifters and focal seals presented large speed variations within the BMC southward jet and in the BMC loop (Fig. 7 and Table 2). Drifters that described an anticyclonic trajectory, similar to the one followed by Bon5 and Mar3 (Fig. 7d), experienced a substantial decrease in drift velocity when approaching the BMC loop (Table 2). Similarly, both focal seals slowed down in this region, suggesting that seals not only follow the high-temperature gradient regions, but also that their velocities are modulated by ocean currents.

Assuming geostrophic balance, surface currents must leave warm waters to their left; thus the mean flow direction can be inferred from the SST distributions. Noticeably, the travel direction of focal seals was not arbitrary: all paths along high-temperature gradients were in the direction of the surface currents (e.g., Fig. 4c–e). In contrast, part of the path of Bon5 required active swimming across isotherms and against currents. As described above, after September 20 this seal swam across surface currents, into and against the Malvinas Return Current (Fig. 1a and Fig. 2c).

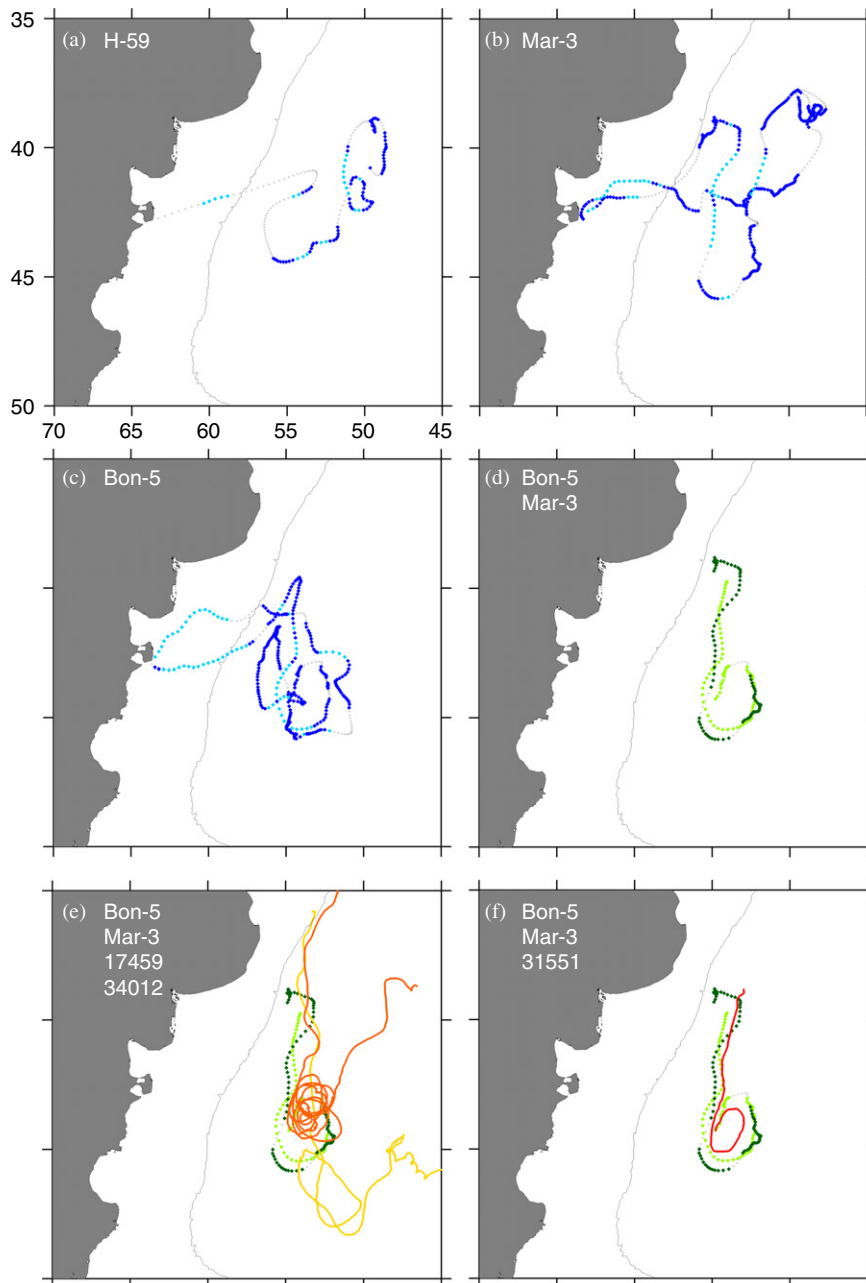


Fig. 7. (a–c) Locations of focal seals H59 (a), Mar3 (b) and Bon5 (c) plotted at 6-h intervals after fitting a cubic smoothing spline to the position data. Locations are plotted according to travel speed: blue <math>< 1\text{ m/s}</math>, light blue $> 1\text{ m/s}$. Gray dots indicate paths during location gaps of a day or more. (d) Mean 6-hourly positions of Bon5 (light green) and Mar3 (dark green) during the period 14 August–8 September, 2005. (e) Same as (d) (Bon5 in light green, Mar3 dark green), with non-simultaneous drifter trajectories 17459–2002 (orange) and 34012–2003 (yellow). (f) Same as (d), with quasi simultaneous drifter trajectory 31551–2005 (red).

5. Discussion

Elephant seals from Península Valdés forage in the large, bathymetry-dependent ocean fronts of the Patagonian shelf and shelf break. A foraging trip to

the deep Argentine Basin and offshore transitions, such as eddies and meanders of the mixed waters of the Confluence, is not dominant in this population. However, at least some young, pre-reproductive females may exploit alternative foraging places,

Table 2
Speed statistics from surface drifters and elephant seals (BMC: Brazil/Malvinas Confluence)

ID	Dates (mm/dd/yy)	BMC speed (m/s)			Time (days)	Dates (mm/dd/yy)	BMC loop speed (m/s)			Time (days)
		Mean	Max	Min			Mean	Max	Min	
17459	12/19/01, 12/27/01	1.11	1.62	0.63	9	12/29/01, 01/02/02	0.77	1.14	0.41	5
27131	01/18/03, 01/24/03	0.80	1.14	0.32	7					
28904	07/19/99, 07/24/99	0.43	0.78	0.08	6					
32051	11/04/01, 11/08/01	1.06	1.24	0.43	5	01/16/02, 01/22/08	0.81	1.07	0.30	7
34012	05/01/03, 05/10/03	1.12	2.05	0.37	10	05/13/03, 05/17/03	0.53	0.66	0.28	5
32433	01/02/00, 01/09/00	0.68	0.98	0.33	8					
9422068	04/12/96, 04/21/96	0.45	0.90	0.11	10					
31551	08/17/05, 08/26/05	0.84	1.75	0.38	9	08/27/05, 08/31/05	0.45	0.62	0.33	5
Mean		0.81	1.31	0.33	8		0.64	0.87	0.33	5.5
Bon5	08/15/05, 08/22/05	0.99	1.51	0.58	8	08/23/05, 08/26/05	0.80	1.22	0.50	4
Mar3	08/20/05, 08/25/05	1.06	1.55	0.42	6	08/28/05, 09/04/05	0.51	1.34	0.12	8

Drifter trajectories following paths similar to Bon5 and Mar3 were selected. Means, maxima and minima of 6-h velocities are given for the indicated dates. BMC loop refers to the sharp anticyclonic turn observed at the southernmost extension of the BMC.

Table 3
Speed statistics from surface drifters and elephant seals in anticlockwise, warm (W) and clockwise, cold (C) core eddies

ID	Dates (mm/dd/yy)	Speed (m/s)			Time (days)
		Mean	Max	Min	
17459-W	01/02/02, 02/09/02	0.66	1.43	0.03	66
34012-W	05/25/03, 06/18/03	0.37	0.80	0.03	25
9525790-W	10/07/97, 11/18/97	0.62	1.01	0.07	43
Mean		0.55	1.08	0.04	45
Bon5a-W	08/24/05, 09/10/05	0.46	0.98	0.07	17
Bon5b-W	09/26/05, 10/13/05	0.46	1.17	0.01	18
32456-C	12/13/03, 02/03/04	0.39	1.07	0.04	53
34393-C	11/12/02, 01/05/03	0.18	0.51	0.01	55
7707628-C	05/15/94, 06/27/94	0.46	1.28	0.02	44
Mean		0.34	0.95	0.02	51
Mar3a-C	10/01/05, 10/07/05	0.33	0.52	0.08	7
Mar3b-C	10/17/05, 10/21/05	0.40	0.88	0.14	5

Means, maxima and minima of 6-h velocities are given for the indicated dates.

perhaps more ephemeral but relatively predictable, productive and less congested. A fine-scale association was found between the movements of these animals and localized gradients in surface temperatures created at the convergence of the Brazil and Malvinas currents and its associated eddy field. Results from other species suggest that the strategy is relatively common in highly migratory, pelagic

vertebrates that must find patches of food in extraordinarily large areas.

An elephant seal that leaves Península Valdés on a foraging trip and cues on depth contours and thermal signals would unmistakably locate the transition between mixed coastal and stratified shelf waters, the continental shelf break, the water masses of the Malvinas and Brazil currents and their

confluence and the deep waters of the Argentine Basin (Campagna et al., 2000). From these alternative habitats, males and some adult females (Campagna et al., 1999) travel predominantly to the seasonal frontal areas of the outer shelf and shelf break regions described by Acha et al. (2004) and Saraceno et al. (2004). These animals would take advantage of productive areas that depend on the bathymetry and are thus predictable in location (Romero et al., 2006). The open ocean physical environment of the subantarctic zone, where most southern elephant seal colonies occur, is less predictable: prey distribution is often patchy and the foraging pattern of seals reflects considerable individual differences (Bornemann et al., 2000; Field et al., 2001; McConnell et al., 2002).

Females from Península Valdés are more distant travelers than males (Campagna et al., 1998). They traverse the shelf and disperse into the deep Argentine Basin, where bathymetry does not play the same role as on the shelf and slope. In these less predictable environments, females find the most productive areas associated with mesoscale features and adapt their behavior to their dynamics. Our results are also consistent with sex segregation of foraging areas at early stages of development, already reported for the northern elephant seal (Stewart, 1997). A study of juveniles of the southern species from Macquarie Island (Field et al., 2005) found that young seals show temporal and spatial age segregation in the foraging pattern, with older individuals covering a larger area of the Southern Ocean and spending time in different oceanographic regions than younger juveniles. Sex differences in the foraging pattern were not found.

There is a general understanding of how foraging seals respond to the physical environment, but it is not yet known how they decide on their migratory paths and find foraging grounds. Seals follow isotherms or continental margins, use temperature discontinuities and avoid sea ice to direct their travel and reach productive areas (Bornemann et al., 2000; Field et al., 2001; van den Hoff et al., 2002). For example, the Subantarctic Front, the Antarctic Polar Front and the Antarctic Circumpolar Current are important for seals from South Georgia, Campbell and Macquarie Islands (McConnell and Fedak, 1996; Jonker and Bester, 1998; van den Hoff et al., 2002). Special bathymetric profiles characterize the foraging grounds of juveniles from the South Shetlands (Bornemann et al., 2000) and Macquarie (van den Hoff et al., 2002).

But the most frequently studied relationship between the physical environment and behavior involves SST (e.g., Field et al., 2001; McConnell et al., 2002; Bradshaw et al., 2004b).

For a deep diver, such as an elephant seal, oceanographic features at depth may have even more relevant behavioral consequences than temperature at the surface (Bradshaw et al., 2004b).

The regular diel pattern of Bon5, evident only when she was traveling in the MC waters (Fig. 6), suggests mid-water foraging, following prey whose vertical distribution varies with time of day (Le Boeuf et al., 1989; Hindell et al., 1991). Diurnal changes in dive depth have been described for juvenile elephant seals from their first foraging trip (e.g., Hindell et al., 1999). But when Bon5 was at the edge of or inside the eddy, either a diel pattern did not occur (Fig. 6b) or the behavior consisted of deep dives during most of the day (Fig. 6e). Relatively shallow dives throughout the day at the edge of the eddy may be explained by a concentration of prey in a near-surface convergence zone (Polovina et al., 2004).

In situ SST agrees with data derived from satellite imagery only within the more homogeneous MC waters (Fig. 6i). The agreement is poor at the edge of the eddy (Fig. 6c). While temperature sensors measure instantaneous SST, satellite-derived SST maps integrate 8 days of data. The use of the long-term composites is necessary because of the frequent cloud cover. In addition, the long time response of the seals temperature sensors leads to low SST estimates after ascents in stratified waters. When elephants remain in relatively homogeneous waters, the agreement between in situ and satellite derived SST is good. However, even small displacements produce relatively large temperature changes near eddy edges and fronts, where horizontal temperature gradients are large. The detailed temperature profile recorded by the instruments carried by the seal is consistent with hydrographic data, revealing a vertical temperature structure of fronts and eddies that reaches several hundred meters within the subtropical waters (Roden, 1986; Gordon, 1989). Diving seals within BMC eddies would then traverse subsurface water masses that are related to those at the surface.

5.1. Travel pattern associated to transient oceanographic features

Focal seals in the Basin traveled along strong SST gradients and within the intense ($>1\text{ m/s}$)

southward flow associated with the BMC and the warm-core eddy located further south. A high temperature gradient band occurs across the BMC throughout the year (Saraceno et al., 2004). Bon5 and Mar3, and probably H59, closely followed this gradient during their first southward journeys (in late August). This observation and the range of speeds of seals and surface drifters suggest that focal seals were embedded within the high-velocity jet associated with the Confluence (e.g., Olson et al., 1988; Peterson et al., 1996; Piola and Matano, 2001).

The trajectories of seals inside the Basin focal area follow both CW and ACW directions. Warm-core eddies, arising from instabilities of the BC, are associated with anticyclonic rotation, in contrast to cyclonic cold-core eddies. Along these high-temperature gradient paths, seal travel direction is always consistent with the direction of surface currents, except for the transit of Bon5 across the BMC and against the Malvinas Return Current. The seal was already at the rim of warm-core eddy A of Fig. 4 when she swam into subantarctic waters. She later repositioned herself in the eddy rim further upstream.

5.2. Seals as active swimmers and surface drifters

If seals were drifting passively, their trajectories and speeds should resemble those described by surface drifters. Results partially confirm this hypothesis, as seals that follow the main circulation features, e.g., the BMC and the eddy field, have trajectories and speeds of translation within each of the regimes comparable with those of passive drifters (Tables 2 and 3).

There are, however, critical problems that arise because the surface trajectory of a seal integrates its diving behavior. A diving seal, contrary to a floating object, is exposed to variable current speeds at different depths. In the BMC, and also around eddies, the current speed decreases substantially with depth (e.g., Roden 1986; Gordon 1989). Therefore, a diving seal that travels at a speed similar to the surface current would have to actively swim to keep up with the latter. To evaluate the seal tracks relative to ocean currents, we assumed a theoretical dive to a depth of 400 m lasting 20 min, consistent with known elephant seal diving behavior (Hindell et al., 1991; Campagna et al., 1998, 1999; Le Boeuf et al., 2000 and Fig. 3). Based on baroclinic shear retrieved from historical hydro-

graphic data collected within the high velocity jet associated with the Confluence (see Piola and Bianchi, 1992), we estimated the average current speed at which the animal would have been exposed during the theoretical dive. Surface currents in this region reach 1.10–1.15 m/s (ca. 95 km/day), and decrease linearly downward to an average of 0.35 m/s (30 km/day) at 400 m. The mean current speed experienced by a seal during a complete diving cycle as describe above would then be 0.67 m/s (58 km/day). If a diel pattern is considered, and 40% of the dives are assumed to occur to 200 m (the rest to 400 m), the mean daily drift velocity is 0.77 m/s (66 km/day). These speed estimates support the conclusion of a combined swimming-drifting behavior of focal seals. Since these high-current velocities occur only in relatively narrow jets (20–30 km), our time-depth averaged velocity estimate should be considered an upper limit. Thus, to achieve speeds comparable to the surface currents, as suggested by Table 2, some degree of swimming is required most of the time. However, swimming along the SST gradients is always in the flow direction, strongly suggesting that seals use ocean currents to travel along the fronts.

5.3. Productivity of ephemeral fronts

In the western South Atlantic, mixed waters downstream of the Confluence present sufficient stratification and nutrient availability to produce modest phytoplankton blooms near the Confluence axis and around the periphery of eddies (e.g., Brandini et al., 2000; Saraceno et al., 2005). Chlorophyll images suggest that the edges of young warm-core eddies (Fig. 4i and Fig. 4j) and the centers of cold-core eddies (surrounded by H59 in 2004 and by Mar3 in 2005; Fig. 4f and Fig. 5b) are areas of enhanced productivity. These observations are consistent with the recent study of Souza et al. (2006), who found increased surface chlorophyll concentrations (0.6 mg/m^3) around the rim of a BC warm-core ring detached from the Confluence, and with studies of Gulf Stream eddies (Yentsch and Phinney, 1985). Likewise, models and observations suggest that upwelling at the core of cold-core cyclonic eddies may enhance phytoplankton growth (e.g. McGillicuddy et al., 1998; Oschlies and Garçon 1998; Garcia et al., 2004).

Focal seals tend to remain on the colder side of areas with high SST gradient. Although they do not remain in the center of cold eddies (Fig. 4f and j),

the detailed trajectory of Mar3 in mid October 2005 reveals that she did travel around the eddy, occupying the productive waters of the outer core. Similarly, loggerhead sea turtles, *Caretta caretta*, occupied the edge of productive cold-core, cyclonic eddies and meanders that develop along the southern edge of the Kuroshio Extension (Polovina et al., 2004). Antarctic fur seals, *Arctocephalus gazella*, were described to forage in the cold side of high SST gradient associated with the Polar Front (Guinet et al., 2001).

Eddies would attract diverse species assemblages of zooplankton, micronekton, and top predators (e.g., Olson and Backus, 1985; Rodhouse et al., 1992; Davis et al., 2002; Polovina et al., 2004). It is, however, rare to obtain in situ measures of productivity or prey availability linked with almost simultaneous predator position fixes (but see Guinet et al., 2001). In October 2005, about the same time as our animals were at sea, an independent study on species abundance conducted transects across the shelf break, MC and BMC, between 38°30'S and 45°30'S (Anonymous, 2005). This study partially covered our Basin focal area, and results indicate that, excluding the shelf break front, the highest concentration of young stages of *Illex* squid occurred at the BMC and at the western rim of eddy A.

The use of eddies as foraging grounds has been suggested by data on abundance of cetaceans in the Gulf of Mexico (Davis et al., 2002) and on trajectories of loggerhead sea turtles in the central North Pacific. Individuals of this species spend months at the edge of cyclonic, mid-ocean eddies related to the Kuroshio Extension, where surface convergence zones result in enhanced surface chlorophyll (Polovina et al., 2004).

The ephemeral temperature fronts of the Argentine Basin could then be potential foraging areas for the elephant seals of Península Valdés and other top predators that reproduce along the coast of Patagonia, such as Magellanic penguins, *Spheniscus magellanicus*, and South American sea lions, *Otaria flavescens*. Data suggest however that only young female seals may travel and remain associated with temperature fronts of the BMC. Adult seals, Magellanic penguins and sea lions forage in bathymetry-dependent fronts of the Patagonian continental shelf and slope (Campagna et al., 2001; Boersma et al., 2002; Pütz et al., 2002; Wilson et al., 2005). In summary, the use of mesoscale temperature fronts in the western Argentine Basin

more likely represents an alternative foraging strategy that benefits juvenile females via decreased competition from other marine mammals or diving birds.

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References

- Anonymous, 2005. Informe preliminar de campaña Kaiyo Maru 2005. Crucero conjunto argentino-japonés para el estudio de los juveniles del calamar argentino (*Illex argentinus*). Instituto Nacional de Investigación y Desarrollo Pesquero, Informe Técnico Interno 94, 22p.
- Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M., Bava, J., 2004. Marine fronts at the continental shelves of austral South America physical and ecological processes. *Journal of Marine Systems* 44, 83–105.
- Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, Ch.J., Boustany, A., Teo, S.L.H., Seitz, A., Walli, A., Fudge, D., 2001. Migratory movements, depth preferences, and thermal biology of Atlantic Bluefin Tuna. *Science* 293, 1310–1314.
- Block, B.A., Teo, S.L.H., Walli, A., Boustany, A., Stokesbury, M.J.W., Farwell, Ch.J., Weng, K.C., Dewar, H., Williams, T.D., 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* 434, 1121–1127.
- Boehlert, G.W., Costa, D.P., Crocker, D.E., Green, P., O'Brien, T., Levitus, S., Le Boeuf, B.J., 2001. Autonomous pinniped environmental samplers: using instrumented animals as oceanographic data collectors. *Journal of Atmospheric and Oceanic Technology* 18, 1882–1893.
- Boersma, P.D., Stokes, D.L., Strange, I.J., 2002. Applying ecology to conservation: tracking breeding penguins at New Island South reserve, Falkland Islands. *Aquatic Conservation: Marine and Freshwater Ecosystems* 12, 63–64.

- Bornemann, H., Kreyscher, M., Ramdohri, S., Martinz, T., Carlinp, A., Sellmann, L., Plotz, J., 2000. Southern elephant seal movements and Antarctic sea ice. *Antarctic Science* 12, 3–15.
- Bost, C.A., Georges, J.Y., Cherel, Y., Pütz, K., Charrassin, J.B., Handrich, Y., Zorn, T., Lage, J., Le Maho, Y., 1997. Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Marine Ecology Progress Series* 150, 21–33.
- Boyd, I.L., Hawker, E.J., Brandon, M.A., Stranilad, I.J., 2001. Measurement of the ocean temperatures using instruments carried by Antarctic fur seals. *Journal of Marine Systems* 27, 277–288.
- Bradshaw, C.J.A., Hindell, M.A., Sumner, M.D., Michael, K.J., 2004a. Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour* 68, 1349–1360.
- Bradshaw, C.J.A., Higgins, J., Michael, K.J., Wotherspoon, S.J., Hindell, M.A., 2004b. At-sea distribution of female southern elephant seals relative to variation in ocean surface properties. *ICES Journal of Marine Sciences* 61, 1014–1027.
- Brandini, F., Boltovskoy, D., Piola, A.R., Koçmur, S., Rottgers, R., Abreu, P., Mendes Lopes, R., 2000. Multiannual trends in fronts and distribution of nutrients and chlorophyll in the southwestern Atlantic. *Deep-Sea Research I* 47, 1015–1033.
- Campagna, C., Le Boeuf, B.J., Blackwell, S.B., Crocker, D.E., Quintana, F., 1995. Diving behaviour and foraging location of female southern elephant seals from Patagonia. *Journal of Zoology (London)* 236, 55–71.
- Campagna, C., Quintana, F., Le Boeuf, B.J., Blackwell, S., Crocker, D., 1998. Diving behaviour and foraging ecology of female southern elephant seals from Patagonia. *Aquatic Mammals* 4, 1–11.
- Campagna, C., Fedak, M.A., McConnell, B.J., 1999. Post-breeding distribution and diving behavior of adult male southern elephant seals from Patagonia. *Journal of Mammalogy* 80, 1341–1352.
- Campagna, C., Rivas, A.L., Marin, M.R., 2000. Temperature and depth profiles recorded during dives of elephant seals reflect distinct ocean environments. *Journal of Marine Systems* 24, 299–312.
- Campagna, C., Werner, R., Marin, M.R., Karesh, W., Koontz, F., Cook, R., Koontz, C., 2001. Movements and location at sea of South American sea lions (*Otaria flavescens*). *Journal of Zoology (London)* 257, 205–220.
- Charrassin, J.B., Park, Y.H., Le Maho, Y., Bost, C.A., 2002. Penguins as oceanographers, unravel hidden mechanisms of marine productivity. *Ecology Letters* 5, 317–319.
- Chelton, D.B., Schlax, M.G., Witter, D.L., Richman, J.G., 1990. Geosat altimeter observations of the surface circulation of the Southern Ocean. *Journal of Geophysical Research* 95, 17877–17903.
- de Boor, C., 2001. A Practical Guide to Splines. Applied Mathematics. Sciences, 27, revised edition. Springer, New York, 346p.
- Davis, R.W., Ortega-Ortiz, J.G., Ribic, C.A., Evans, W.E., Biggs, D.C., Ressler, P.H., Cady, R.B., Leben, R.R., Mullin, K.D., Würsig, B., 2002. Cetacean habitat in the northern oceanic Gulf of Mexico. *Deep-Sea Research I* 49, 121–142.
- Fadely, B.S., Robson, B.W., Sterling, J.T., Greig, A., Call, K.A., 2005. Immature Steller sea lion (*Eumetopias jubatus*) dive activity in relation to habitat features of the eastern Aleutian Islands. *Fisheries Oceanography* 14, 243–258.
- Field, I., Hindell, M., Slip, D., Michael, K., 2001. Foraging strategies of southern elephant seals (*Mirounga leonina*) in relation to frontal zones and water masses. *Antarctic Science* 13, 371–379.
- Field, I.C., Bradshaw, C.J.A., Burton, H.R., Hindell, M.A., 2004. Seasonal use of oceanographic and fisheries management zones by juvenile southern elephant seals (*Mirounga leonina*) from Macquarie Island. *Polar Biology* 27, 432–440.
- Field, I.C., Bradshaw, C.J.A., Burton, H.R., Sumner, M.D., Hindell, M.A., 2005. Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals (*Mirounga leonina*). *Oecologia* 142, 127–135.
- Garcia, C.A.E., Sarma, Y.V.B., Mata, M.M., Garcia, V.M.T., 2004. Chlorophyll variability and eddies in the Brazil–Malvinas Confluence region. *Deep Sea Research II: Topical Studies in Oceanography* 51, 159–172.
- Goni, G.J., Wainer, I., 2001. Investigation of the Brazil Current front variability from altimeter data. *Journal of Geophysical Research* 106, 31117–31128.
- Gordon, A.L., 1989. Brazil–Malvinas Confluence—1984. *Deep-Sea Research* 36, 573–585.
- Gordon, A.L., Greengrove, C., 1986. Geostrophic Circulation of the Brazil–Falkland Confluence. *Deep-Sea Research* 33, 573–586.
- Guerrero, R.A., Piola, A.R., 1997. Masas de agua. In: Boschi, E. (Ed.), *El Mar Argentino y sus recursos pesqueros*. Tomo 1, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, pp. 107–118.
- Guinet, C., Dubroca, L., Lea, M.A., Goldsworthy, S., Cherel, Y., Duhamel, G., Bonadonna, F., Donnay, J.P., 2001. Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Marine Ecology-Progress Series* 219, 251–264.
- Hansen, V.H., Poulain, P.-M., 1996. Quality control and interpolations of WOCE/TOGA drifter data. *Journal of Atmospheric and Oceanic Technology* 13, 900–909.
- Hays, G.C., Åkesson, S., Godley, B.J., Luschi, P., Santidrian, P., 2001. The implications of location accuracy for the interpretation of satellite-tracking data. *Animal Behaviour* 61, 1035–1040.
- Hindell, M.A., Burton, H.R., Slip, D.J., 1991. Foraging areas of southern elephant seals (*Mirounga leonina*) as inferred from water temperature data. *Australian Journal of Marine and Freshwater Research* 42, 115–128.
- Hindell, M.A., McConnell, B.J., Fedak, M.A., Slip, D.J., Burton, H.R., Reijnders, P.J.H., McMahan, C.R., 1999. Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea. *Canadian Journal of Zoology* 77, 1807–1821.
- Hindell, M.A., Bradshaw, C.J.A., Sumner, M.D., Michael, K.J., Burton, H.R., 2003. Dispersal of female southern elephant seals and their prey consumption during the austral summer: relevance to management and oceanographic zones. *Journal of Applied Ecology* 40, 703–715.
- Jonker, F.C., Bester, M.N., 1998. Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarctic Science* 10, 21–30.
- Legeckis, R., Gordon, A.L., 1982. Satellite observations of the Brazil and Falkland currents—1975 to 1976 and 1978. *Deep-Sea Research Part A-Oceanographic Research Paper* 29, 375–401.

- Le Boeuf, B.J., Naito, Y., Huntley, A.C., Asaga, T., 1989. Prolonged, continuous, deep diving by northern elephant seals. *Canadian Journal of Zoology* 67, 2514–2519.
- Le Boeuf, B.J., Crocker, D.E., Costa, D.P., Blackwell, S.B., Webb, P.M., Houser, D.S., 2000. Foraging ecology of northern elephant seals. *Ecological monographs* 70, 353–382.
- Lentini, C.A.D., Olson, D.B., Podestá, G.P., 2002. Statistics of Brazil Current rings observed from AVHRR: 1993–1998. *Geophysical Research Letters* 29, 16.
- McConnell, B.J., Fedak, M.A., 1996. Movements of southern elephant seals. *Canadian Journal of Zoology—Revue Canadienne de Zoologie* 74, 1485–1496.
- McConnell, B.J., Chambers, C., Fedak, M.A., 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science* 4, 393–398.
- McConnell, B., Fedak, M., Burton, H.R., Engelhard, G.H., Reijnders, P.J.H., 2002. Movements and foraging areas of naïve, recently weaned southern elephant seal pups. *Journal of Animal Ecology* 71, 65–78.
- McGillicuddy Jr., D.J., Robinson, A.R., Siegel, D.A., Jahanasch, H.W., Johnson, R., Dickey, T.D., McNeil, J., Michaels, A.F., Knap, A.H., 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature* 394, 263–266.
- Niiler, P.P., Sybrandy, A.L., Bi, K., Poulain, P.M., Bitterman, D., 1995. Measurements of the water following capability of holey-sock and TRISTAR drifters. *Deep-Sea Research I* 42, 1951–1964.
- Olson, D.B., Backus, R.H., 1985. The concentrating of organisms at fronts: a cold-water fish and a warm-core Gulf Stream ring. *Journal of Marine Research* 43, 113–137.
- Olson, D.B., Podestá, G.P., Evans, R.H., Brown, O., 1988. Temporal variations in the separation of the Brazil and Malvinas currents. *Deep-Sea Research* 35, 971–990.
- Oschlies, A., Garçon, V., 1998. Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean. *Nature* 394, 266–269.
- Peterson, R.G., Johnson, C.S., Krauss, W., Davis, R.E., 1996. Lagrangian measurements in the Malvinas Current. In: Wefer, G., Berger, W.H., Siedler, G., Webb, D.J. (Eds.), *The South Atlantic: Present and Past Circulation*. Springer, Berlin, Heidelberg, pp. 239–247.
- Piola, A.R., Bianchi, A.A., 1992. Southwest Atlantic boundary currents. *WOCE Newsletter* 12, 14–17.
- Piola, A.R., Matano, R.P., 2001. Brazil and Falklands (Malvinas) Currents. In: Steele, J.H., Thorpe, S.A., Turekian, K.K. (Eds.), *Encyclopedia of Ocean Sciences*, vol. 1. Academic Press, London, UK, pp. 340–349.
- Piola, A.R., Figueroa, H.A., Bianchi, A.A., 1987. Some aspects of the surface circulation south of 20°S revealed by First GARP Global Experiment Drifters. *Journal of Geophysical Research* 92, 5101–5114.
- Polovina, J.J., Balazs, G.H., Howell, E.A., Parker, D.M., Seki, M.P., Dutton, P.H., 2004. Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fisheries Oceanography* 13, 36–51.
- Pütz, K., Ingham, R.J., Smith, J.G., 2002. Foraging movements of Magellanic penguins *Spheniscus magellanicus* during the breeding season in de Falkland Island. *Aquatic Conservation: Marine and Freshwater Ecosystems* 12, 75–87.
- Rodhouse, P.G., Symon, C., Hatfield, E.M.C., 1992. Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. *Marine Ecology Progress Series* 89, 183–195.
- Roden, G.I., 1986. Thermohaline fronts and baroclinic flow in the Argentine Basin during the austral spring of 1984. *Journal of Geophysical Research* 91, 5075–5093.
- Romero, S.I., Piola, A.R., Charo, M., Garcia, C.A.E., 2006. Chlorophyll-*a* variability off Patagonia based on SeaWiFS data. *Journal of Geophysical Research* 111, C05021.
- Saraceno, M., Provost, C., Piola, A.R., Gagliardini, A., Bava, J., 2004. The Brazil Malvinas Frontal System as seen from nine years of advanced very high resolution radiometer data. *Journal of Geophysical Research* 109, C05027.
- Saraceno, M., Provost, C., Piola, A.R., 2005. On the relationship of satellite-retrieved surface temperature fronts and chlorophyll *a* in the Western South Atlantic. *Journal of Geophysical Research* 110, C11016.
- Sokolov, S., Rintoul, S.R., Wienecke, B., 2006. Tracking the Polar Front south of New Zealand using penguin dive data. *Deep-Sea Research I* 53, 591–607.
- Souza, R.B., Mata, M.M., Garcia, C.A.E., Kampel, M., Olivera, E.N., Lorenzetti, J.A., 2006. Multi-sensor and in situ measurements of a warm core ocean eddy south of the Brazil–Malvinas Confluence region. *Remote Sensing of Environment* 100, 52–66.
- Stewart, B.S., 1997. Ontogeny of differential migration and sexual segregation in northern elephant seals. *Journal of Mammalogy* 78, 1101–1116.
- Sumner, M.D., Michael, K.J., Bradshaw, C.J.A., Hindell, M.A., 2003. Remote sensing of Southern Ocean sea surface temperature: implications for marine biophysical models. *Remote Sensing of Environment* 84, 161–173.
- Tremblay, Y., Shaffer, S.A., Fowler, S.L., Kuhn, C.E., McDonald, B.I., Weise, M.J., Bost, C.A., Weimerskirch, H., Crocker, D.E., Goebel, M.E., Costa, D.P., 2006. Interpolation of animal tracking data in a fluid environment. *The Journal of Experimental Biology* 209, 128–140.
- van den Hoff, J., Burton, H.R., Hindell, M.A., Sumner, M.D., McMahon, C.R., 2002. Migrations and foraging of juvenile southern elephant seals from Macquarie Island within CCAMLR managed areas. *Antarctic Science* 14, 134–145.
- Vincent, C., McConnell, B.J., Ridoux, V., Fedak, M.A., 2002. Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. *Marine Mammal Science* 18, 156–166.
- Wilson, R.P., Ropert Coudert, Y., Akiko, K., 2002. Rush and grab strategies in foraging marine endotherms: the case for haste in penguins. *Animal Behaviour* 63, 85–95.
- Wilson, R.P., Sclaro, J.A., Gremillet, D., Kierspel, M.A.M., Laurenti, S., Upton, J., Gallelli, H., Quintana, F., Frere, E., Müller, G., Strate, M.T., Zimmer, I., 2005. How do magellanic penguins cope with variability in their access to prey? *Ecological Monographs* 75, 379–401.
- Yentsch, C.S., Phinney, D.A., 1985. Rotary motions and convection as a means of regulating primary production in warm core eddies. *Journal of Geophysical Research-Oceans* 90, 3237–3248.