Marine Mammal Science

MARINE MAMMAL SCIENCE, **(*): ***–*** (*** 2015)

DOI: 10.1111/mms.12199

Status, population trend and genetic structure of South American fur seals, *Arctocephalus australis*, in southwestern Atlantic waters

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Abstract

The South American fur seal (SAFS), *Arctocephalus australis*, was severely depleted during the 18th century. This work updates information on distribution, abundance, seasonal movements, and genetic structure along the southwestern South Atlantic. Its distribution in Argentine waters includes nineteen rookeries on the Patagonian coast, Isla de los Estados, and islets of the Beagle Channel. Censuses were carried out in rookeries from Isla Escondida to Isla de los Estados from 1996 to 2014. The largest concentrations are found in Chubut, (4,500–15,500 seals) and Isla de los Estados (4,500). Pups were recorded on Isla Escondida, Rasa, and Isla de los Estados. An increasing number of SAFS were recorded in northern Patagonia, including seals marked in Uruguay. Skin samples were taken from southern Brazil to Tierra del Fuego in order to evaluate population structure and demographic trends. Genetic results indicated no population subdivisions (Φ_{st} = –0.0292, F_{st} = –0.00716, $P > 0.05$). Bayesian skyline plots constructed for the entire data set indicated evidence of rapid population expansion discernible in *Nef* between the last 20,000 and 17,000 yr. Genetics results and observation data from marked fur seals support the hypothesis of ancient gene flow and a single Atlantic population.

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Therefore, SAFS should be managed under international and integrated conservation policies.

Key words: South American fur seal, *Arctocephalus australis*, distribution, abundance, population trend, genetic structure, seasonal movements, southwestern South Atlantic.

The South American fur seal, *Arctocephalus australis*, is one of the two resident otariids in waters of the southwestern South Atlantic Ocean, along with the South American sea lion, *Otaria byronia*.[2] The species occurs on the coasts and offshore islands of South America between southern Brazil on the Atlantic coast and central Perú on the southeastern Pacific Ocean (King 1983, Vaz-Ferreira 1982). Their northern limit for breeding groups on the Atlantic side is at Islas del Castillo (Uruguay) (34°21′S, 53°44′W), while individual males and juveniles move north to Ilha dos Lobos, Torres, Brazil (29°20′S, 49°42′W) (Rosas *et al.* 1994, Sanfelice *et al.* 1999) or even farther (Castello and Pinedo 1977). On the Pacific side, the northern limit seems to be Isla Foca, Peru (5°12′S, 81°18′W) (LRO, unpublished data). At the extreme south, the fur seals are found along the Tierra del Fuego archipelago and at the Falkland Islands (Islas Malvinas).

Total population estimates for the entire distribution area are rather fragmentary, scarce, and out of date. According to Vaz-Ferreira (1982) there was a total population estimated at 320,000 individuals: 12,000 from Peru, 40,000 from Chile, 14,000–16,000 from the Falkland Islands (Malvinas), <3,000 from Argentina, and 250,000 from Uruguay. Recent estimates for Peru by the Instituto del Mar del Perú (2006) indicate a figure close to 16,000 individuals. Strange (1992) estimated a population of between 18,000 and 20,000 animals in the Falkland Islands (Malvinas), but there have not been any recent censuses or monitoring of colonies (Otley 2008). In Uruguay, although the population size has been estimated during the 1990s at 300,000 individuals, this information comes from simulations based on a previously estimated pup number (Páez 2000). More recent information indicates that these figures for Uruguay are overestimated and that the overall population size estimated from aerial surveys would be around half of those figures (VF-T, unpublished data). Nevertheless, Páez (2006) estimated a finite population trend of 1.02% between 1988 and 2005.

In Argentina, size estimations of this and other pinnipeds were carried out during the 1930s (Godoy 1960) and the late 1940s (Carrara 1952). However, as Carrara warned, his survey on Isla de los Estados (Tierra del Fuego) was incomplete because weather conditions restricted the complete survey of the coastline. The rookeries of Chubut Province were surveyed during the 1970s (Ximénez and Scolaro 1974) and the total estimation for those days was around 2,000 individuals. The total population in Argentina was considered to be very low and the South American fur seals fairly rare. After 50 yr the population was surveyed again during the 1990s and continued until recent years.

However, all these figures come from estimates done at different times in each country between the 1950s and the 1970s. What is still lacking is an estimation of the total population for recent years.

[2]The authors consider *Otaria flavescens* (Shaw 1800) as the valid specific name for the South American sea lion, following Cabrera (1940), Vaz-Ferreira (1984), and Rodríguez and Bastida (1993).

The South American fur seal has a long history of exploitation in the southwestern South Atlantic from Uruguay to Cape Horn, and from the very beginning of colonization by Europeans. The first kills of this species go back in time to the trips of Cavendish and Davis in 1586. By 1515, the Spanish were carrying out fur seal exploitation at Isla de Lobos, Uruguay (Vaz-Ferreira and Ponce de León 1987). Nevertheless, the hunting of South American fur seals was much more severe during the 18th and 19th centuries, when most of the species of *Arctocephalus* along the South American coast and the Antarctic Peninsula were driven to the edge of extinction. As an example, in 1775 the ship *States*, from Boston, loaded 13,500 skins from the Falkland Islands (Malvinas) area (Bonner 1982). The Argentine explorers and navigators Vernet and Piedrabuena also hunted fur seals at Isla de los Estados during the 19th century. The hunting extended to the beginning of the 20th century at the southernmost tip of South America. During the 1970s and part of the 1980s, South American fur seals were hunted illegally in southern Chile and Argentina (among other wildlife) to bait traps for southern king crab (*Lithodes santolla*) (Cárdenas *et al.* 1987). No direct estimation of the number of fur seals killed is available, but the overall estimation of amount of illegal wildlife bait utilized between 1976 and 1980 reached values between 200 and 400 tons per year (Cárdenas *et al.* 1987). In Uruguay, between 1873 and 1900, 438,445 fur seals and sea lions were sacrificed, as well as 71,860 more from 1910 to 1942, 17,000 from 1943 to 1947 and 273,738 from 1950 to 1991; in total 801,043 fur seals were taken (tables I and II in Ponce de León 2000). Uruguay was the last country to ban the sealing in South American continent in 1991 (Ximénez and Langguth 2002).

The population reduction during the last two centuries leads to two other questions: (1) how strong was the impact of sealing in the genetic diversity of these populations? and (2) how connected are the fur seal settlements in the South Atlantic at present, given that the original distribution was more extended? The first question was recently answered by Oliveira *et al*. (2009), who detected a genetic bottleneck exclusively in the Peruvian population of *A. australis*, probably as an indirect result of the synergic effect between the repetitive ENSO events (Oliveira 2011) and the human impact in the past (sealing and prey overfishing).

However, the second question remains open. It is only known that fur seal remains are found in many archeological sites where no settlements are found today (Borella 2014). Vaz-Ferreira (1976) stated that the Uruguayan populations were not migratory and that part of the herd maintained its year-round attachment to land, which is true for females and juveniles. Nevertheless, King (1964) suggested that possibly part of the Falkland Islands (Malvinas) population migrates to Uruguayan waters during the winter. Marked fur seals from Uruguayan colonies were previously recorded in northern Argentina (Vaz-Ferreira 1965, 1982), whereas pelagic records for the outer continental shelf are also available (Bastida and Lichstchein de Bastida 1984, Ximénez 1986).

The genetic diversity and population structure of South American fur seals was analyzed using mitochondrial DNA haplotypes, along with *O. byronia*, from colonies located along the Atlantic and Pacific coasts of South America (Túnez *et al.* 2007, 2013). Colonies of the these two areas did not share haplotypes, and this result, based on a limited number of samples for the comparisons between oceans, suggests that populations from each ocean correspond to different, evolutionarily significant units. Recently, the same analysis was carried out using microsatellite loci for *A. australis* (Oliveira *et al.* 2008). Nevertheless, in all these studies the fur seal samples only came from Uruguay and Peru while the Argentine and Chilean coasts were not sampled.

Given this background, the objectives of this paper were: (1) to update the records of distribution and abundance of the South American fur seal along the Argentine coast, (2) to report changes in the seasonal pattern and movements, and (3) to analyze the genetic structure and demography of the fur seal population in the southwestern South Atlantic Ocean.

Materials and Methods

Area Surveyed

The surveys for South American fur seals were carried out between Isla Escondida and the islands of the Beagle Channel in the southwestern South Atlantic (Table 1, Fig. 1) between 1992 and 2013. The census were carried out by means of aerial, boat, and land surveys during and between the breeding seasons of the species, which occurs from the second half of November to mid-January.

Survey Methods

Aerial censuses—The whole coast of Chubut Province was surveyed by air on 2 February 1989, 22 and 26 November 1990, 5 December 1990, 27 January 1995, and 17 November 1995. Both in 1989 and 1990 the surveys were carried out by means of a Cessna B-182 high wing single-engine aircraft, at an altitude of 150 m on the coastal area, and 500–1,000 m on the offshore islands. In 1995, both censuses were made by an Aero Commander twin-engine aircraft, at an altitude of 100–150 m. The whole coast of Santa Cruz Province was surveyed on 24 January 1995 by means of a Piper

Table 1. Geographic position, type, and seasonality of South American fur seal settlements along the Argentine coast.

No.	Settlement	Latitude	Longitude	Type	Seasonality
1	Mar del Plata	38°06′00″S	57°32′59″W	haul-out	seasonal
2	Islote Lobos	41°24′00″S	65°03′00″W	haul-out	seasonal
3	Isla Escondida	43°43′18″S	65°17′00″W	breeding	permanent
4	Cabo Dos Bahías	44°55′47″S	65°31′09″W	haul-out	seasonal
5	Isla Arce	45°00′15″S	65°29′00″W	haul-out	permanent
6	Isla Rasa	45°06′30″S	65°23′30″W	breeding	permanent
7	Cabo Blanco	47°13′00″S	65°44′00″W	haul-out	permanent
8	Islote del Cabo	48°15′09″S	66°13′20″W	haul-out	–
9	Islote Les Eclaireurs Oeste	54°52′17″S	68°06′13″W	haul-out	seasonal
10	Islote Blanco	55°03′40″S	66°32′49″W	haul-out	–
11	Islets south of Cabo Hall	54°58′37″S	65°41′41″W	haul-out	–
12	Islote Veleros	54°55′28″S	65°19′27″W	haul-out	–
13	Is. Barrionuevo (Is. Dampier)	54°51′05″S	64°09′41″W	breeding	–
14	Punta Achával	54°50′16″S	64°10′58″W	breeding	–
15	Punta Jira	54°45′25″S	63°48′51″W	breeding	–
16	Punta Leguizamo	54°43′33″S	63°47′47″W	breeding	–
17	Caleta Ojeda	54°43′25″S	63°48′26″W	haul-out	–
18	Cabo Furneaux	54°43′08″S	63°53′31″W	haul-out	–
19	Pta. Dorgambide and Pta. Shank	54°43′37″S	63°56′23″W	haul-out	–

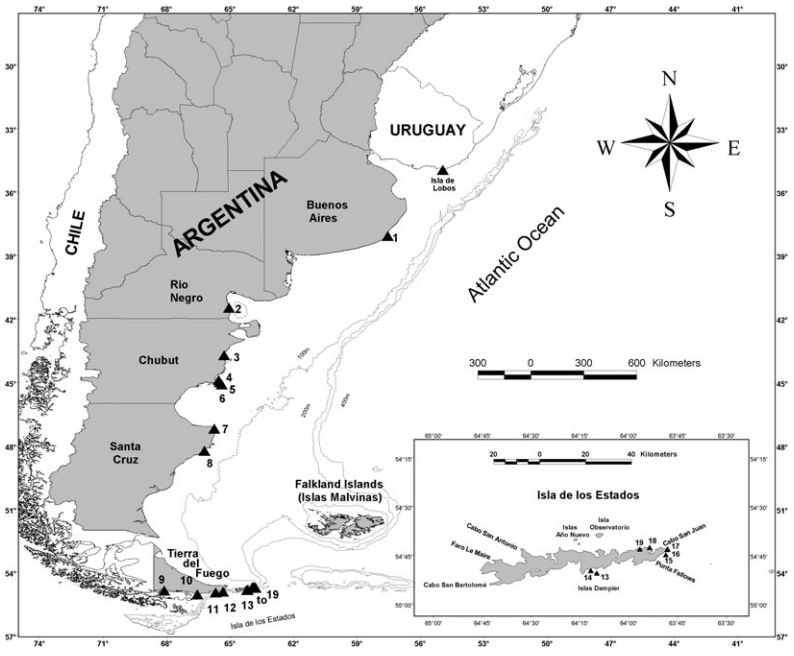

Figure 1. Map showing current distribution of South American fur seal, *Arctocephalus australis*, colonies and rookeries along the coast of Argentina, including Isla de Lobos, Uruguay, and isobaths of 100, 200, and 400 m.

Lance single-engine aircraft. The coast of Tierra del Fuego was surveyed the 14 November 1994, 1 December 1994, and 17 February 1995 with a Coast Guard high wing twin-engine CASA 212, flying at 100–150 m and a speed of 120 knots. Another survey of the 23 March 1994 was performed with an ARAVA high wing twin-engine at 100–150 m and a speed of 110 knots. Finally the surveys made on 30 December 1991 and 27 January 1992 were conducted with a Piper Lancer flying at 100–150 m and 80–90 knots.

On every aerial census each rookery was photographed using 35 mm photographs and slides, with telephoto lenses. Animals were censused later from the projected slides or from black and white photographs. Ektachrome Film 200 ASA was used with the exception of one flight (27 January 1995) in which 100 ASA forced to 200 ASA was used in order to compensate scarce illumination. More recent surveys were photographed with digital cameras.

Boat and land surveys—Isla Escondida, Isla Arce, and Isla Rasa (Chubut Province) were surveyed from a zodiac and were landed upon on several occasions from 1996 to 2013 (see Table 2). Nevertheless, landing or not, the islands were circumnavigated several times in order to carry out direct counts, take photographs, video films, and to record information on a tape recorder. The only colony located in the Beagle Channel was surveyed from tour boats and rubber boats almost weekly from 26 July 1991 to 23 February 1994 (Table 3). Colonies at Staten Island and Islote Veleros were surveyed from the R/V *Polar Duke* from 25 to 31 May 1986 (Schiavini 1987), from a 12 m sailing vessel from 13 November to 8 December 1995 (Parera *et al.* 1997) and

Table 2. Counts performed in South American fur seal colonies along the continental Patagonian coast between 1996 and 2013.

Date	Platform	Total	SD	Pups	Adult males	Subadult males	Females	Juveniles	1-yr-old juveniles
Isla Escondida									
16 December 1996	boat	3,150	150	230					
6 March 2012	boat	2,754							
Isla Arce									
17 December 1996	boat	239	± 13		8	16			
14–16 December 1998	boat/land	609	± 73						
8 December 1999	land	80			9			25	
15 December 2000	land	150							
14 December 2001	boat	50							
12–16 December 2002	boat/land	125	± 9						
20 December 2006	land	30			5		5		20
18 December 2007	boat	70						59	
17 December 2008	boat	45	± 5					45	
12 December 2009	boat	94							
19 February 2013	boat	780	± 20						
Isla Rasa									
26 November 1996	boat	4,430	± 86						
20 December 1996	boat	8,190							
24 February 1998	boat	11,246	± 526						
1 December 1999	boat/land	3,690		18					
16 December 2001	boat/land	2,700		12					
10 December 2002	land	4,011		16					
16 December 2007	land			80	16				
14 December 2008	land	3,759	± 511						
12 December 2009	boat	6,190							
15 February 2012	boat	12,404	± 1,369						
21 February 2013	boat/land	12,955	± 655	550					

(Continued)

Table 2. (Continued)

Date	Platform	Total	SD	Pups	Adult males	Subadult males	Females	Juveniles	1-yr-old juveniles
13 December 2013	boat/land			410					
Cabo Blanco									
27 January 1994	flight/land	322						215	
4 February 2010	land	350		35					
29 May 2011	land	22	± 1					22	

Table 3. Counts performed in South American fur seal colonies along the Fuegian coast.

Locality name	Date	Total count	Pups	Locality name	Date	Total count	Pups
Islotes Les Eclaireurs				Punta Jira			
	19 March 1992	895			27 January 1992	949	
					23 March 1994	P	
Islote Blanco					20 November 1995	1,758	
	11 November 1995	14			18 January 1997	1,743	358
Islets South of Cabo Hall				Punta Leguizamo			
	30 December 1991	93			23 March 1994	251	
	27 January 1992	98			20 November 1995	157	
	23 March 1994	444			18 January 1997	200	P
	1 December 1994	A					
	17 February 1995	P		Caleta Ojeda			
Islote Veleros					20 November 1995	205	
	30 December 1991	181			18 January 1997	333	
	27 January 1992	379					
	23 March 1994	191		Cabo Furneaux			
	14 November 1994	52			25–31 May 1986	50	
	14 January 1997	411			23 March 1994	P	
					22 November 1995	318	
Isla Barrionuevo (Islas Dampier)					18 January 1997	734	
	25–31 May 1986	100					
	27 January 1992	48		East of Punta Shank			
	18 November 1995	130			22 November 1995	86	
	16 January 1997	222	54		18 January 1997	31	

(Continued)

Table 3. (Continued)

Locality name	Date	Total count	Pups	Locality name	Date	Total count	Pups
Punta Achával							
	25–31 May 1986	200					
	23 March 1994	154					
	18 November 1995	400					
	16 January 1997	400	P				

Note: A = surveyed but animals absent. P = animals present but not estimated.

from 10 to 30 January 1997. The counts were made by direct counts and/or count on 35 mm slides of the animals on the islet, and an estimation of animals in the water at the time of the census.

Age and sex categories—During the field census or on photographs, the animals were classified, when possible, into the following age and sex categories: adult males, adult females, juveniles of unknown sex, and pups. In the field or on the projected slides at least two series of counts were carried out within a maximum 10% fixed error (Crespo 1988, Crespo and Pedraza 1991, Reyes *et al.* 1999). The final value is the average between values of the series being considered.

Genetic Structure

Genetic analysis—Sixty-five skin samples were taken from specimens collected on the southern Brazilian coast (= Uruguay) (n = 27), Mar del Plata (n = 9), Puerto Madryn (n = 5), Chubut Islands (n = 24) and Tierra del Fuego (n = 1) in order to evaluate gene diversity, population structure, and expansion through the analysis of the control region (267 bp) from the mitochondrial DNA (mtDNA). Samples from Brazilian coast were considered from Uruguay, because there are no breeding colonies in the coast of Brazil, only two haul-out areas in southern region, specially used by fur seals and sea lions during the austral autumn and spring months (Rosas *et al.* 1994). These areas occur along the coast of the Rio Grande do Sul state and are the result of the dispersal of individuals from their natal colonies after the breeding period. In this sense, it is well accepted that sea lions and fur seals rest along the southern Brazilian coast during their northward foraging trips after their depart from breeding colonies in Uruguay (Vaz-Ferreira 1982).

DNA extraction was performed according to Sambrook *et al*. (1989). The mitochondrial $tRNA^{thr}$-control region was amplified by the polymerase chain reaction (PCR; Saiki *et al*. 1985) using primers Thr/Pro and Cent (Wynem *et al.* 2000). Polymerase chain reactions (PCR) were performed in a 20 mL final volume using Pharmacia kit, 0.2 mM dNTPs, 1 mM of each primer, and 25 ng of DNA template. PCR conditions were as follows: 90 s at 94°C, 39 cycles of 94°C for 30 s, 45 s at 56°C, 70 s at 72°C, 10 min at 72°C. PCR products were purified using Shrimp alkaline phosphatase and Exonuclease I. Sequencing reactions were performed using the APBiotech DYEnamic ET Dye Terminator Cycle Sequencing Kit and read on a MegaBACE 1000 automated sequencer (Amersham Biosciences).

Sequence Analysis

Sequence electropherograms were checked with the software Chromas (Technelysium). Finished sequences were aligned using Clustal X (Thompson *et al*. 1997), manually edited with Bioedit 6.0.7 (Sequence Alignment Editor, Hall 1999) and corrected by eye. A highly variable TC-rich region from site 91 to 118 ("TC landmark," as recognized by Lento 1995) exhibited ambiguous alignment, and was removed from the data set prior to analysis as in Lento (1995) and Wynen *et al.* (2000).

The genetic variability was estimated using the following indices: haplotype (h) and nucleotide (π) diversity, calculated with Arlequin 3.1 (Schneider *et al.* 2000). Assessments of population genetic structure based on the sequence data were also performed with Arlequin, using an analysis of molecular variance (AMOVA) approach. Two variants of the AMOVA were performed to assess consistency of population

subdivision patterns: (1) haplotype frequency only (F_{st}; Weir and Cockerham 1984) and (2) *P*-distance F_{st}.

For each AMOVA variant, the same subdivision scenario was tested: five population units (each sampling locality treated as a distinct population). The pairwise F_{st} and F_{st} values were calculated with Arlequin 3.1 (Schneider *et al.* 2000). We also analyzed the sequences in order to test and infer possible events of population oscillation. The genetic diversity of each locality was tested against the null hypothesis of neutrality and we inferred possible events of population expansions using Fu's *Fs* (Fu 1997) and the Tajima's *D* (Tajima, 1989). However, Bayesian skyline reconstructions were implemented using BEAUTi 1.7.4 and BEAST 1.7.4 (Drummond *et al.* 2012) for all data pooled as whole population, according to population structure results. We used a HKY substitution model gamma site heterogeneity (generated by likelihood with PAUP 4.0b10, Swofford 2002) with eight categories and a strict molecular clock prior with Dickerson *et al*. (2010) mutation rate of 5.74×10^{-7} s/s/gen derived for *Callorhinus ursinus* (Hoffman *et al*. 2011). 30,000,000 Markov Chain Monte Carlo (MCMC) iterations were implemented and a Bayesian skyline plot was generated using Tracer 1.5 (Drummond *et al.* 2012).

Results

Distribution and Abundance

South American fur seals are distributed along the Patagonian and Fuegian coasts in 19 colonies (Fig. 1). Geographic position, type, and seasonality of each colony are shown in Table 1.

Punta Mogotes (Mar del Plata)—These rocky reefs are located *ca*. 1,000 m off Punta Mogotes, and are formed by three main underwater ridges not connected to the coastline and only occasionally exposed during exceptional spring low tides and strong winds (Bastida and Rodríguez 1994, Dassis *et al.* 2012). Some 50–400 fur seals concentrate and float around these reefs between May and December each year, with a highly predictable annual cycle.

Islote Lobos (Río Negro)—This islet is located in the Golfo San Matías. Around 1,600 fur seals are found there between May and October. The highest numbers are found in August, with a decline in September. No fur seals are sighted in the area in November (Svendsen *et al.* 2013).

Isla Escondida—This is a rocky island with a 300 m long east-west axis and around 50 m wide in the north-south axis, located at 5 nmi from the coast. It is shared by the South American fur seal and the South American sea lion. The latter occupies the flattest areas of the island while fur seals occupy mainly the steep and abrupt rocky zones. Both species breed on the island, but avoid overlapping during the peak of their respective breeding seasons. Between November and January a maximum of 2,300 South American fur seals were recorded, while there was a maximum of 570 South American sea lions at the end of its breeding season in February. One census carried out in October 1999, before the breeding season, counted some one thousand animals, rapidly increasing throughout November and December, when at least 230 fur seal pups were recorded on the southwest corner of the island (Table 2). Most of the social components of the fur seals of this rookery are juveniles of both sexes. The

South American sea lion had the typical reproductive structure of other breeding rookeries of the area (Crespo and Pedraza 1991, Dans *et al.* 1996, Reyes *et al.* 1999).

Isla Arce—This is a rocky 400 × 100 m island. It was surveyed several times from boats and aircraft. This is one of the few islands where it is possible to land. About 1,000 adult and subadult male fur seals populate mainly the southeast side of the island (Table 2). No evidence of females, pups or reproductive behavior was detected. This island is also shared by breeding groups of about 540 South American sea lions with pups.

Isla Rasa—This is a flat island 700 m long and 150 m wide with multiple creeks. It has the largest rookery of South American fur seals along the Argentine Patagonian coast. After the breeding season it contains more than 12,000 individuals, about 60% of the total population of Argentina from Mar del Plata to the Beagle Channel, including Isla de los Estados. The lowest number of individuals was recorded before the breeding season in October and November. This island could not be surveyed between March and August. The social component of Isla Rasa is mainly juveniles of unknown sex. Although the island was surveyed many times by boat or aircraft, breeding (pupping, lactating females, or any evidence of social reproductive behavior) was not detected until landings were made on 8 December 1999, and several times from 2001 to 2014. In 1999 18 females were recorded with pups and a few breeding groups at the top of the island. The number of pups increased to 55 in more recent years (2008–2010). Landings could not be made in 2011 and 2012, but in February 2013 550 pups were counted on the island, as well as 410 and 600 pups in December 2013 and February 2014 respectively. This means an increase of the pups born for the period 1999–2014 of 34.11% (CI: 13.8%–54.4%). As in other rookeries, some 500 South American sea lions share the island with the South American fur seals during the breeding season.

Cabo Blanco—This is one of the few rookeries located in a group of abrupt and steep rocky islets at the tip of this cape. It is of very difficult access from land and almost continuously battered by the sea. The number of fur seals varies between 300 and 500 individuals, mainly juveniles with few adult individuals. In February 2010 a few pups were counted. As in other colonies, this area is shared with few South American sea lions, approximately 350 to 600 individuals (Carrara 1952).

Islote del Cabo—This is a small islet in Santa Cruz Province on which South American fur seals are found. Individuals on this islet were counted on photographs taken during the aerial survey carried out in January 1995 and January 2012. Less than one hundred individuals shared the islet with 52 South American sea lions in 1995, while in 2012 140 fur seals were counted with 15 sea lions.

Islotes Les Eclaireurs—This is a group of flat rocky islets in the Beagle Channel about 13 km east of Ushuaia. South American fur seals occupy one small islet exposed to the prevailing winds and swell. Fur seals are present from late February to mid-September. They gather in very high densities, reaching a maximum record of 895 in March 1992, in an area of less than 2,000 m^2.

Islote Veleros—This is a rocky triangular-shaped rock, located 4.5 km northeast of Cabo Buen Suceso, the eastern extreme of the Isla Grande de Tierra del Fuego. The rookery here is of juvenile and nonbreeding adults that seem to peak during January (Table 3). No pups were observed although it was visited in the middle of the breeding period (13 January 1997).

Islets south of Cabo Hall—South of Cabo Hall there is a series of islets and rocks exposed to the prevailing swell and wind. One of these islets is occupied by South

American fur seals. It represents a nonbreeding aggregation with peak numbers of 44 animals recorded in March 1994 (Table 3).

Isla de los Estados—Located to the east of the Isla Grande de Tierra del Fuego, it has a steep relief with rocky coasts and deep fjords and coves. This island holds four breeding colonies (Table 3) and three other rookeries. The colonies are located in places exposed to the swell and wind, which makes it difficult to take a census from a sailboat or zodiac or even a photographic record from an airplane. At least Isla Barrionuevo, Punta Achával and Cabo Furneaux have permanent colonies recorded during both the breeding and nonbreeding seasons. The total count for the entire island was 3,663 individuals. The pup production of Isla de los Estados can be estimated at about 546 pups, based on the average number of pups present in the colonies at Punta Jira and Isla Barrionuevo, applied to the total counts made at Punta Achával and Punta Leguizamón. Summarizing, the total population of Argentine Tierra del Fuego can be estimated as 4,174 animals, including the aggregate of animals present on the islets of Cabo Hall (estimated at 100).

Seasonal Pattern and Movements

Although the fur seal colonies could not be followed throughout the entire year, it was clear that the number of fur seals varied between seasons. Most of the surveys by land, air, or sea were carried out between October and February when the weather conditions are fairly acceptable. Of the colonies surveyed only Islote Lobos in Golfo San Matías, and Isla Escondida and Isla Rasa in Chubut showed a clear seasonal pattern (Fig. 2). While the peak in numbers at Islote Lobos is in August (Svendsen *et al.* 2013), the number of fur seals increase in on the Chubut Islands from October to February, which coincides with weaning in Uruguay (September–December). In fall the numbers decrease. However, the time of the year in which the animals abandon the area is not clear. A similar seasonal movement was detected throughout the Beagle Channel. The number of fur seals increases from late February to mid-September reaching a maximum by March. We believe that these seals move westward to the many islands and islets located in southernmost Chile.

Movements within the distribution range of the South American fur seals come from records of individuals marked at birth in the breeding colony at Isla de Lobos, Uruguay. The first record was made in October 2007 at Bahía Blanca, Argentina, where an individual marked in Uruguay during January 2007 was found. Subsequently, in January 2009 an individual tagged in December 2006 in Uruguay was observed at Isla Escondida, Argentina. Another case was documented at Pehuen Co, Argentina, during July 2011, corresponding to an individual marked in February, 2010, which had been observed on Isla de Lobos until November 2010. Another individual tagged in Uruguay in December 2010, and seen in Uruguay in October 2011, was observed in Araranguá, Santa Catarina, Brazil, in August 2012. Finally, an individual marked at Isla de Lobos in February, 2012 was observed in Golfo San Matías in February 2013. It is interesting to note that a proportion of animals tagged at birth at Isla de Lobos were resighted four years later in the birth area. Therefore, these records indicate that young South American fur seals, after weaning, perform migrations between different rookeries within their range, traveling more than 1,000 km.

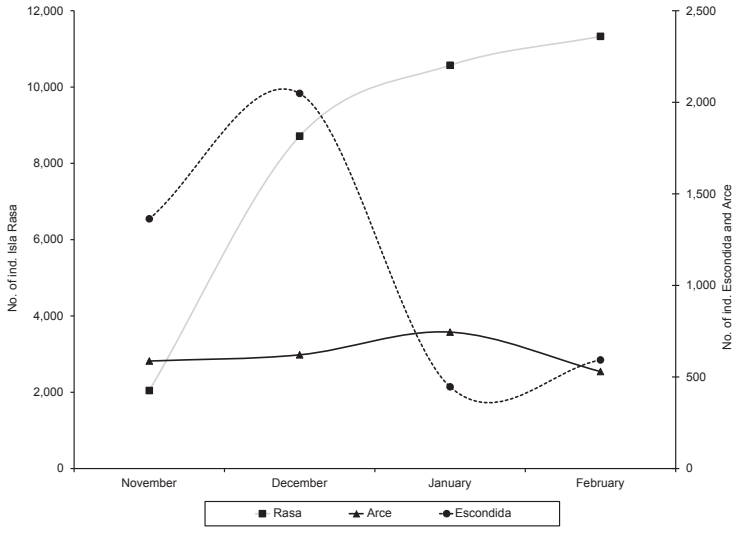

Figure 2. Seasonal changes in numbers recorded during reproductive season of South American fur seal, *Arctocephalus australis* rookeries off central Patagonia, Argentina.

Genetic Analysis

Sixty-five sequences of mtDNA control region were obtained for analysis, which comprised 267 bp. The segment contained 29 variable sites, defining 29 different haplotypes (see Table 4 for GenBank accession numbers). The most common and widespread haplotype was shared by 21 individuals from several sampled localities, absent only in Tierra del Fuego (Table 5). High levels of genetic diversity were observed among individuals of *A. australis*. Haplotypes 18 and 19 are exclusively from Mar del Plata. The genetic diversity (h) and the nucleotide diversity (π) calculated for the species as a whole along the Atlantic coast of South America were 0.8769 ± 0.0340 and 0.011288 ± 0.006623, respectively.

The analyses of population structure based on the molecular variance conducted considering the scenario using haplotype frequency only (F_{st}; Weir and Cockerham 1984) indicated no population subdivisions along the southwestern South Atlantic ($F_{st} = -0.00716$, $P = 0.84$). Similarly, the second scenario based on P-distance Fst ($\Phi_{st} = -0.0292$, $P = 0.78592$) gave the same results. Furthermore, nonsignificant pairwise F_{st} and Φ_{st} values observed among these samples (see Table 5) suggest that the specimens from Brazil, Uruguay, and different places in Argentina belong to the same population.

Both neutrality tests and Bayesian skyline plots detected population oscillation. The Fu's *Fs* neutrality tests detected a rapid population expansion from a small effective size in the fur seals from Uruguay (Fu's *Fs*: -10.85149, $P < 0.0001$) and the islands of Chubut (Fu's *Fs*: -6.58459, $P < 0.001$) (Table 6). Most of Tajima's D values were also negative suggesting population expansion. However, they were not significant for $P < 0.05$. Puerto Madryn was the only population with no signal of population oscillation in both neutrality tests (see Table 6). We were not able to calculate for the Tierra del Fuego population due to its small sample size ($n = 1$) (Table 5).

Table 4. List of individuals that bear each mitochondrial DNA control region haplotype. Absolute frequency in the sample and geographic distribution of haplotypes.

Haplotype	Individuals	GenBank accession number	Frequency	Locality	Country
1	CP1	KM593065	1	Cabo Polonio	Uruguay
2	CP2, GEMARS 660, GEMARS 671, GEMARS 676, GEMARS 687, GEMARS 705, GEMARS 712, GEMARS 729, AF01-2001-MDP, BV-MDP, 78-00-MDP, 85-00-MDP, 110-00-MDP, Aa38, Aa29, Aa101, Aa105, Aa112, Aa113, Aa119, Aa121	KM593066	21	Cabo Polonio Rio Grande do Sul Mar del Plata Chubut Islands Puerto Madryn	Uruguay Brazil Argentina Argentina Argentina
3	CP3, Aa110	KM593067	2	Cabo Polonio Chubut Islands	Uruguay Argentina
4	GEMARS 556	KM593068	1	Rio Grande do Sul	Brazil
5	GEMARS 586	KM593069	1	Rio Grande do Sul	Brazil
6	GEMARS 591, Aa114, Aa34	KM593070	3	Rio Grande do Sul Puerto Madryn	Brazil Argentina
7	GEMARS 656	KM593071	1	Rio Grande do Sul	Brazil
8	GEMARS 657	KM593072	1	Rio Grande do Sul	Brazil
9	GEMARS 662	KM593073	1	Rio Grande do Sul	Brazil
10	GEMARS 664	KM593074	1	Rio Grande do Sul	Brazil

(Continued)

Table 4. (Continued)

Haplotype	Individuals	GenBank accession number	Frequency	Locality	Country
11	GEMARS 668, GEMARS 689, GEMARS 708, GEMARS 722, 24-99-MDP, 86-00-MDP, Aa130, Aa124, Aa125	KM593075	9	Rio Grande do Sul Mar del Plata Chubut Islands	Brazil Argentina Argentina
12	GEMARS 683, Aa05	KM593076	2	Rio Grande do Sul Chubut Islands	Brazil Argentina
13	GEMARS 694	KM593077	1	Rio Grande do Sul	Brazil
14	GEMARS 696	KM593078	1	Rio Grande do Sul	Brazil
15	GEMARS 714	KM593079	1	Rio Grande do Sul	Brazil
16	GEMARS 728	KM593080	1	Rio Grande do Sul	Brazil
17	GEMARS-PARNA-LNRS	KM593081	1	Rio Grande do Sul	Brazil
18	71-00-MDP	KM593082	1	Mar del Plata	Argentina
19	87-00-MDP	KM593083	1	Mar del Plata	Argentina
20	Aa25	KM593084	1	Puerto Madryn	Argentina
21	Aa102	KM593085	1	Chubut Islands	Argentina
22	Aa103, Aa104	KM593086	2	Chubut Islands	Argentina
23	Aa106, Aa116, Aa122	KM593087	3	Chubut Islands	Argentina
24	Aa107	KM593088	1	Chubut Islands	Argentina
25	Aa108	KM593089	1	Chubut Islands	Argentina
26	Aa109	KM593090	1	Chubut Islands	Argentina
27	Aa111	KM593091	1	Chubut Islands	Argentina
28	Aa115, Aa118	KM593092	2	Chubut Islands	Argentina
29	Aa125	KM593093	1	Chubut Islands	Argentina

Table 5. Pairwise F_{st} (below diagonal) and Φ_{st} values (above diagonal) based on *P*-distance method from mtDNA control region analysis among five Atlantic populations of South American fur seal. n = number of samples.

Population	BR + UY (n = 27)	MDP (n = 9)	PM (n = 5)	CI (n = 24)	TF (n = 1)
Southern Brazilian coast (= Uruguay) (BR + UY)	–	-0.01005	0.0001	-0.00733	-0.65156
Mar del Plata (MDP)	-0.00503	-0.02439	-0.01600	0.01253	-0.56507
Puerto Madryn (PM)	-0.07192	–	-0.04142	-0.02241	-0.7037
Chubut Islands (CI)	-0.00186	0.02408	–	–	-0.59667
Tierra del Fuego (TF)	-0.06020	0.10714	-0.33333	0.05482	–

Table 6. Fu's *Fs* (1997) and Tajima's *D* (Tajima, 1989) neutrality tests for population expansion event. Negative values and statistically smaller than zero (*P*) indicate a deviation from expected values under neutral evolution model and an indicative of population expansion event.

Population	Fu's *Fs*	*P*	Tajima's *D*	*P*
Southern Brazilian coast (= Uruguay) (BR + UY)	-10.85149***	0	-1.23309	0.109
Mar del Plata (MDP)	0.97375*	0.695	-0.51253	0.355
Puerto Madryn (PM)	-0.88390*	0.139	0.03892	0.663
Chubut Islands (CI)	-6.58459***	0.001	-1.03146	0.184
Tierra del Fuego (TF)	–	–	–	–

Note: $^{*}P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Bayesian Skyline Plot constructed for the entire data set indicated evidence for population expansion, discernible in *Nef* between the last 20,000 and 17,000 years (Fig. 3).

Discussion

The present study updates the current information about the distribution, abundance, seasonal changes and the genetic structure of the South American fur seal along the southwestern Atlantic coast.

Most of the 16 rookeries surveyed are located on coastal islands. The most remote localities are Isla de los Estados, which includes six rookeries, and Isla Rasa. The northernmost settlement on the Argentine coast is located at Punta Mogotes, close to Mar del Plata in the Province of Buenos Aires (38°06′S), which was surveyed by Bastida and Rodríguez (1994). The remaining rookeries are located along the Patagonian coast and reported in this paper.

Among the Patagonian colonies, Isla Escondida was always recognized as a fur seal rookery and surveyed repeatedly throughout the 20th century. It was also perceived as the settlement containing the residual population of the species. Nevertheless, in Chubut Province, other locations were indicated as settlements of fur seals during the 1970s. For the islands of Chubut Province, where censuses were carried out by the late 1940s, early 1970s and during the 1990s, a rough estimation of the rate of

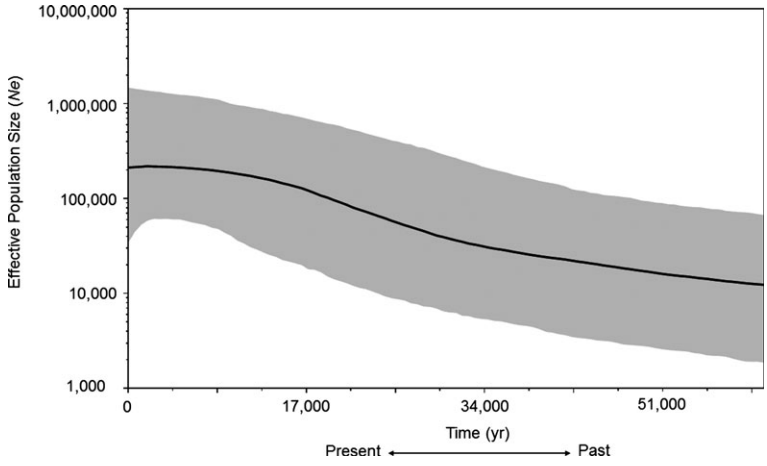

Figure 3. Bayesian skyline plot of historical female effective population size (straight line) and the corresponding 95% posterior probability interval (gray area).

increase in the number of fur seals was calculated at about 8%. Other rookeries along the coast of Argentina do not allow this calculation because of the lack of data. Carrara (1952) presented a total figure of 250 individuals, based mainly on counts at Isla Escondida, for the triennial period 1946–1949. No mention was made in his surveys about other fur seal rookeries in the Province of Chubut. Ximénez and Scolaro (1974) totalize an estimated figure of 2,980 fur seals based at Isla Escondida, Cabo Dos Bahías, Isla Rasa, and Isla Arce. These latter three rookeries are located within a distance of at least 15 nautical miles. During the end of the 1970s and the 1980s, Cabo Dos Bahías was abandoned, probably as a consequence of human interference, given that it is a game reserve.

Although the number of newborn pups increased in recent years, the remarkable number of animals at Isla Rasa cannot be explained by the number of pups produced in colonies at Isla Escondida and Tierra del Fuego. On the other hand, a potential immigration factor could be proposed. These animals most likely are coming from colonies located either in the Falkland Islands (Malvinas) to the east or Isla de Lobos at Uruguay in the north, as indicated by the displacement between rookeries registered through tagged animals. During the last few years the increase in number of South American fur seals sighted along the coast of the Province of Buenos Aires, the city of Buenos Aires, and the Paraná River delta was noteworthy,[3] a fact which could be related to the ending of the fur seal harvest in Uruguay since 1991.

The fur seal colonies in Tierra del Fuego hold the larger breeding aggregations identified along the Patagonian and Fuegian coast. Comparison with previous numbers for the area is difficult due to the almost absolute lack of data. The oldest records available are those described in the journal of a sailor, Saráchaga (Ministerio de Marina 1884) and those of a narrative from a navy captain (Bescoechea 1966). They mention colonies that undoubtedly refer to the ones at Punta Jira, Punta Lequizamo, and

[3]Personal communication from D. Albareda, Acuario ZOO Buenos Aires, República de la India 3000, Buenos Aires, Argentina, October 1996.

Caleta Ojeda. Then, these colonies were present at least from the late 19th century. These colonies could not be surveyed by Carrara (1952) due to weather conditions.

The colony at Islotes Les Eclaireurs is a remarkable example of the trend that the species experienced during the late 1980s and early 1990s. By the year 1987 the islet held no more than 10 animals, with the same seasonal pattern discussed above. However, in only 5 yr the islet held close to 1,000 animals. Although we did not conduct more surveys after the 1993/1994 season, the presence of animals followed the same seasonal pattern, and their peak number always was close to the peak aforementioned. Animals are present out of the breeding season, from late February to September, when they move to unknown breeding grounds, probably located in the Chilean Fuegian archipelago. The increase at this colony was due to migratory movements. Isla Rasa is another example of an explosive increase; this colony went from 55/60 pups in 2011 to almost 600 in 2012/2014.

Summarizing the surveys carried out during the 1990s, the four rookeries totaled about 15,000 individuals, mainly located at Isla Rasa and Isla Escondida. Adding the colonies located at Tierra del Fuego (about 4,200), the total figure for the Argentine Patagonian and Fuegian coast can be estimated as at least 20,000 individuals.

In general, the number of animals and pups may be considered as a lower bound of the actual numbers. South American fur seals prefer to gather in very inaccessible places, and their colonies are characterized by their exposure to wind and swell: only two colonies allowed landings. As pups and even larger animals can hide behind rocks or into small caves, counts must be considered as a lower estimate.

The present evidence does not allow assessing trends. There are no figures on South American fur seal numbers related either to the presealing or for the sealing period (17th–19th centuries). It is clear from the scarce historic evidence, that the southwestern South Atlantic Ocean was one of the first sealing grounds in the southern hemisphere and that the South American fur seal was one of the first *Arctocephalus* fur seals subjected to exploitation. Therefore, the low numbers available early in the 20th century are the base of our comparisons.

There are indications of population increases both in the aggregations located in Uruguay (Páez 2006) and Chile (Sielfeld 1999) and a decline in the Falkland Islands (Malvinas) (Otley 2008, 2012). In the case of Tierra del Fuego, the decrease in fishing effort for southern king crab during the late 1980s and 1990s probably triggered the population increase reported (Lescrauwaet and Gibbons 1994). The only evidence of population for this area comes from Islotes Les Eclaireurs.

Even though some census populations have shown strong signs of recent recovery (see results), the population expansion detected in the mtDNA sequences present a sign of an old expansion near the end of the Pleistocene. This period coincides with the Last Maximum Glacial (LMG), moment that exposed the continental shelf along the Atlantic coast of South America. According to molecular and paleontological data (see Fraser *et al*. 2012 for a review), on the Atlantic coast, the shoreline was attached to the continental shelf at that time, which facilitated the access to breeding and foraging areas and consequently created a favorable scenario for population expansion for the fur seals. Moreover, the later retreat of glacial coverage of the LMG ice sheet along the Pacific coast of South America changed local currents, temperature and salinity, and generated productive oceanic areas (Cassens *et al.* 2005) and top predator population expansions. Similar results were observed for the dusky dolphin (*Lagenorhyncus obscurus*) in Argentine waters (~16,000 yr, Loizaga de Castro 2013) and South Africa (~20,000 yr, Cassens *et al.* 2005).

With regards to genetic diversity and population structure of fur seals, Túnez *et al*. (2008) used mitochondrial DNA haplotypes and compared populations from Peru on the Pacific coast and Uruguay on the Atlantic coast, which did not share haplotypes. Oliveira *et al*. (2008) conducted extensive genetic and morphometric analyses to determine the level of differentiation between the same populations of fur seals (but with much larger sample sizes), and discussed these results in the light of Evolutionarily Significant Units (ESUs) (Moritz 1994) and suggested that each ocean basin represented a different ESU of the species. More recently, Túnez *et al*. (2013) analyzed the mtDNA control region of fur seals from Uruguay and Isla Guaffo in southern Chile, corroborating this suggestion that these breeding areas would correspond to different conservation units. Moreover, Abreu (2011), analyzing microsatellite loci and mtDNA loci samples from Brazil, Uruguay and Argentina, found no population structure as well. According to Vaz-Ferreira (1982) and Páez (2000, 2006) the Uruguayan population could be the potential original source for most of migrants to the remaining populations. Even after a long period of commercial sealing pressure in its islands (from the 17th century to 1991), the fur seal does not show a particularly reduced level of genetic variability along the Atlantic coast as observed along the Pacific coast (Oliveira 2011).

Accordingly, our mtDNA results support the hypothesis that migration among breeding colonies sustains an ancient gene flow that results in a single Atlantic population. Also, the nuclear loci indicate current gene flow among Atlantic colonies (Abreu 2011). The migratory implications of these findings for the conservation or management plans of South American fur seals are important. Based on the current gene flow detected among South Atlantic colonies, this population should be managed in an international and integrated manner by the authorities of the South Atlantic countries that have not only breeding colonies, but also haul-out areas of the species, since they share the same population and eventually similar conservation problems.

Acknowledgments

The surveys carried out for the South American Fur Seals were supported by National Geographic Society (Grant 4245/95 to EAC and ACMS), the Patagonian Coastal Zone Management Plan (1993–1996), the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT PICT 4025/1998, 01763/2007 and 1834/2011), Universidad Nacional de Mar del Plata, (PI15/E471, 15/E335 and 15/E564), the Scientific Program of Cooperation between Spain and Latinoamerica (1996–1998), the United Nations Development Program (2005–2007), the Mohamed Bin Zayed Species Conservation Fund Project No. 0925516 (2011–2013), the Amnéville Zoo (France) (2004–2013) and the IBOL Fund (2012). Logistic support was provided by Fundación Patagonia Natural, Centro Nacional Patagónico and Centro Austral de Investigaciones Científicas (CONICET), Universidad Nacional de la Patagonia (CIUNPAT PI-033), the National Coast Guard of Argentina CASA 212, the Government of Tierra del Fuego through the Museo del Fin del Mundo and Organismo Provincial de Turismo de Chubut. We thank the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 00/00248-2, 00/01340-0), Society for Marine Mammalogy (grants-in-aid program) and CNPq/Prosul (CNPq 490281/2005-2) for funding the collection of samples and the genetic analyses. VF-T was funded by a Ph.D. scholarship from the ANII (National Agency for Research and Innovation, Uruguay) and by the CAP (Postgraduate Academic Commission–UdelaR). The authors are indebted to J. Owen, M. Sanemeterio, M. Coscarella, F. Grandi, D. Vales, R. Loizaga, N. Ortíz R. Vera, J. L. Esteves, E. Frere, J. Brunet, A. Chizzini, D. Danilewicz, M. Tavares,

R. Machado, P. H. Ott, I. B. Moreno, M. Borges-Martins, R. Bastida, M. A. Mandiola, and M. Dassis for their collaboration during field work. Sample collection was allowed under permits given by the Provinces of Chubut, Buenos Aires, and Tierra del Fuego. The authors are also indebted to the Editor, Dr. Daryl Boness, the Associate Editor, Dr. Jaume Forcada, and two anonymous reviewers for their help improving the manuscript.

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Received: 3 February 2014
Accepted: 5 November 2014