



Foraging strategies of Southern sea lion females in the La Plata River Estuary (Argentina–Uruguay)

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ABSTRACT

The stocks of Southern sea lions (*Otaria flavescens*, SSL) and South American fur seals (SAFS) that breed on coastal islands of Uruguay constitute the most important focal concentration of pinnipeds in South America, with a significant increase in SAFS and a steady decrease of SSL over the past decades. Because females are a key element of population dynamics and no information exists on the post-breeding pup rearing period, we studied the foraging patterns of SSL females in the La Plata River Estuary (LPRE) during mid and late lactation (late austral autumn and winter), analyzing the foraging performance, geographic coverage and ontogenetic differences in foraging strategies for a period of 1–5 months. At-sea movements of 22 SSL females (6 subadults and 16 adults) from Isla de Lobos (IL, 35°01'28"S–54°52'59"W, Uruguay) were monitored using satellite transmitters (SPOT4, SPOT5 and STD-R-S16, Wildlife Computers) in 2007 and 2010. An algorithm [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. *Antarct. Sci.* 4, 393–398.] with a maximum transit speed of 3 m s⁻¹ was applied to the Argos information, resulting in a total of 2522 filtered locations. A daily mean of 3.5 ± 1.74 filtered locations per animal was received. One hundred and eighty three foraging trips (FT) were recorded with no significant differences ($p < 0.05$) between subadults and adults in the duration of FT (6.1 ± 3.15 day), distance traveled per FT (237.2 ± 105.25 km), mean distance from IL (57.2 ± 25.90 km), maximum straight line (Spider) distance (100.2 ± 41.40 km) and transit speed (1.1 ± 1.04 m s⁻¹). SSL showed directional fidelity to foraging sites, indicated by high mean vector (r) values (0.74 ± 0.14) calculated from FT mean bearings. Kernel ranges for 50% and 95% of all FT locations were 5420 km² and 36,222 km², respectively, and the extension of the foraging areas appeared to be influenced by a combination of bathymetry and ecological boundaries within LPRE. Regardless of their reproductive condition, females showed a strong fidelity to IL, and their foraging activity was restricted to relatively shallow areas (10–100 m) on the continental shelf. During autumn and winter, SSL females made significantly longer FTs than during the breeding season, when lactating females decrease FT duration by increasing transit speed but maintain a similar spatial coverage compared with FT later in lactation. Although several aquatic areas of high priority for conservation in LPRE have been identified and proposed, only 15% of the foraging habitat of SSL females is currently included in these areas. This emphasizes the importance of the inclusion of the at-sea foraging distributions of central point foragers in marine protected areas. If conservation efforts focus only on coastal breeding concentrations, key elements of the life cycle are excluded with potential unpredictable effects.

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1. Introduction

The Río de la Plata, located between Argentina and Uruguay (Fig. 1), is one of the largest open estuaries in the world that discharges into the Atlantic Ocean an average flow of about

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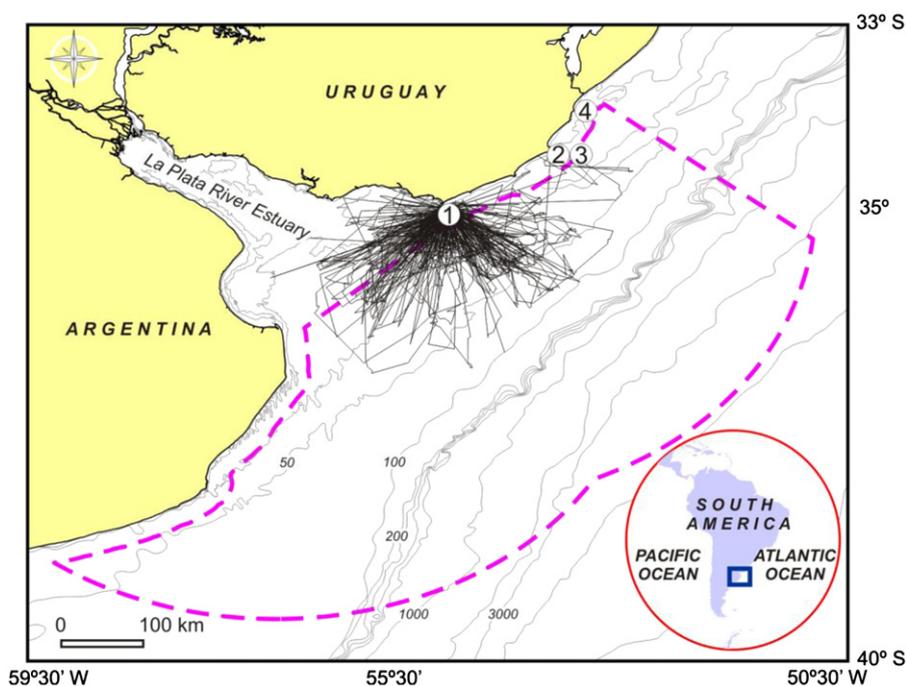


Fig. 1. The La Plata River Estuary and continental shelf between Argentina and Uruguay located in southeastern South America. The dashed pink line demarcates the Argentina–Uruguay Joint Fisheries Management Zone. Numbers indicate the Southern sea lion rookeries in Uruguay: Isla de Lobos (1; study area), Islas de Torres (2), Islas de Castillo Grande (3) and Isla Verde—Isote Coronilla (4). Individual Southern sea lion (SSL) foraging trips are indicated as black lines. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

22,000 m³ s⁻¹ (Framiñán and Brown, 1996). With industrial and urban areas located along the river and its estuary with more than 15 million inhabitants, it constitutes a highly complex fluvial transporting system with important economic impacts. Because of the high productivity, very active artisanal and coastal fisheries have developed in Uruguay and Argentina, focusing mainly on the whitemouth croaker (*Micropogonias furnieri*) (Acha et al., 2008).

The stocks of Southern sea lions (SSL, *Otaria flavescens* Shaw, 1800¹) and South American fur seals (SAFS, *Arctocephalus australis*

Zimmermann, 1783) that breed on four groups of coastal islands of Uruguay constitute the most important focal concentration of pinnipeds in South America, with current populations of ca. 400,000 animals (Ponce de León and Pin, 2006; Ponce de León, unpublished data). Both species were heavily exploited since the XVI century and sustained a long-term commercial exploitation that ended in 1978 and 1991 respectively. Actual population trends of both species are very different, with a constant increase in SAFS (Lima and Páez, 1997) and a decrease of SSL (Campagna, 2008; Páez, 2005; Ponce de León and Pin, 2006) for several years and a total abundance of SSL currently not exceeding 10,000 animals (Ponce de León, unpublished data).

South American sea lions are highly polygynous, with the breeding season beginning in ca. mid-December throughout their breeding range (Campagna, 1985; Hamilton, 1934; Vaz Ferreira, 1982a). The peak concentration of males and females ashore occurs during the second half of January, and pups are born from mid-December to early February. The peak number of copulations and births was suggested to be earlier at higher latitudes (Campagna, 1985). Lactating females begin to forage 8–10 days after parturition, and the breeding aggregations dissolve by late February. However, females and pups remain together for 8–10 months (Ponce de León and Pin, 2006; Vaz Ferreira, 1982a).

Opportunistic observations indicate that Uruguayan stocks of SSL and SAFS forage on the continental shelf off northern Argentina, Uruguay and Southern Brazil (Vaz Ferreira, 1982a,

¹ The controversial validity of the specific name for the Southern sea lion is disputed between *Otaria flavescens* (type—*Phoca flavescens* Shaw, 1800) and *Otaria byronia* (type—*Phoca byronia* de Blainville, 1820). Shaw's holotype was a two feet long yellowish otariid pup collected near the Straits of Magellan (Argentina–Chile) and lost from the Leverian Museum. Taking into consideration the International Code of Zoological Nomenclature (ICZN), the *Otaria flavescens* priority is undisputed because is the earliest available name applied to this taxon (Art.23). Because only Southern sea lions and South American fur seals are reported to breed in southern South America during the last 6000 years, Shaw's holotype could only have been a pup of one of these two otariid species. The revisions rejecting the validity of *Phoca flavescens* Shaw (King, 1978; Oliva, 1988) considered the type specimen as unidentifiable, but Cabrera (1940), Vaz Ferreira (1984) and Rodríguez and Bastida (1993) presented data supporting that body length, ear size, and coloration correspond only to that of a Southern sea lion pup. A tangible specimen also confirmed that this combination of characteristics is found in *Otaria* pups (Rodríguez and Bastida, 1993; Fig. 1, p. 376), and no reports are available supporting that these characters are found in *Arctocephalus australis* pups. Recently, Brunner (2004) supported the use of *O. byronia* instead of *O. flavescens*, but did not present tangible data to refute the concordance of the characteristics of *Phoca flavescens* with SSL pups. The arguments suggest that the validity of the senior synonym would be accepted only after ruling out several non-South American otariid pups, a requirement that has no biogeographical justification and is against the stability principle of the ICZN. The ICZN Opinion 1962 (2000) added some confusion to the Southern sea lion nomenclature issue, because some authors misinterpreted its scope. In this opinion, *Phoca leonina* Molina 1782 was stated as the type species of *Otaria* Peron 1816, and *Phoca byronia* de Blainville 1820 was placed in the Official Lists of Names in Zoology and erroneously considered as the first available subjective synonym of *Phoca leonina* Molina. This statement only established that *P. byronia* is equivalent to *P. leonina* and did not reject *Phoca flavescens* Shaw because this name was not mentioned. Thus

(footnote continued)

P. flavescens should not be considered as rejected because in terms of the ICZN, the rejection of a name must be clearly explicit and justified. That being the case, the statement that *Phoca byronia* is the first available synonym is not correct because *Phoca flavescens* has priority. *Otaria flavescens* (Shaw 1800) is based on a tangible specimen collected in a valid type locality, with body size, coloration and ear size fully compatible with a Southern sea lion pup. This name is used in this manuscript because is the oldest available name, has no nomenclatural act rejecting it and meets the requirements to be considered the valid name under the ICZN (Art.23).

1982b; Ximénez, 1986), but the at-sea behavior is almost unknown. The location of critical foraging areas and foraging performance is crucial for our understanding of the inter-specific interactions and the overlap with fisheries in the La Plata River Estuary and the nearby coastal area.

The SSL is one of the least known members of the family Otariidae, with very limited information on foraging behavior. The diving behavior and foraging activity of lactating female SSL has been described for Patagonia (Campagna et al., 2001; Werner and Campagna, 1995), the Malvinas-Falkland Islands (Thompson et al., 1998) and Isla de Lobos (Riet Sapiza et al., 2011). These studies were focused on the activity of females during the peak of the breeding season, but no information exists during the post-breeding pup rearing period.

Recent studies have confirmed that the declining SSL population off Uruguay is a discrete genetic stock (Feijoo et al., 2011; Túnez et al., 2007) and, although this species is classified as Least Concern by the IUCN (version 3.1, 2008), the decline in some populations may require a further reclassification to Near Threatened status (Campagna, 2008). Because females are a key element of population dynamics, we studied the foraging patterns of SSL females in the La Plata River Estuary (LPRE) during mid- and late-lactation period (late austral autumn and winter), analyzing the foraging performance, geographic coverage and ontogenetic differences in foraging strategies. Actual pup production on Isla de Lobos has declined to ca. 6% of that during the 1950s and 15% of the 1980s pup counts (Ponce de León, unpublished data; Vaz Ferreira et al., 1984), and pup provisioning is directly associated with the success of the mother foraging cycle. Therefore, the results of the present study will be relevant to understand the maternal foraging strategies during least known part of the lactation period in this declining stock.

2. Material and methods

2.1. Study site, animal handling and instrumentation

The study was performed on Isla de Lobos (35°01'28"S–54°52'59"W; Uruguay) in the La Plata River Estuary in May 2007 and 2010 (Fig. 1). Animal capture and handling was

conducted at the former sealing facility currently administered by the Uruguayan government (Dirección Nacional de Recursos Acuáticos de Uruguay—DINARA).

Twenty two SSL females (Table 1) were captured by DINARA staff and held in a corral under veterinary observation for 24 h. The animals were physically restrained using a squeeze cage and anesthetized with isoflurane using a mask and later with an endotracheal tube (Heath et al., 1996). Mask anesthesia induction lasted 14 ± 7 min (range=7–43 min) with a constant oxygen flow of $5\text{--}10 \text{ L min}^{-1}$ and 5% of isoflurane. After intubation, anesthesia was maintained with $2\text{--}3 \text{ L min}^{-1}$ oxygen and an isoflurane concentration of 0.75–1.5% in most of the animals (with some cases of deeper anesthesia around 2.5% isoflurane). Animals breathed constantly and regularly by themselves, but one assisted ventilation with the bag was performed every 5–7 min to expand the lungs, with particular care of not exceeding normal-lung inflation. Total anesthesia time ranged between 0.5 and 2 h. Animals were extubated 5 ± 3 min (range=1–17) after isoflurane administration stopped and anesthesia machine disconnected. Time between isoflurane anesthesia interruption and recovery (walking or head up behavior) also varied among animals, with a mean time of 21 ± 17.3 min (range=1–90; Dassis et al., unpublished data.). Heart rate, breathing rate, body temperature, oxygen in tissues, electrocardiographic recording and oral mucosa condition were monitored each 5 min with both manual techniques and a multi-parametric monitor (Guoteng, Science and Technology). All animals recovered with no difficulty, except for one adult female that died during anesthesia. A gross inspection during the field necropsy revealed no evident cause of death, and possible causes may have been the accidental lost of the endotracheal tube from the upper breathing way, although pre-existing lung pathologies could not be ruled out. Sea lions were weighed to the nearest 0.5 kg and measured (axillary girth and standard length) to the nearest 0.1 cm and considered adults at 147 cm (Grandi et al., 2010).

The animal instrumentation was performed 2–3 months after breeding aggregations ended, so most of the females captured were found solitary or in very small groups (2–4 animals) surrounded by groups of SAFS. Only a few SSL pups were seen, and they could not be assigned to a particular female; no pups were captured with a female. As a consequence, reproductive

Table 1
Deployment year, sex, age and morphometrics of the Southern sea lions (SSL) used in this study. Satellite transmitter programming included instruments transmitting daily (1) and every other day (2). The reproductive stage of adult females includes lactating adults (LA), non-lactating (NL) and not assessed (NA).

Animal	Deployment	PTT type (transmission)	Age	Weight (kg)	Length (cm)
L01	2007-05-12	STDR (1)	Adult (NL)	83.1	168.0
L02	2007-05-12	STDR (1)	Subadult	77.6	146.0
L03	2007-05-13	STDR (1)	Adult (NL)	77.1	159.0
L06	2007-05-14	STDR (1)	Adult (NL)	76.5	160.0
L07	2007-05-14	SPOT 4 (1)	Adult (NL)	61.3	148.0
L08	2007-05-14	STDR (1)	Adult (LA)	81.7	160.0
L09	2007-05-14	SPOT 4 (1)	Adult (NL)	61.6	149.0
L10	2007-05-15	SPOT 4 (1)	Subadult	64.7	146.0
L11	2007-05-15	SPOT 4 (1)	Subadult	54.9	141.0
L13	2007-05-16	SPOT 4 (1)	Adult (LA)	113.8	175.0
L14	2007-05-16	STDR (1)	Adult (LA)	130.3	181.0
L15	2007-05-16	SPOT 4 (1)	Subadult	51.9	139.0
OF01	2010-05-14	SPOT 5 (1)	Subadult	62.0	145.5
OF02	2010-05-15	SPOT 5 (1)	Adult (NA)	77.0	153.0
OF03	2010-05-16	SPOT 5 (2)	Adult (NA)	71.4	151.0
OF04	2010-05-17	SPOT 5 (2)	Adult (NA)	145.8	193.0
OF06	2010-05-18	SPOT 5 (2)	Adult (NA)	109.6	184.0
OF07	2010-05-18	SPOT 5 (2)	Adult (NA)	64.1	153.0
OF09	2010-05-20	SPOT 5 (2)	Adult (NA)	69.2	162.0
OF10	2010-05-20	SPOT 5 (2)	Adult (NA)	67.4	151.0
OF11	2010-05-21	SPOT 5 (2)	Adult (NA)	64.8	152.0
OF12	2010-05-21	SPOT 5 (2)	Subadult	56.3	143.0

status was determined after capture with a solid phase progesterone radioimmunoassay (RIA) (Diagnostic Products Corporation, Los Angeles, USA) with unextracted SSL serum. Hormone concentrations were determined after a log-logit transformation of the standard curve (Rodbard, 1974), and all concentrations were corrected for dilution.

At-sea movements were monitored using satellite transmitters (SPOT4, SPOT5 and STDR-S16, Wildlife Computers, Redmond, WA, USA; Table 1). The satellite transmitters were glued to the fur on the mid-dorsal line of the head (SPOT4&5) or back (STDRs) using neoprene cement.

2.2. Foraging trip analysis

At-sea locations of SSL were provided by the Argos System (CLS Group, Toulouse, France, <http://www.argos-system.org>) in seven accuracy categories: Class 3, accurate to 150 m; Class 2, accurate to 350 m; Class 1, accurate to 1 km; Class 0, accurate to ≥ 1 km; Classes A and B, limited (not estimated) accuracy and Class Z or invalid positions. The location-class Z positions were omitted, and the rest of the locations were filtered using the algorithm of McConnell et al. (1992) with a maximum transit speed of 3 m s^{-1} . This iterative forward/backward averaging filter identifies consecutive positions that would require an unrealistic speed of travel. The time invested in foraging was calculated as the sum of the foraging trip durations divided by the total time (on shore and at sea) of individual of an animal's transmission.

Filtered locations were used to estimate distance traveled by linear interpolation between consecutive positions in the ArcGIS 9.8 (ESRI Inc., Redlands, CA, USA) using the Hawth's Analysis Tools extension 3.27 (Beyer, 2004). Trip duration was calculated from ARGOS satellite time data. Linear distance between each position and Isla de Lobos was estimated using the Spider Distance command of the Animal Movement extension (Hooge and Eichenlaub, 1997) in the ArcView 3.2 (ESRI Inc., Redlands, CA, USA). Estimates of mean distance traveled, mean duration, mean linear distance and mean speed were calculated for each individual foraging trip, defined as the path from Isla de Lobos and back with a minimum linear distance of at least 40 km. Directional preference between consecutive foraging trips was analyzed by calculating the statistic r (mean vector) (Zar, 2010). Bottom depth was estimated for each location extracted from the General Bathymetric Chart of the Oceans (<http://www.gebco.net>; version 20090202).

Kernel areas (Worton, 1989) of 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90% and 95% locations were calculated using the Home Range Tools extension (Rodgers et al., 2007) in the ArcGIS 9.8. All kernel areas for adults ($n=16$ animals) and sub-adults ($n=6$ animals) were included on the maps, but only 95% and 50% values were statistically analyzed. A smoothing factor of 70% of reference bandwidth was applied to estimate a reliable home range area according to Kie et al. (2010). For comparative purposes, 100% Minimum Convex Polygons (MCPs; Mohr, 1947) were also estimated.

Homoscedasticity was tested by Levene tests and, in the case of proportions, the arcsine of the square root was used to fulfill the statistical assumptions (Zar, 2010). Significance was considered at $p=0.05$ unless otherwise stated.

3. Results

Twenty-two instrumented females yielded 2522 filtered locations consisting of the following location classes: 3 (7.9%), 2 (16.4%), 1 (19.3%), 0 (6.9%), A (21.0%) and B (28.5%). A daily mean of 3.5 ± 1.74 (range 0.7–12.5) filtered locations per animal were received, with an overall mean of 115 ± 50 locations (range

Table 2
Foraging trips (FT) recorded by month and number of weeks (in brackets) in 2007 and 2010.

Month [weeks]	2007		2010		Total
	Subadults	Adults	Subadults	Adults	
May [2]	10	22	4	21	57
June [4]	8	26	7	25	66
July [4]	2	2	7	23	34
August [4]	0	0	2	8	10
September [4]	0	0	2	9	11
October [2]	0	0	1	4	5
Total [20]	20	50	23	90	183

32–209) for each animal. Sea lions with instruments programmed to transmit every other day yielded significantly longer transmission periods (108.0 ± 40.91 day; range 45.6–157.3; $n=8$) than animals transmitting every day (48.3 ± 12.11 day; range 25.3–62.4; $n=14$) (Mann-Whitney U test, $p < 0.001$, $n=22$).

A total of 183 foraging trips (FT) were recorded with a significantly higher mean number for sea lions transmitting with every other day (12.6 ± 4.87 FT; 3–19; $n=101$) than daily transmitting instruments (5.9 ± 1.99 FT; 2–9; $n=82$) ($t=-0.463$; $df=20$; $p < 0.001$). FT were recorded for approximately 20 weeks from mid May to mid-October (Table 2) covering approximately the last two thirds of the lactation period.

Mean FT duration was 6.1 ± 3.15 day (range 1.2–17.1; $n=183$) with no significant difference between subadults ($n=28$) and adults ($n=155$; $t=-0.491$; $df=181$; $p=0.624$) (Table 3). Lactating and non-lactating adult females showed no significant differences in their mean FT duration ($t=-1.323$; $df=48$; $p=0.192$). The sea lions spent $69 \pm 15.9\%$ (range 21–93) of their time at sea foraging. No significant differences were found in the mean percentage of time at sea invested by subadults ($59 \pm 15.3\%$; range 39–76), non-lactating ($59 \pm 22.3\%$; range 21–78) and lactating females ($72 \pm 8.2\%$; range 63–80) (ANOVA F [arcsin transformed]=0.599; $p=0.570$; $df=2$, 9).

In addition, no significant differences between subadults and adults were found in the distance of foraging trips from Isla de Lobos, computed as the mean daily distance ($t=-0.178$; $df=181$; $p=0.859$), total distance covered per FT ($t=-0.333$; $df=181$; $p=0.740$), the mean ($t=-0.235$; $df=181$; $p=0.815$) or maximum straight line (Spider) distances ($t=-0.036$; $df=181$; $p=0.971$) (Table 3).

Mean transit speed between consecutive locations was $1.1 \pm 1.04 \text{ m s}^{-1}$, with no differences between subadults and adults ($t=0.523$; $n=2514$; $p=0.601$). Transit speed was negatively correlated with FT duration in both subadults (Pearson $r=-0.605$; $p < 0.001$) and adults (Pearson $r=-0.454$; $p < 0.001$), suggesting that increasing FT durations were associated with a lower mean transit speed, independent of age. A positive correlation was found for FT duration and distance traveled (Pearson $r=0.302$; $p < 0.001$) and mean (Pearson $r=-0.454$; $p < 0.001$) and maximum straight line (Spider) distances (Pearson $r=0.318$; $p < 0.001$) in adult females.

Foraging trip duration, daily distance traveled and maximum straight line (Spider) distance did not show within year differences during the study period (Fig. 2). No individual correlations (Pearson's r , $p < 0.05$) with time were found for these variables in most of the SSLs. Significant increase in FT duration was found in only one SSL (OF10, $p=0.009$), however, significant decreases in daily distance traveled were found in two animals (L14, $p=0.008$; OF12, 0.036), and three decreased the maximum straight line (Spider) distance with time (L08, $p=0.009$; OF01, $p=0.008$; OF12, $p=0.036$).

Table 3Summary of foraging patterns of 22 Southern sea lions (SSL) instrumented in Isla de Lobos (Uruguay). Values are expressed in mean \pm SD.

Animal ID	Foraging Trips	Locations	Transmission period (days)	FT duration (days)	Forage time (%)
L01	5	46	62.2	2.6 \pm 0.8	20.9
L02	8	209	62.4	4.6 \pm 2.5	58.4
L03	5	84	41.6	4.9 \pm 2.7	59.4
L06	9	200	60.7	5.2 \pm 1.6	77.5
L07	6	91	38.4	4.0 \pm 0.8	62.0
L08	8	169	60.1	6.0 \pm 1.0	79.7
L09	4	65	36.5	6.6 \pm 5.9	72.6
L10	6	83	44.5	4.8 \pm 1.9	64.1
L11	2	62	42.5	8.2 \pm 0.8	38.8
L13	6	143	47.7	5.7 \pm 1.1	72.0
L14	7	79	57.5	5.2 \pm 4.2	63.3
L15	4	72	25.3	4.8 \pm 1.4	75.5
OF01	8	127	60.1	5.3 \pm 1.5	70.2
OF02	4	87	36.4	5.4 \pm 4.6	59.3
OF03	3	32	45.6	11.2 \pm 4.8	74.0
OF04	12	124	77.2	5.6 \pm 3.4	87.2
OF06	19	175	157.3	7.0 \pm 2.8	84.6
OF07	12	97	81.1	5.0 \pm 1.5	73.7
OF09	17	155	147.5	7.1 \pm 4.0	81.9
OF10	13	110	133.3	7.2 \pm 2.7	70.1
OF11	10	132	83.5	6.4 \pm 1.6	77.1
OF12	15	180	138.3	8.6 \pm 4.3	93.4
Subadults	8.5 \pm 4.7	117.9 \pm 49.3	70.4 \pm 39.8	6.3 \pm 3.4	69.7 \pm 15.6
Adults	8.0 \pm 4.5	111.5 \pm 49.5	66.7 \pm 36.7	6.1 \pm 3.1	66.7 \pm 18.2
Overall	8.3 \pm 4.6	114.6 \pm 50.5	70.0 \pm 38.9	6.1 \pm 3.1	68.9 \pm 15.9

Animal ID	FT traveled distance (km)	Daily traveled distance (km)	Mean spider distance (km)	Maximum spider distance (km)	FT Speed (m s ⁻¹)
L01	156 \pm 86.3	70 \pm 62.8	29 \pm 8.7	58 \pm 24.5	0.8 \pm 0.7
L02	245 \pm 109.1	60 \pm 20.9	61 \pm 25.0	98 \pm 37.5	0.7 \pm 0.2
L03	261 \pm 93.8	65 \pm 28.1	76 \pm 27.4	123 \pm 35.5	0.8 \pm 0.3
L06	253 \pm 55.9	52 \pm 14.7	70 \pm 11.7	107 \pm 27.1	0.6 \pm 0.2
L07	139 \pm 29.0	37 \pm 15.6	28 \pm 7.0	58 \pm 12.4	0.4 \pm 0.2
L08	254 \pm 48.9	43 \pm 8.0	78 \pm 14.4	112 \pm 24.7	0.5 \pm 0.1
L09	277 \pm 175.7	66 \pm 56.1	57 \pm 28.9	122 \pm 60.2	0.8 \pm 0.6
L10	257 \pm 110.4	55 \pm 11.0	54 \pm 19.4	120 \pm 53.0	0.6 \pm 0.1
L11	282 \pm 117.2	34 \pm 10.8	50 \pm 14.4	80 \pm 20.9	0.4 \pm 0.1
L13	336 \pm 73.4	60 \pm 14.8	81 \pm 14.1	142 \pm 23.6	0.7 \pm 0.2
L14	197 \pm 79.6	44 \pm 11.4	36 \pm 11.3	68 \pm 11.7	0.5 \pm 0.1
L15	135 \pm 10.9	31 \pm 10.4	30 \pm 2.2	50 \pm 10.1	0.4 \pm 0.1
OF01	347 \pm 122.5	66 \pm 13.2	88 \pm 25.6	157 \pm 41.8	0.8 \pm 0.2
OF02	234 \pm 181.2	46 \pm 12.1	41 \pm 16.4	64 \pm 12.0	0.5 \pm 0.1
OF03	323 \pm 126.9	29 \pm 2.9	59 \pm 19.4	125 \pm 36.9	0.3 \pm 0.0
OF04	199 \pm 68.9	46 \pm 31.2	48 \pm 18.7	77 \pm 18.8	0.5 \pm 0.4
OF06	324 \pm 49.1	51 \pm 16.0	82 \pm 17.5	146 \pm 23.0	0.6 \pm 0.2
OF07	166 \pm 47.7	35 \pm 11.6	36 \pm 9.7	75 \pm 20.5	0.4 \pm 0.1
OF09	214 \pm 164.7	31 \pm 13.0	49 \pm 32.9	84 \pm 45.5	0.4 \pm 0.2
OF10	200 \pm 66.5	30 \pm 10.7	49 \pm 20.1	93 \pm 30.4	0.3 \pm 0.1
OF11	259 \pm 71.5	42 \pm 11.7	75 \pm 24.6	124 \pm 34.4	0.5 \pm 0.1
OF12	201 \pm 79.1	27 \pm 11.1	46 \pm 11.3	78 \pm 17.4	0.3 \pm 0.1
Subadults	242 \pm 110.6	45 \pm 21.1	56 \pm 24.7	100 \pm 45.8	0.5 \pm 0.2
Adults	236 \pm 103.9	44 \pm 23.1	57 \pm 26.3	100 \pm 40.2	0.5 \pm 0.3
Overall	237 \pm 105.2	44 \pm 22.6	57 \pm 25.9	100 \pm 41.4	0.5 \pm 0.3

Animal ID	K50 (km ²)	K95 (km ²)	MCP (km ²)	Mean vector (r)	Mean depth (m)
L01	1026	4125	3197	0.60	22.2 \pm 3.4
L02	2803	10,535	8476	0.86	28.5 \pm 6.3
L03	4048	13,729	12,189	0.86	15.5 \pm 3.6
L06	1601	7249	7360	0.94	29.4 \pm 6.9
L07	643	2581	2140	0.70	21.7 \pm 1.6
L08	1483	6989	5352	0.96	33.2 \pm 12.4
L09	2820	10,171	7059	0.84	32.7 \pm 11.3
L10	2567	12,323	9506	0.64	25.0 \pm 2.3
L11	1756	7748	5212	0.79	23.1 \pm 1.5
L13	4622	16,940	12,128	0.93	39.2 \pm 8.6
L14	1904	7966	7433	0.55	17.2 \pm 2.5
L15	466	2121	1696	0.70	21.4 \pm 2.1
OF01	9013	35,704	27,116	0.59	29.9 \pm 12.1
OF02	1739	6517	4450	0.60	21.8 \pm 1.8
OF03	3944	15,446	6723	0.80	18.8 \pm 2.3
OF04	1978	7184	7564	0.65	17.3 \pm 4.4
OF06	5224	21,302	20,746	0.69	16.1 \pm 2.8
OF07	1783	8116	6368	0.80	24.4 \pm 3.3
OF09	7085	32,378	24,864	0.42	20.4 \pm 5.1
OF10	2775	11,696	14,930	0.69	18.7 \pm 3.8
OF11	3593	12,101	7286	0.83	20.9 \pm 3.6
OF12	2119	8839	8892	0.78	24.2 \pm 3.3
Subadults	2892 \pm 1742.1	11531 \pm 7411.8	9362 \pm 6236.6	0.74 \pm 0.15	25.9 \pm 6.6
Adults	3121 \pm 3001.4	12878 \pm 11706.3	10150 \pm 8814.7	0.73 \pm 0.10	22.0 \pm 8.0
Overall	2952 \pm 2079.3	11898 \pm 8499.6	9577 \pm 6812.6	0.74 \pm 0.14	22.9 \pm 7.8

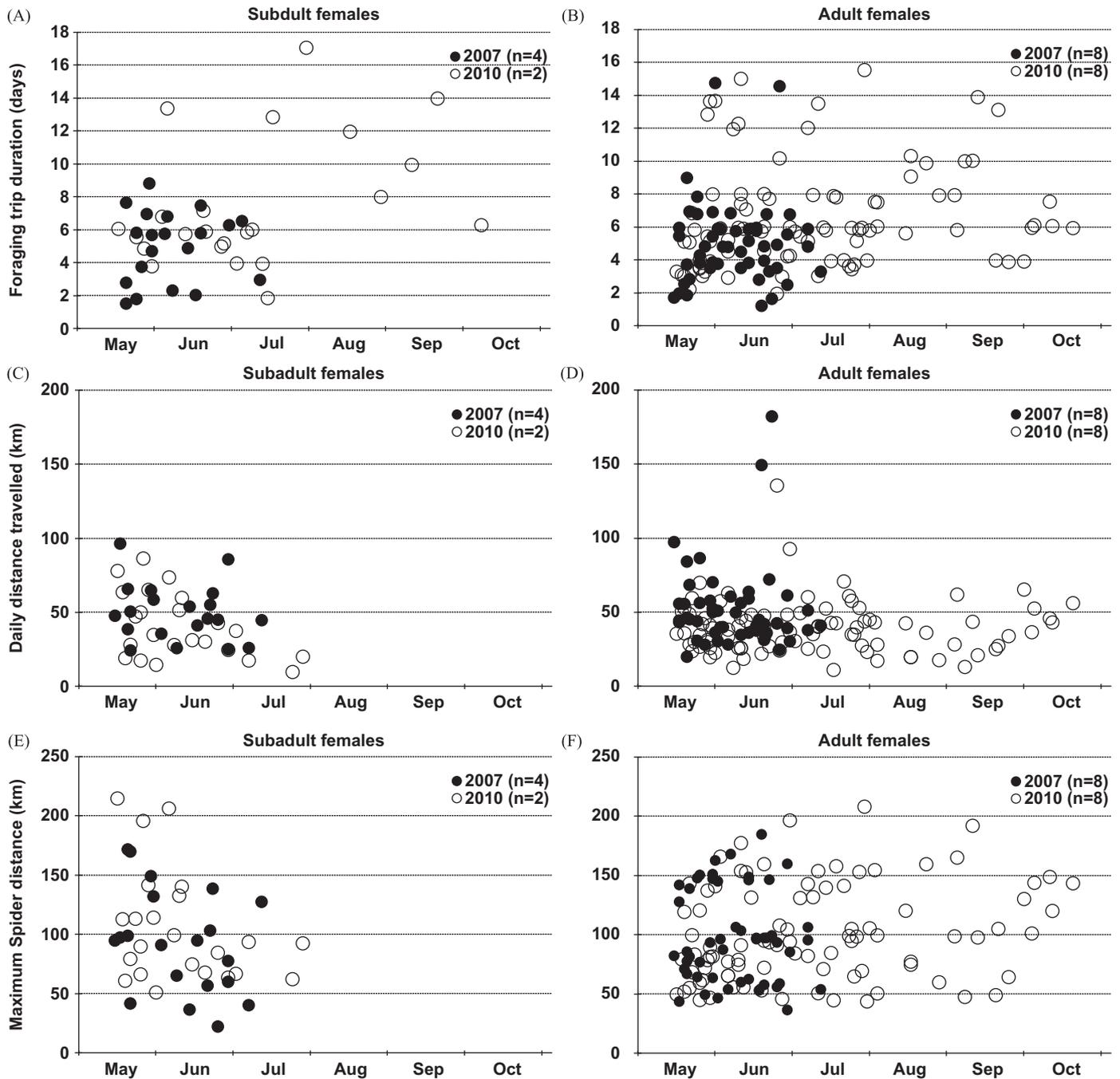


Fig. 2. Changes of FT duration (A and B), daily distance traveled (C and D) and maximum straight line (Spider) distance (E and F) with time for both subadult (left) and adult (right) SSLs in 2007 and 2010.

Interannual differences in the same three variables were checked for the May–July period, with no differences in FT duration (ANOVA $F=2.542$; $df=3, 153$; $p=0.058$) and maximum straight line (Spider) distance (ANOVA $F=1.019$; $df=3, 153$; $p=0.386$). Significant differences were only found in daily distance traveled (ANOVA $F=2.904$; $df=3, 153$; $p=0.037$) due to a significant decrease for adults in 2010 (Post-hoc Tukey's HSD test for unequal n, $p=0.040$). This difference may be due to a small number of single, exceptionally fast (≥ 80 km day⁻¹; Fig. 2d) and short (1.6 ± 0.28 day) foraging trips in four non-lactating adult females (L01, L03, L06 and L09) during 2007.

SSL showed high mean vector (r) values (0.74 ± 0.14 ; 0.42 – 0.96) calculated from FT mean bearings, indicating directional fidelity to foraging sites (Table 3). There was a positive correlation

between mean vector (r) and mean location bottom depth only for adults (Pearson's $r=0.572$, $p=0.021$), suggesting the individuals with higher directional fidelity foraged in deeper areas.

Kernel ranges for 50% (K50) and 95% (K95) of all FT locations for each female were calculated to estimate the areas in which females concentrated their foraging activity. The K95 covered by all sea lions was 25,656 km² in 2007 and 34,846 km² in 2010, with a combined area of 36,222 km². The overall core activity area (K50) was 4337 and 5824 km² in 2007 and 2010, respectively, and 5420 km² combined. No significant differences were found in the mean individual K50 (Mann–Whitney U Test Z [adj.] = -1.912 ; $p=0.056$) and K95 (Mann–Whitney U Test $-Z$ [adj.] = -1.714 ; $p=0.086$) between years. Kernel ranges showed a high variability among animals (K50 CV = 70.4%; K95 CV = 71.4%; Table 3), with

core activity area (K50) ranging from ca 500 to 9000 km² and general use area (K95) from 2000 to 35,000 km² (Table 3).

The size of the individual foraging areas (K95) was positively correlated with the distance traveled per FT (Pearson's $r=0.605$, $p=0.003$) and the maximum straight-line (Spider) distance traveled from Isla de Lobos (Pearson's $r=0.803$, $p<0.001$), with no effect of the satellite transmitter performance ($p=0.108$) and the number ($p=0.065$), duration ($p=0.233$) and mean speed of the FTs ($p=0.172$).

Regardless their reproductive condition, SSL showed strong fidelity to Isla de Lobos, with almost no exchange of animals with other rookeries and foraging activity restricted to the continental shelf off La Plata River Estuary (Fig. 1). Both age classes showed the highest frequency of at-sea activity (K50) near Isla de Lobos, with the adults having a secondary area of activity to the east close to the 50 m isobath (Fig. 3A). Adult female K95 areas were dispersed along an east–west axis covering an extensive shallow area (10–20 m) in the inner part of the estuary and reaching the outer shelf near the 100 m isobath. Subadult females foraged mainly between the 20 and 50 m isobaths along a northeast–southwest axis with coastal movements nearly reaching the rookeries of Islas de Torres and Castillo Grande (Fig. 3B).

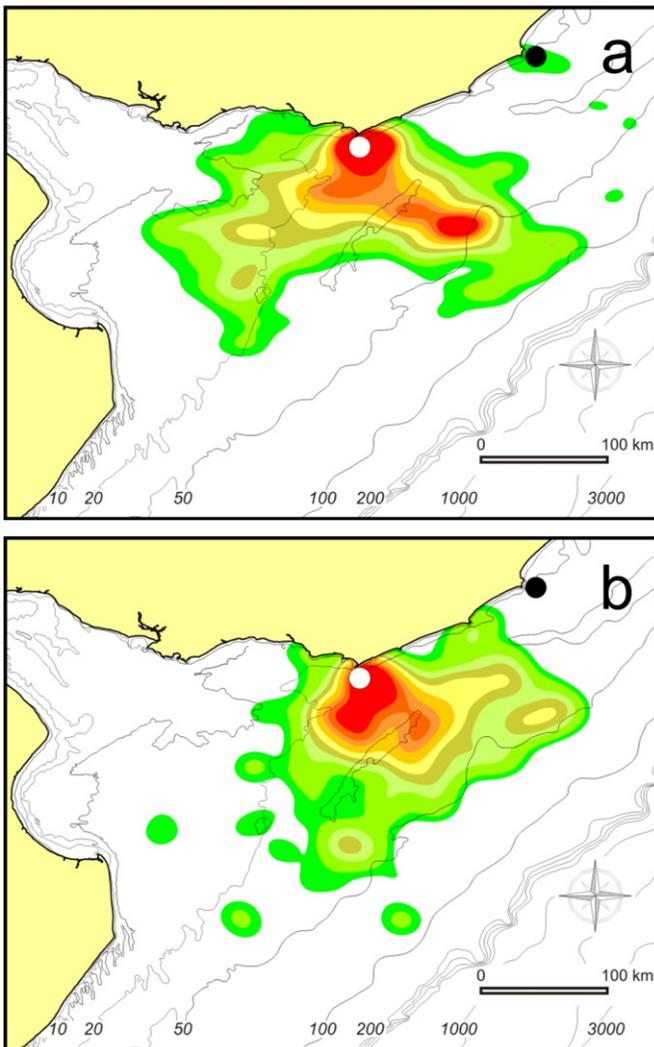


Fig. 3. Kernel areas of adult (A) and subadult (B) female Southern sea lions (SSL). Red indicates the 50% (K50) Kernel area and the entire colored region is the 95% (K95) Kernel area. The white circle marks the location of Isla del Lobos and the black circle the rookery at Islas de Torres and Castillo Grande.

The six animals that carried STDRs yielded a total of 62,556 (10426.0 ± 3227.4 per animal), 64,762 (10793.7 ± 3309.5 per animal) and 286,949 (47824.8 ± 17465.3 per animal) histograms of duration, depth and time at depth, respectively. Almost all dives (99.3%) were shorter than 2 min (the 1.0–1.5 min interval was the most frequent duration bin), with very few dives (0.2%) longer than 8 min. Most (96.5%) dives were less than 50 m in depth (2–10 m and 20–30 m were the two most frequent depth bins containing 36.4% and 25.6% of the dives, respectively). Coincidentally with the dive data, 96.1% of total K95 area corresponded to shallow waters of less than 50 m. Time at depth histograms revealed that animals spend the 73.9% of their time at depths less than 10 m.

4. Discussion

Our study was conducted during the late austral autumn and winter, when we monitored SSL female foraging behavior for a period of 1–5 months. The peak of births for SSL in Uruguay occurs during the second half of January, and the breeding aggregations dissolve by late February (Ponce de León and Pin, 2006; Vaz Ferreira, 1982a). As a result, the lactating females at the beginning of the current study had pups that were ca 3.5 month old. As the lactation period is thought to last 8–11 months (Ponce de León and Pin, 2006), our study covered the last two thirds of the lactation period. Previous studies of diving and foraging behavior in SSL focused on the peak of breeding in Patagonia (Campagna et al., 2001; Werner and Campagna, 1995), Malvinas-Falkland Islands (Thompson et al., 1998) and Isla de Lobos (Riet Sapriza et al., 2011). Our results therefore complement previous studies and provide for the first time information on sea lion foraging behavior during the non-breeding phase and mid-late lactation in autumn and winter.

The FT of adult female sea lions from Isla de Lobos during autumn and winter (May–October; 6.1 ± 3.1 day; $n=22$) were 4.6 times longer than during the peak of the breeding (January–February; 1.3 ± 0.8 day; $n=10$; Riet Sapriza et al., 2011). Shorter FT were also reported during early lactation for female sea lions in both Malvinas-Falkland Islands (0.75 ± 0.46 day; $n=3$; Thompson et al., 1998) and northern Patagonia (3.4 ± 1.4 day; $n=15$; Campagna et al., 2001). The FT duration on Isla de Lobos was also 2.5 times longer than for SSL females during strong 1998 El Niño events in Perú (2.37 ± 0.23 day; range 0.45–4.41; Soto et al., 2006). A more detailed comparison of the FT performance of adult females during the summer in Patagonia and autumn–winter on Isla de Lobos indicates that FT during the breeding season are significantly shorter and faster but with similar travel distance and area covered (Table 4; Fig. 4). It appears that during the peak of the breeding season when pups are young, lactating females decrease FT duration by increasing transit speed but maintain a similar spatial coverage compared with FT later in lactation. This suggests that FT travel distance, area covered and maximum straight line (Spider) distance from the colony are more conserved than FT duration and speed. Nevertheless, increasing FT duration was associated with greater distances traveled and foraging at more distant locations off Isla de Lobos. An early lactation shift to more coastal resources has been described through isotopic signatures in lactating SSL females from Patagonia (Drago et al., 2010) and Uruguay (Franco Trecu et al., 2012), indicating that foraging pattern changes can be associated with dietary shifts.

SSL females off Isla de Lobos performed longer FT than the adult females of most of the sea lion species (*Phocartos hookeri* [1.6–4.6 day; Chilvers et al., 2005, 2010; Costa and Gales, 2000; Crocker et al., 2001], *Neophoca cinerea* [1.50–2.86 day; Costa and Gales, 2003], *Eumetopias jubatus* [0.8 ± 0.5 day; Waite et al.,

Table 4

Comparison of FT performance between adult female Southern sea lions (SSL) in the present study during the autumn–winter with those during the summer breeding season in Patagonia (Campagna et al., 2001). Only adult females with ≥ 2 FT were included. Median speed is expressed in km h^{-1} for comparative purposes. MCP=Minimum Convex Polygon. Maximum values are in brackets. Values are expressed in mean \pm SD. NS=Non significant. **Highly significant ($p < 0.01$).

Parameter	Isla de Lobos (autumn–winter) [n=16]	Patagonia (summer) [n=12]	Statistical differences
Mean FT duration (days)	6.0 \pm 1.9 [11.2]	3.7 \pm 1.3 [6.9]	** [$t=3.608$; $df=26$; $p=0.001$]
Longest FT duration (days)	10.4 \pm 4.0 [15.5]	5.3 \pm 2.0 [9.5]	** [$Z(\text{adj.})=3.157$; $df=16, 12$; $p=0.001$]
Median FT transit speed (km h^{-1})	1.8 \pm 0.5 [2.9]	2.9 \pm 0.8 [4.2]	** [$Z(\text{adj.})=3.668$; $df=16, 12$; $p < 0.001$]
Mean travel distance (km)	237.0 \pm 60.0 [683]	243.8 \pm 133.8 [864]	NS [$Z(\text{adj.})=0.557$; $df=16, 12$; $p=0.599$]
Maximum distance from colony (km)	140.9 \pm 42.7 [214]	126.7 \pm 62.5 [258]	NS [$t=0.716$; $df=26$; $p=0.480$]
MCP (km^2)	9362 \pm 6237 [24,864]	6584 \pm 5041 [17,054]	NS [$t=1.263$; $df=26$; $p=0.218$]

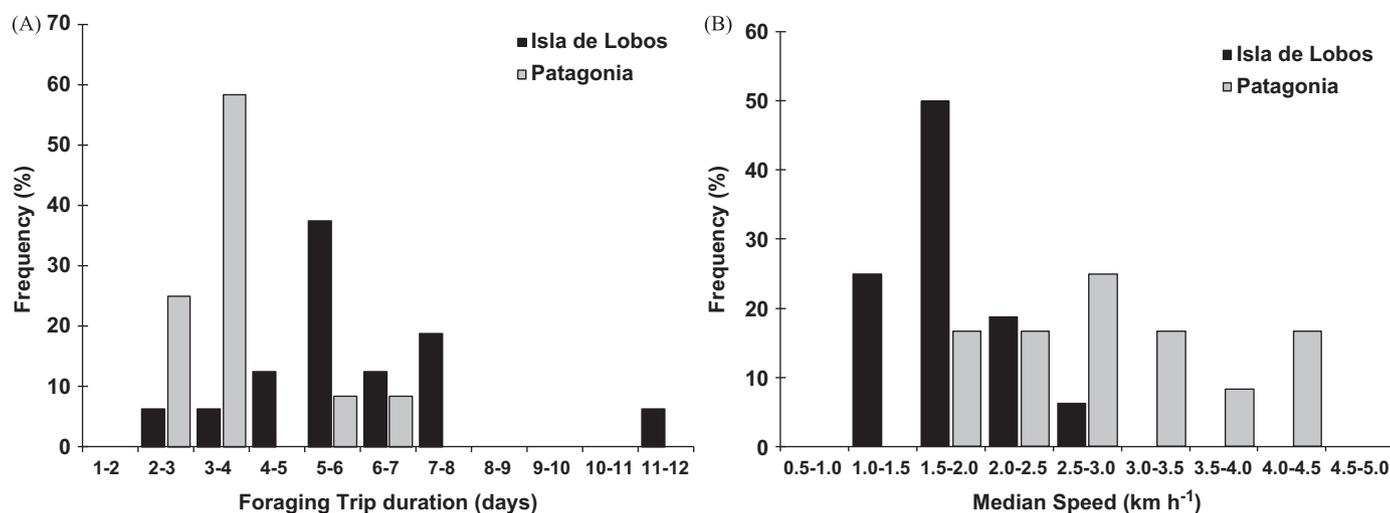


Fig. 4. Comparison of foraging trip (FT) duration (A) and transit speed (B) for Southern sea lions (SSL) from Isla del Lobos ($n=16$) and northern Patagonia ($n=12$; Campagna et al., 2001). Only adult females with ≥ 2 FT were included. Median speed is expressed in km h^{-1} for comparative purposes.

2012], *Zalophus wollebaeki* [0.5–1.7 day; Villegas Amtmann et al., 2008], *Zalophus californianus* [2.0–3.1 d; Antonnelis et al., 1990; Costa et al., 2007; Feldkamp et al., 1989]). Nevertheless, the percentage of the time at sea (≈ 60 –70%; references above) and the maximum distance from the colony (≈ 90 –170 km; references above) are consistently similar across species. This pattern indicates that SSL females later in the pup rearing season have significantly longer foraging trips, with the consequent extension of the fasting time of the pups, but the general balance between at-sea foraging and colony attendance is similar to other sea lions.

SSL are considered to be benthic foragers with restricted to continental shelf waters (Campagna et al., 2001; Thompson et al., 1998; Werner and Campagna, 1995). A non-lactating adult female from the present study (L06) was instrumented with an accelerometer (W1000–3MPD3GT, Little Leonardo Ltd., Japan; Suzuki et al., 2011) for a complete FT confirmed that females from Isla de Lobos are also benthic divers that begin to dive as soon as they leave the colony. The distribution of diving depths and time at depth indicates that SSL females off Isla de Lobos dive at or near the bottom. As a result, the entire area covered during FT could be considered as potential foraging habitats.

During almost all foraging trips, both subadults and adults returned to Isla de Lobos indicating high site fidelity even for those females without pups. Breeding site fidelity also occurs in lactating females from northern Patagonia (Campagna et al., 2001), although Thompson et al. (1998) reported that females in the Malvinas-Falkland Islands hauled out at sites remote from their breeding rookery during 40% of FT. Fidelity of SSLs to Isla de Lobos in conjunction with some directional fidelity to foraging sites suggest a degree of space structuring in Uruguayan colonies,

although the existence of segregated foraging areas should be investigated. Lowther et al. (2012) recognized foraging specialization within discrete, fine-scale foraging areas and habitats in adult female Australian sea lions and hypothesized that this behavior may drive population structure. Due to female philopatry, the Uruguayan colonies are considered to be a separate genetic female stock, with rare or non-existent female exchange with Patagonia (Feijoo et al., 2011; Túnez et al., 2007). Therefore, fine scale foraging segregation in Isla de Lobos females may influence population structure.

SSL foraging habitat covered an extensive area in La Plata River Estuary (LPRE), with a clear center of activity around Isla de Lobos and a significant overlap between subadults and adults (Fig. 5). The extension of the foraging area (K95) appeared to be influenced by a combination of bathymetry and ecological boundaries within the estuary. The LPRE has a salt-wedge regime with distinct horizontal and vertical salinity gradients (Boschi, 1988; Framiñán et al., 1999; Guerrero et al., 1997) that define three main habitats. The upstream limit of the salt wedge in combination with the bottom topography defines a Bottom Salinity Front (BSF, Fig. 5) that delimits an inner tidal riverine habitat (Guerrero et al., 1997; Mianzan et al., 2001). The Surface Salinity Front (SSF, Fig. 5) is the downstream limit of the wedge, being a dynamic and wind-driven boundary between estuarine and offshore marine waters.

The central area of activity (K50) was located in the area of direct influence of the SSF, and adults used the estuarine area as a foraging habitat more extensively than subadults (Fig. 5). The K50 area (mean $\approx 3000 \text{ km}^2$) off Isla de Lobos was 4–5 times the one recorded for other sea lions in insular colonies (i.e., *P. hookeri*,

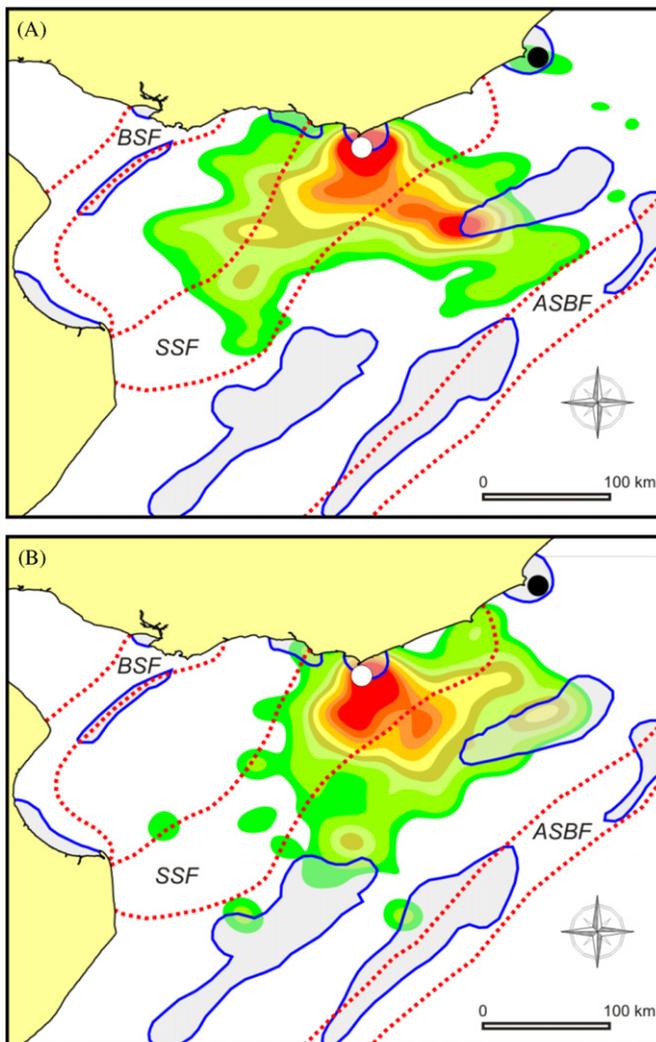


Fig. 5. Kernel areas of adult (A) and subadult (B) female Southern sea lions (SSL). Red indicates the 50% (K50) kernel area and the entire colored region is the 95% (K95) kernel area. The white circle marks the location of Isla del Lobos and the black circle the rookery at Islas de Torres and Castillo Grande. References: Dotted red lines demarcate the Bottom Salinity Front (BSF), Surface Salinity Front (SSF) and Argentine Shelf Break Front (ASBF). Blue areas demarcate proposed areas of High Priority for Conservation (Brazeiro et al., 2003). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

≈ 380–700 km², Chilvers et al., 2005, 2010; *Z. californianus*, ≈ 600 km², Costa et al., 2007). The estuarine area is dominated by homogeneous, muddy sediment with a benthic community less diverse but with higher densities and biomass than those of the adjacent marine areas (Giberto et al., 2004). The retentive properties of the frontal areas of the LPRE favor intense spawning activity of fishes, with some species associated with the SSF (Acha et al., 2008; Berasategui et al., 2004).

Bottom fish assemblages are strongly influenced by horizontal gradients of salinity, and the most important prey of sea lions from Isla de Lobos (whitemouth croaker [*M. furnieri*], striped weakfish [*Cynoscion guatucupa*], large head hairtail [*Trichiurus lepturus*] and anchovy [*Anchoa mitchilli*]; Naya et al., 2000; Ponce de León and Pin, 2006) are key species in the estuarine and marine habitats under different stratification scenarios (Acha et al., 2008; Jaureguizar et al., 2003). Based on N-isotopic values, Botto et al. (2011) suggested that *M. furnieri* and *C. guatucupa*—the most important preys of SSL in the LPRE— probably act as a link between the benthic and planktonic communities. Although

marine mammals have not been integrated into the theoretical framework for trophic relationships in LPRE (i.e., Acha et al., 2008), they may play an important role in the pelagic–benthic coupling with important implications for fisheries management.

Offshore limits of the foraging area were different for sub-adults and adults, with the former restricted to shallower waters (< 50 m) than the latter (up to 100 m). Hence, adult females could exploit the productive areas of the Argentine Shelf Break Front (ASBF; Fig. 5). The beginning of the permanent and highly productive continental shelf-break thermohaline front is located between the 90 and 100 m isobaths (Lutz and Carreto, 1991; Martos and Piccolo, 1988).

The conservation status of the Southern sea lion colonies in Uruguay is of a major concern because of steady population declines (≈ 2–5%) during the past several years (Páez, 2005 [in Campagna, 2008]). Currently, ca. 10,000 sea lions (≈ 2000 pups year⁻¹) are sympatrically distributed with an expanding population (annual increase ≈ 3%; Lima and Páez, 1997) of ca. 400,000 SAFS (Ponce de León and Pin, 2006; Ponce de León, unpublished data). Our results confirm that SSL females forage in extensive shelf benthic habitats of ca. 10–100 m depth in the La Plata River Estuary and the nearby marine area, with a significant directionality in foraging and with no ontogenetic differences in FT performance (duration, speed, proportion of the time at-sea) and coverage (distance traveled, dispersion from the colony and Kernel ranges). Although benthic–demersal fish assemblages are consistently associated with particular salinity habitats (Acha et al., 2008; Jaureguizar et al., 2003), constraints in benthic foraging plasticity have been associated with stable or declining population trends in some pinniped species, especially sea lions (Arnould and Costa, 2006; Costa and Gales, 2003). Human induced habitat disruption by benthic and demersal trawl fisheries can additionally affect the foraging patterns of SSL and induce changes in foraging trip performance or coverage. This is of particular importance as a significant percentage of the area used by SSL (K50=67%; K95=56%) is included in the Argentina–Uruguay Joint Fisheries Management Zone (Figs. 1 and 2).

Although several aquatic areas of high priority for conservation in LPRE have been identified and proposed (Brazeiro et al., 2003), only 15% of the foraging habitat of SSL females is currently included in this area (Fig. 5); if protected breeding rookeries are not considered, this percentage drops to 12%. Moreover, most of the foraging area determined in this study overlaps with trawling operations of the Uruguayan and Argentine fleet targeting SSL prey. This emphasizes the importance of including the at-sea foraging distributions of central place foragers in marine protected areas. If conservation efforts focus only on coastal breeding concentrations, key elements of the life cycle are excluded with potential unpredictable effects.

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