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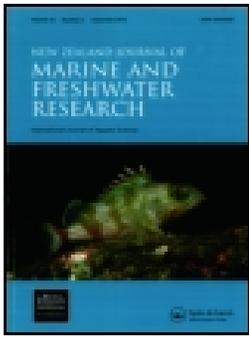
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REVIEW ARTICLE

Review of the current distribution of southern elephant seals in the eastern South Pacific

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ABSTRACT

The eastern South Pacific southern elephant seal population was extinguished by extensive hunting and the current presence of this species in this area is not well understood. We reviewed existing records from the 1900s to 2014 in the eastern South Pacific, as well as tagged seals and movement records in order to assess the potential immigration source of these individuals. A total of 409 confirmed sightings were compiled, ranging from the southern tip of South America (Cape Horn Archipelago) as far north as Ecuador, including some oceanic island groups. The evidence shows also that recolonisation of its former Pacific distribution has started, with slow population growth in three incipient pupping sites in southern Chile (south of 51°S). Although the source of all of the individuals in the growing colonies is unknown, evidence from tags and satellite tagging indicates that some seals come from subpopulations on the Peninsula Valdes and the Falkland/Malvinas Islands, although mtDNA analysis showed, preliminarily, a greater genetic relationship only with the Falkland/Malvinas Islands rookery.

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Introduction

The southern elephant seal (SES) (*Mirounga leonina* Linnaeus, 1758) is the largest of the true seals and is one of the principal consumers of squid and small fish in the Southern Ocean (Laws 1977; McCann 1985; Boyd et al. 1994; Bradshaw et al. 2003; Hindell et al. 2003; Carlini et al. 2005). The annual cycle of this species is characterised by two terrestrial phases: one for breeding (September to November) and one for moulting (December to March); and two pelagic foraging phases: post-breeding (for about 2–3 months) and post-moult (lasting 7 months) (Campagna et al. 1993, 2000). This species has a nearly circumpolar distribution in the Southern Hemisphere. Although the SES can reach the Antarctic continent and even very high-latitude locations such as Ross Island, the major breeding populations are located close to the Antarctic Polar Front (Laws 1994), especially

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at the sub-Antarctic islands, where populations are densely concentrated (Aguayo-Lobo & Torres 1967; Ling & Bryden 1992; Jefferson et al. 2008). The only exception is the Peninsula Valdes rookery which is located on the mainland of South America (Ling & Bryden 1992) and has increased in size consistently over the past three decades (Campagna & Lewis 1992, <http://www.seals.scar.org/pdf/statusofstocs.pdf>). Vagrant SESs have occasionally been reported farther north in the Southern Hemisphere (Mills et al. 1977; Oosthuizen et al. 1988; Pemberton & Skira 1989; Mawson & Coughran 1999; Reeves et al. 2002; Magalhães et al. 2003; Vargas & Steinfurth 2004; Alava & Carvajal 2005; Daneri 2009; Mertz & Bester 2011) and even in the Northern Hemisphere (Johnson 1990).

Historical records from previous centuries indicate that SESs in the eastern South Pacific (ESP) were distributed on the oceanic islands of the Juan Fernández Archipelago and on the mainland of Chile, at least from 37°S to Cape Horn Archipelago (see Dampier 1729; Anson's 1748; Molina 1782; Burney 1813; Perón 1816; Vicuña 1883). In fact, Linnaeus (1758) described the type locality of this species (cited as *Phoca leonina*) as restricted to Más a Tierra Island (currently Robinson Crusoe Island) in the Juan Fernández Archipelago (Thomas 1911), whereas Molina (1782) stated that the type locality of the species (cited as *Phoca elephantina*) was the mainland coast of Chile (near Arauco), including the Juan Fernández Archipelago. However, this population was decimated by extensive hunting by whalers and sealers (see Gay 1847; Philippi 1892; Albert 1901; Allen 1905; Trouessart 1907; Murphy 1914; Mathews 1929; Murphy 1936; Cabrera & Yepes 1940; Osgood 1943; Torrejon et al. 2013) and the last individual was observed in 1840 (Philippi 1892).

From the 1970s, SESs have been reported again on the ESP coast, mainly on the southern tip of Chile (e.g. Markham 1971; Sielfeld 1978; Torres et al. 2000; Gibbons & Miranda 2001), suggesting that this species may be recolonising the traditional sites of its former Pacific distribution (Torres 1981). Nevertheless, some publications have solely attributed these sightings to vagrant individuals (e.g. Venegas & Sielfeld 1998; Wilson & Reeder 2005; Sepúlveda et al. 2007). Given that the concern regarding the current status of SESs on the Pacific coast of South America is not well understood, this paper reviews previously published records and presents a high number of new unpublished sightings along the ESP coast of South America in order to document the range extension and status of the current SES population, provide information on sex and age class, seasonality and breeding groups. Additionally, tagged seals and movement records were examined in order to assess the potential original source of these individuals.

Materials and methods

The study area encompasses the ESP coast of South America. It comprises the west coast of Colombia, Ecuador, Peru and Chile, including oceanic islands of Galápagos, Eastern and Juan Fernández Archipelago (Figure 1). In this review, the Antarctic region is not included. In order to evaluate the occurrence of the species along the ESP coast, we searched both the published and unpublished literature to extract records reported from 1900 to 2014. Moreover, information provided by qualified observers, newsletters and newspapers, among other sources, where individual southern elephant seals were observed or reported along the ESP, were also included after careful examination of the reliability of the information and of available photographs or video. All available

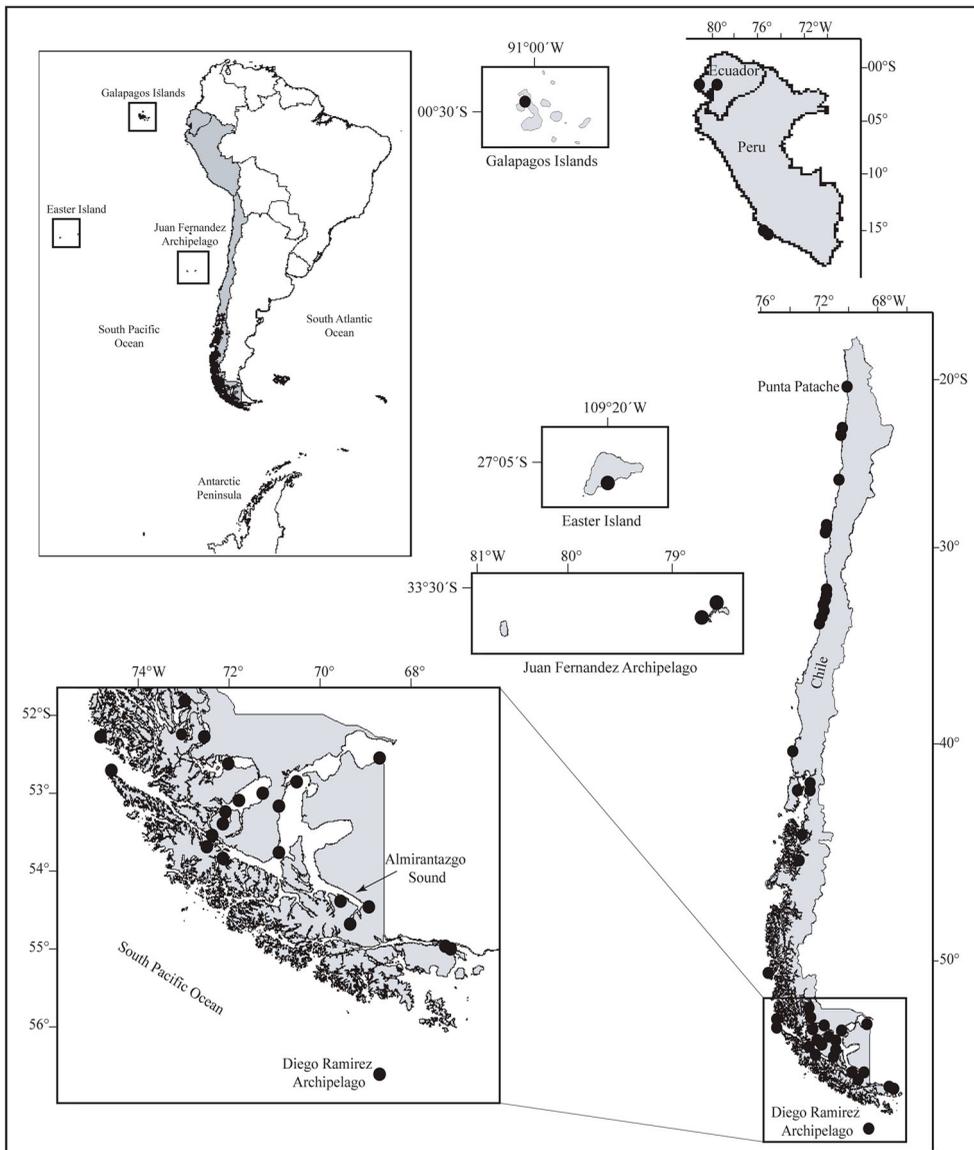


Figure 1. Distribution of SES sightings along the ESP of South America between 1944 and 2014.

records of SESs of which the location could be determined with an accuracy of greater than 5 km were entered into a database, together with information on date, position, locality, group size and reference or source.

Records were also obtained from a database of marine mammal surveys conducted by four long-term monitoring programmes in Chile and one in Peru. The first survey programme was initiated between 1965 and 1973 by two of the authors (A. Aguayo-Lobo and D. Torres) in an agreement between the Universidad de Chile and Instituto Antártico Chileno (INACH), covering the coastline from north ($18^{\circ}30'S$) to central/south ($39^{\circ}27'S$) Chile (e.g. Aguayo-Lobo & Maturana 1973), the oceanic islands of the Juan Fernández

Archipelago (e.g. Aguayo-Lobo & Maturana 1970; Aguayo-Lobo et al. 1971) and from Puerto Montt (41°28'S) to Cape Horn (56°S) (e.g. Aguayo-Lobo & Torres 1967). The second marine mammal survey began in 1991 to date by the Wildlife Rescue and Rehabilitation Centre of the Museo Municipal de Ciencias Naturales y Arqueología de San Antonio (MUSA), in central Chile (32°–35°S). The third marine mammal survey was initiated in 2002 to date by Fundación CEQUA in the austral zone of Chile (52°20'–55° S) including Almirantazgo Sound (c. 54°20'S), Tierra del Fuego; while the fourth marine mammal survey was initiated in 2007 to date by the Wildlife Conservation Society—Chile (WCS), particularly in Almirantazgo Sound, Tierra del Fuego. The fifth programme (Punta San Juan Program) initiated in 1978 to date is conducted by the Center for Environmental Sustainability of the Universidad Peruana Cayetano Heredia (CSA-UPCH) at Punta San Juan Natural Reserve (c. 15°21'S), Peru.

Additionally, data on the occurrence of SESs at Tierra del Fuego Island (Chile) were provided by a tour guide that periodically visits the area of Almirantazgo Sound on board a cruise ship between September and April of each year from 2003 to 2012. These data form part of an undergraduate thesis (Cáceres 2013) and provide partial information about the number and occurrence of SESs in that locality.

The records analysed included details of sex and age classes. When possible, the sex of the individuals was assessed by direct observation by colleagues who had extensive experience in marine mammal identification or by an analysis of available photos of the genital area of the animals as well as from the information reported in both published and unpublished records. The age classes were divided into four categories: pup, juvenile, subadult and adult based on the descriptions of Laws (1953). The data also include records of individuals tagged in the interdigital webbing of their hind flippers or with black dye by stamping an alphanumeric code on a visible part of the body.

Results

Summary of records

A total of 409 records were collected along the ESP coast of South America. Of these, 62 sightings came from 18 published papers, 266 other sightings came from one undergraduate thesis and 81 sightings from unpublished data. Only four records were found for Ecuador, six from Peru and 399 sightings from Chile. A summary of the data set is shown in Table 1; a copy of the detailed database is also available (Table S1).

The sightings ranged from single to more than 100 animals. It should be noted that, in the austral Chilean coast (mainly the locality of Ainsworth Bay), several seals may have been sighted more than once during repeated visits (intervals of 2–15 days) to Tierra del Fuego, and therefore the total number of animals sighted would be overestimated by potential duplicate records. Considering the highest value per month for the records of Tierra del Fuego Island, at least 1926 seals would have been sighted along the ESP. In seven published notes, the numbers of seals were reported as 'several' or 'some'.

The earliest report found after the presumed disappearance of the seal on the ESP coast is dated 1944, when an animal (mistakenly called dugong) was photographed and then shot and killed in Punta Arenas. However, it was not until the 1970s that sightings on

Table 1. Summary of the sightings of SES along the ESP coast of South America from 1944 to 2014.

Country	Area	Total sightings	Total seals sighted	Source
Ecuador	Mainland	2	2	Alava & Carvajal (2005), Lewis et al. (2006)
	Oceanic Island	2	2	Vargas & Steinfurth (2004), Lewis et al. (2006)
Peru	Mainland	6	6	P. Majluf (pers. comm. 2015), Lewis et al. (2006), CSA-UPCH database
Chile	Mainland North 51°S	43	46	Sielfeld (1978), Torres (1981), Crovetto (1987), Reyes (1987), Guerra (1989), Torres et al. (2000), Aguayo-Lobo et al. (2006), Lewis et al. (2006), Sepúlveda et al. (2007), Pacheco et al. (2011), Hausserman et al. (2012), Sielfeld (pers. comm. 2004), Mancilla (pers. comm. 2005), Castillo (pers. comm. 2011), Grupo de acción ecológica Chinchimén (pers. comm. 2014), Toro (pers. comm. 2014), Majluf (pers. comm. 2015), MUSA database, CEQUA/INACH database
	South 51°S	351	1865	Magallanes newspaper (1944), Markham (1971), Torres et al. (1979, 2000), Sielfeld (1978), Clark (1988), Gibbons & Miranda (2001), Godoy et al. (unpubl. data), El Pingüino newspaper (2010), Cáceres (2013), Sernapesca Magallanes (unpubl. data), Gibbons et al. (unpubl. data), CEQUA/INACH database, WCS database, Gallardo (pers. comm. 2002), Illanes (pers. comm. 2007), Farias (pers. comm. 2012), Garrido (pers. comm. 2014).
	Oceanic Island	5	5	Schlatter (1981), Aguayo-Lobo et al. (1995), Lewis et al. (2006), Teran (pers. comm. 2009), Gutiérrez (pers. comm. 2010), Tabilo (pers. comm. 2011),
Total		409	1926	

*Re-sighted individuals were excluded. †Potential duplicate records were excluded.

the ESP coast became more frequent and the reported numbers of animals became greater in Fuegian fjords and other remote places in Chile.

Sightings distribution

The sightings recorded here occurred between latitudes of 00°14'S (Ecuador) and 56°30'S (Chile). On the Ecuadorian mainland, SESs have been reported in the vicinity of Guayaquil (02°05'S and 02°10'S), while in Peru all the sightings have been recorded in Punta San Juan Natural Reserve (15°21'S). On the Chilean mainland, SESs have been reported in the north, central and south regions, from Punta Patache (20°48'S) to Diego Ramirez Islands (56°30'S). SESs have also been sighted on Pacific oceanic islands, with two seals at Galapagos Islands (00°14'S, 91°23'W), an individual at Easter Island (27°09'S, 109°23'W) and at least five records for the Juan Fernández Archipelago (33°36'S, 78°51'W). The SES records on the ESP range are illustrated in Figure 1 and some individuals shown in Figure 2.

Along this distribution range, the species occurred consistently to the south of 51°S and sightings were more often of groups, from two to 39 seals ($n = 298$ records), rather than solitary individuals ($n = 51$ records). Reports north of this latitude usually involved solitary individuals ($n = 58$ records); there were only two groups of two and six individuals. Moreover, to the south of 51°S, the species occurred consistently at three haul-out areas, Ainsworth Bay (54°24'S) and Jackson Creek (54°26'S), both located in Almirantazgo Sound in Tierra del Fuego Island, and Poca Esperanza Estuary (52°14'S). Seventy five per cent of all records from the ESP came from Ainsworth Bay and Jackson Creek.

The presence of SESs at Almirantazgo Sound dates from 44 years ago, when a small group of seven individuals was observed at Parry Fjord in February 1971. The next



Figure 2. SES sightings at ESP of South America. **A**, May 2004 on Galapagos Island, Ecuador; **B**, October 2009 at Juan Fernandez Archipelago, Chile; **C**, April 2012 at Punta San Juan Natural Reserve, Peru; **D**, February 2004 at Ainsworth Bay, Chile. Photographs courtesy of Antje Steinfurth, Diego Tabilo, Marco Cardeña and Jorge Plana.

year, a group of six seals was observed in the same place by A. Aguayo-Lobo and R. Maturana during an overflight. In February 1978, five animals were again reported in this fjord, suggesting that a small stable colony of SESs was establishing itself. Nine years later, 22 sightings of small groups of SESs (from one to 35 seals) were reported in Ainsworth Bay at Almirantazgo Sound, where they are currently still sighted throughout the year in small numbers.

In December 2006, during the third year of monitoring of a new colony of black-browed albatross at Almirantazgo Sound, two of the authors discovered a newly colonised haul-out site of SESs. This site, named Jackson Creek, is located very close to the albatross colony and any SES was observed between 2003 and 2005 spring/summer seasons. The number of SESs in Jackson Creek has shown an increasing trend over the past few seasons, from 46 individuals counted on 15 December 2006 to as many as 100 seals in 2011 and 2012, making it the largest colony in the ESP.

Recently, a third haul-out was reported at Poca Esperanza Estuary, near to Puerto Natales city, by researchers of Magallanes University. A survey conducted by researchers between February and November 2014 reported the presence of small groups of SESs (three to 24 seals) in every month visited ($n = 7$). However, we have no data to establish if is a newly colonised haul-out site or a newly discovered but existing haul-out site.

Annual occurrence

As mentioned previously, the earliest report after the presumed disappearance of the SES on the ESP coast dates to 1944, but it was not until the 1970s that sightings became more

frequent. In the Ecuadorian region, the four sightings were reported in three different years (1998, 2002 and 2004). In the Peruvian coast, the six sightings have also been reported in different years (1989, 1994, 2007, 2009, 2010 and 2012), all with only one seal. For the Chilean region, the sightings include 29 years between 1971 and 2014, with a marked increase in the numbers of animals sighted since 1998 south of 51°S and since 2003 north of 51°S (Figure 3). The highest number of seals sighted in a year along the Chilean region was 247 individuals in 2012.

Sex and age classes

Excluding potential duplicate records by systematic visits to Tierra del Fuego (see summary of records), most records of sightings of individuals of known sex ($n = 93$ records) involved males (85% of 699 sexed individuals), whereas females represented only 15% of these records. Likewise, with regard to sightings of individuals categorised in age classes ($n = 99$ records), most were young animals (42.6%), followed by subadults (38.7%) and adults (12.5%). Pups represented only 6.2% of the total sightings, and all of them were recorded south of 52°S.

In addition, northern sightings (north of 51°S) mainly involved males (93% of 43 sexed seals) and most of them were juveniles (59.6% of 47 seals of known age classes). In fact, the records in Ecuador and Peru are mostly juvenile males. The only three female sightings north of 51°S are not found farther north than 42°22'S, while the northernmost record for an adult male is 23°27'S.

The southern records (south of 51°S) also showed a majority of males (84.4% of 655 sexed seals), and juvenile and subadult SESs were the most common (41.6% and 39.7% of 803 known age classes, respectively). However, the high presence of both age classes had been registered mostly during the austral summer months.

Breeding

Following the discovery of the previously mentioned aggregation of SESs in Almirantazgo Sound in 1971, this site was suggested as the location of a breeding colony by some authors. However, evidence of births was not observed until January 2003, when two of

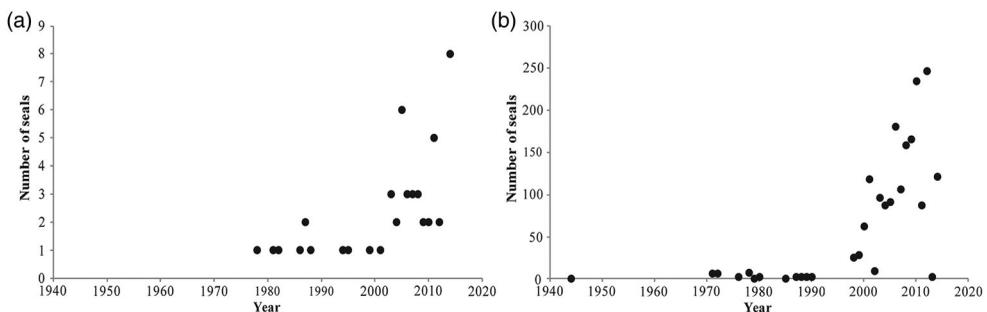


Figure 3. Numbers of SES annually reported from 1944 to 2014, north of 51°S (A) and south of 51°S (B) in the Chilean region, including oceanic islands. In B, potential duplicate records produced by systematic visits to Tierra del Fuego have been excluded.

the authors observed and photographed a recently moulted pup on the coast of Ainsworth Bay. This pup was found alone and isolated from the other SESs observed in the area. Systematic observations conducted between September and December during the period 2003–2014 showed that two to four pups have been born annually (Figure 4) with a total of at least 33 pups born during this time. Only one or two adult males have been observed between September and December during the same breeding period; however, only a small harem of three to five seals was formed annually. Mating has been recorded between late October and early November. The observed alpha male, identified by scars on his back and neck, returned each year from 2003 to 2007.

A second stable breeding area has also been detected in Almirantazgo Sound, on the beaches of Jackson Creek. At least two pups were observed together with their mother in November 2012 and 2013, and in October 2014 a total of 15 pups with their respective mothers were observed at two beaches in this area. Two harems with six and nine adult females with the respective alpha male were recorded, and each harem was separated by a distance of c. 100 m (Figure 4).

One anecdotal birth was reported in Obstruction Sound (south of Puerto Natales city) in October 2010. This sighting involved only a mother with a pup, but no efforts have been made to monitor new births in this locality. However, near this area, at Poca Esperanza Estuary, a small and incipient breeding group was discovered in 2014 and at least two pups were seen in November of that year. No report of the size of harem is available.



Figure 4. **A**, Two pups nursing from their mothers and **B**, a pup resting near a bull at Ainsworth Bay; **C**, harems on the sand and **D**, stone boulders at Jackson Creek, Almirantazgo Sound, Tierra del Fuego Island.

Sightings of identified SESs

The sightings of tagged SESs have been reported only on the Galapagos Islands, Ecuador ($n = 1$) and in Almirantazgo Sound, Chile ($n = 21$). This involved nine animals from the Peninsula Valdés (PV) colony in Argentina and four seals from the Falkland/Malvinas Islands (F/M) (Table 2, Figure 5).

Another nine tagged seals with Dalton Jumbo Rototags of unknown origin have also been sighted at Almirantazgo Sound, Chile. Based on the type and colour of seals M15 and E17, the yellow and green unknown tags may correspond to the F/M Islands (see Table 2). All tagged seals were observed moulting. Two individuals from the F/M Islands (tags M15-D80 and A82-R32) have been re-sighted in consecutive years in the same locality.

Nine of the pups born in Ainsworth Bay at Almirantazgo Sound and two juvenile males of unknown origin have been tagged with green/yellow Allflex Rototags between 2003 and 2007 in the study area. Another six juvenile males were also tagged at Jackson Creek between 2010 and 2011 with the same type of tag. With the exception of an alpha male re-sighted each year between 2003 and 2007 during the breeding season at Ainsworth Bay, re-sightings of locally tagged seals have been scarce. Only four of those seals (two pups and two juveniles) have been re-sighted 2 and 4 years later in the same area.

Other sightings of the same individual in 2 consecutive years have been reported in three localities of northern Chile. A male of 4 m in length resting on a beach in Viña del Mar in January 1986, identified by a prominent scar on his right side, was sighted again in February 1987 in Valparaíso; an immature male with a particular scar on its back was sighted in December 2004 and again in November 2005 at Chañaral Island; and a subadult male was observed on La Portada Beach, Antofagasta, in January 2005 and 2006.

Movement records of satellite-tracked animals

In addition to information on the movements of seals from PV and F/M rookeries that were recorded based on observations of tags, data on the movements of a few SESs in Chilean waters are also available. The first tracked animal was reported by Campagna



Figure 5. Tagged SESs with Dalton Jumbo Rototags from Argentina (left) and the Falkland/Malvinas Islands (right) seen at Almirantazgo Sound, Chile.

Table 2. Summary of the tagged/marked individuals of SES at the ESP of South America.

<i>n</i>	Date	Type of tag	Colour	Sex	Age class	Number	Place of origin
<i>Galapagos Islands, Ecuador*</i>							
1	11 May 2004	Jumbo Rototag	Blue	Male	Juvenile	Unread number	Unknown
<i>Ainsworth Bay, Almirantazgo Sound, Chile</i>							
2	18 Jan 2003	Jumbo Rototag	Light blue	Male	Subadult	3414	Argentina
3	18 Jan 2003	Jumbo Rototag	Light blue	Male	Subadult	2888–3029	Argentina
4	06 Feb 2004	Jumbo Rototag	Light blue	Male	Subadult	3474	Argentina
5	06 Feb 2004	Jumbo Rototag	Light blue	Unknown	Juvenile	Unread number	Argentina
6	06 Feb 2004	Jumbo Rototag†	White	Unknown	Unknown	B93	Falkland/Malvinas Islands
7	06 Feb 2004	Jumbo Rototag†	Light blue	Unknown	Unknown	2866	Argentina
8	30 Oct 2005	Jumbo Rototag†	Light blue	Unknown	Unknown	2859	Argentina
9	26 Feb 2006	Jumbo Rototag	Orange	Male	Subadult	P89	Unknown
10	26 Feb 2006	Jumbo Rototag	Light blue	Male	Adult	5640	Argentina
11	15 Dec 2006	Jumbo Rototag	Yellow/light blue	Male	Subadult	M15–D80 (2002)	Falkland/Malvinas Islands
12	22 Jan 2007	Jumbo Rototag	Light blue	Unknown	Unknown	Unread number	Argentina
13	26 Nov 2007	Jumbo Rototag†	Green	Unknown	Unknown	E17 (2005)	Falkland/Malvinas Islands
14	28 Nov 2007	Jumbo Rototag	Yellow/light blue	Male	Subadult	M15–D80 (2002)	Falkland/Malvinas Islands
15	13 Dec 2007	Jumbo Rototag	Yellow/light blue	Male	Subadult	M15–D80 (2002)	Falkland/Malvinas Islands
16	30 Nov 2009	Jumbo Rototag	Yellow/white	Unknown	Juvenile	A82–R32 (2007)	Falkland/Malvinas Islands
17	16 Dec 2009	Jumbo Rototag	Light blue	Unknown	Unknown	Unread number	Argentina
18	18 Feb 2010	Jumbo Rototag	Yellow/white	Unknown	Juvenile	A82–R32 (2007)	Falkland/Malvinas Islands
19	15 Jan 2011	Jumbo Rototag	Yellow	Male	Subadult	R38	Unknown
<i>Jackson Creek, Almirantazgo Sound, Chile</i>							
20	08 Jan 2011	Jumbo Rototag	Green	Male	Subadult	Unread number	Unknown
21	08 Jan 2011	Jumbo Rototag	Green	Male	Subadult	4942–463?	Unknown
22	08 Jan 2011	Jumbo Rototag	Green	Male	Subadult	4666	Unknown
23	08 Dec 2012	Jumbo Rototag	Green	Male	Subadult	9024	Unknown
24	08 Dec 2012	Jumbo Rototag	Green	Male	Subadult	5181	Unknown
25	08 Dec 2012	Jumbo Rototag	Green	Male	Subadult	5328	Unknown

*Reported by Vargas & Steinfurth (2004). †Tags found on the beach.

et al. (2007) and Falabella et al. (2009). These authors showed the route of a young pre-reproductive female from PV to the Chilean Pacific coast. Her trip started on 17 December 2005 and ended on 2 August 2006; she swam at least 8050 km. She passed through the Drake Passage into the Pacific Ocean, entered the Patagonian channels (near 50°S) and

then returned to PV. Interestingly, during her trip through the Magellan Strait, she visited both the Ainsworth Bay and the Jackson Creek localities in Almirantazgo Sound.

The second reference is to a female pup from Ainsworth Bay that was tracked for 77 days during her first feeding trip (Hückstädt et al. 2008). This pup was equipped with a satellite transmitter on 28 November 2007 but began her trip 36 days after she was captured. During her transit in inland waters, the pup crossed the Magellan Strait and several channels, finally reaching the open waters of the Pacific Ocean at 51°42'S, 75°14'W. In the open ocean, the seal travelled south/southeast for 2101 km and reached 62°38'S, 68°11'W on 14 February 2008, when the last fix was received.

Finally, two subadult males were immobilised in Jackson Creek by a WCS field team on 13 December 2011 and 8 January 2012, respectively. These animals travelled along the inner coastal waters of the channels and fjords of southern Chile and the open Pacific Ocean and returned to the capture area a year later.

Discussion

Narrative historical records from the 16th and mid 19th centuries described SESs distributed on oceanic islands of the Juan Fernández Archipelago and mainland Chile from, at least, Arauco to Cape Horn. Although the identification of this species was not positively confirmed in some of the early reports (e.g. Dampier 1729; Burney 1813; Perón 1816; Vicuña 1877, 1883), both the descriptions and the names given to the animals suggest that the animals involved were SESs.

The available historical records show that extensive hunting during the 17th and 18th centuries was the main cause of the extinction of the species in its range in the eastern South Pacific, and although a small number of individuals could have survived in a few remote places, isolated from human populations, the absence of reports over the next 130 years (1840–1971) suggests that this population vanished completely, as stated by Philippi (1892). In fact, in surveys of Pinnipedia conducted by different researchers from 1901 to 1970 on mainland Chile and oceanic Pacific islands (e.g. Albert 1901; Aguayo-Lobo & Maturana 1970; Aguayo-Lobo et al. 1971; Gilmore 1971; Torres & Aguayo-Lobo 1971; Aguayo-Lobo & Maturana 1973; Torres 1987), no individuals of *M. leonina* were reported. Thus, the current presence of SESs on the Pacific coast of South America may be due to immigration from other breeding sites.

If this hypothesis is correct, the available records suggest that this immigration started at the southern tip of Chile (south of 51°S), where the first group of animals was observed in the 1970s (Markham 1971; Sielfeld 1978; Aguayo-Lobo & Maturana in Torres et al. 1979) and currently includes both regular seasonal haul-outs and breeding sites. This is emphasised by the absence of regular places for moulting/resting and further breeding on both the mainland and the oceanic islands north of 51°S, where individuals would be vagrants, even if they were frequently seen.

The extensive areas in which SESs have been observed on the ESP coast primarily involve juveniles and subadult males. Several studies have suggested that young SESs—particularly males—do not select hauling out sites using the same criteria as older animals, which are expected to be more selective given their previous haul-out experience (Hofmeyr 2000; Mulaudzi et al. 2008). Dispersal to different land sites may also reflect differences in the foraging patterns of different age and sex classes, with females using

the deepest waters in the open ocean and males foraging closer to the coast (Burton 1985; Bester 1988; Hindell et al. 1991; McConnell et al. 1992; Stewart & DeLong 1994; Campagna et al. 1998, 1999, 2006, 2007; Bennett et al. 2001; van den Hoff 2001). The continental shelf of the ESP is narrow and relatively close to land. In this context, juveniles and subadult males would leave their terrestrial haul-out sites and disperse to lower latitudes following the shelf-break front to productive waters of the Humboldt Current. A habit of foraging closer to the coast may explain why males are more frequently re-sighted in locations north of 51°S than females. This pattern of dispersal of males to more distant locations following a productive current has also been suggested for PV seals (Campagna et al. 2000).

Based on the revised records, only three small breeding areas were identified in Chile, two at Almirantazgo Sound and one at Poca Esperanza Estuary. Although the first sightings of groups of seals reported in Almirantazgo Sound included adult females (Markham 1971; Sielfeld 1978; Gibbons & Miranda 2001), the local breeding status of the SES was not confirmed until 2003. In contrast with other well-documented northern SES rookeries, where pup production increased rapidly after founding (Le Boeuf et al. 2011; Ferrari et al. 2013; Lowry et al. 2014), the pup production at Ainsworth Bay has remained low but stable (two to four pups per year) during the past 11 years. Although births at Jackson Creek have been reported only since 2012, the colony shows a rapid increase in pup production (from two to 15 pups per year in 3 years).

One possible explanation for this low production of pups in Ainsworth Bay may be based on the presence of systematic tourism activities during the breeding and post-breeding periods, which has been active in this area since the 2000s (Cáceres 2013). This systematic disruption on a small rookery could cause mature females to move to other, new sites to give birth (e.g. Jackson Creek, next to Ainsworth Bay). Another explanation for this low but stable pup production could be the shortage of suitable habitats for breeding in Almirantazgo Sound. This fjord is principally characterised by a rugged coastline with few grassland and sandy beach areas available. These habitat characteristics could be limiting the growth of the breeding rookeries in the area. Other unknown factors (e.g. food supply, predation pressure) and/or processes (e.g. mortality, female survival), could also be operating at both the population and the local levels to limit the growth of the Chilean breeding groups. However, we do not have information to support either alternative.

Certainly, if the present-day aggregations of SES in the ESP did not originate from the historical population inhabiting these shores, then the source of the animals observed to have immigrated since the 1970s is unclear. With the exception of the few tagged seals re-sighted at Tierra del Fuego and one tagged seal sighted at the Galapagos Islands during the moulting season, none of the animals recorded along the ESP, including the reproductive groups, have a known origin, and therefore there are no conclusive data to confirm the origin of this influx.

Some studies have shown that SESs may travel long distances from their birthplaces. The greatest dispersion discovered from records of telemetric and branded/tag seals to range from 5191–8400 km (Hindell & McMahon 2000; Campagna et al. 2007; Falabella et al. 2009), but such long-distance dispersal appears to be relatively uncommon. The distances reported for males and females usually range from 1000–3600 km from their breeding colonies (Campagna et al. 1998, 1999, 2007; van den Hoff 2001; van den Hoff et al.

2002; Bradshaw et al. 2004; Reisinger & Bester 2010). Under the assumption that these values specify the usual range of movement, four potential breeding colonies are included in this range: PV, F/M, South Georgia and the South Shetland Islands. The PV rookery is located on the coast of Argentina at a distance of approximately 1300 km from Tierra del Fuego Island. The F/M Islands are relatively closer to Tierra del Fuego Island (c. 550 km) than PV. The other two breeding places are located 1100 and 2100 km away, in the South Shetland and South Georgia Islands, respectively.

The species identity of the tagged individual seen in the Galapagos Islands (Vargas & Steinfurth 2004) cannot be ascertained, because the tag was identical in colour and shape to the tags deployed at PV but also similar to tags used on northern elephant seals at Guadalupe Island, Mexico. However, phenotypic features do not match in age to the tagging schedule of northern elephant seals in Guadalupe Island in 2003 (Lewis et al. 2006). The tagged individuals in other places observed in Almirantazgo Sound originated only from the PV and F/M colonies, suggesting that both rookeries are the primary source of the influx of breeding seals to Tierra del Fuego Island in Chile. Although a tracked SES pup born at Ainsworth Bay showed a connection with Antarctic waters (Hückstadt et al. 2008), none of the tagged or satellite-tracked seals from either South Shetland or the South Georgia Islands shows movements to the Pacific coast of South America (see McConnell et al. 1992; McConnell & Fedak 1996; Bornemann et al. 2000; Tosh et al. 2009; Hückstädt et al. 2012). Although tagged or satellite-tracked animals represent only a small portion of the total population, it is unlikely that seals from these locations were the colonisers of the incipient breeding group established in Chile.

Currently, PV is the only large breeding colony of SESs on the mainland of South America (Campagna & Lewis 1992; Le Boeuf & Laws 1994) and is the fifth largest sub-population, after South Georgia, Iles Kerguelen, Macquarie and Heard Islands (<http://www.seals.scar.org/pdf/statusofstocs.pdf>). The F/M Islands have a well-established breeding rookery located at Sea Lion Island, with a few hundred births per year (Galimberti & Boitani 1999; Galimberti et al. 2001). However, suitable habitat in PV for the seals to reproduce and moult is not limited, whereas habitat limitation on land could be more important in the F/M Islands than on the continent (Lewis et al. 2006).

Interestingly, preliminary studies of mtDNA from pups and breeding individuals at Ainsworth Bay, Almirantazgo Sound, have indicated that the breeding aggregation has a high haplotype diversity ($H_d = 0.8899$, $SD = 0.091$; Acuña et al. 2005). Of the 11 maternal lineages found, three haplotypes cluster with the F/M genetic structure, suggesting immigration of breeding individuals only from the F/M rookery. Although the possibility that not all maternal lineages have been sampled at PV or F/M, or even at other locations, these eight other maternal lineages are noteworthy, as they are not present in any other known population to date. This finding makes it necessary to infer another possible origin from well-established rookeries or opens the possibility of the resurgence of the historical population, from which a few individuals may have survived in remote locations. The recovery of some pinniped populations considered virtually extinct or believed to be extinct has been documented, e.g. the Antarctic fur seal (Bonner & Laws 1964) and the Juan Fernandez fur seal (Aguayo-Lobo & Maturana 1970; Aguayo-Lobo et al. 1971; Hubbs & Norris 1971). Further analysis of both mtDNA and nuclear DNA may be helpful to identify the source population(s) and the possible processes that have created the Chilean breeding rookeries.

In summary, due to incomplete information and the absence of systematic survey data, erroneous conclusions have been made about the current presence of SESs along the ESP coast. In this review, we showed that *M. leonina* is a common species, at least in Chile. Although different biological processes govern SES distribution in the different areas, the presence of three incipient pupping sites in southern Chile suggest that the small population is growing slowly and expanding its range on the Pacific coast of South America. Observations of tagged individuals in other places seen at Almirantazgo Sound during the moulting season suggest that SESs from the PV and F/M breeding colonies are the primary source of the animals observed in the ESP. However, mtDNA analysis showed, preliminarily, a greater genetic relationship only with the F/M Islands, but also shows maternal lineages that stand out as distinct from the genetic structure observed in any other population to date. Because the SESs population vanished completely on the ESP of South America, we have a long-term interest in monitoring its status and predicting its future growth.

Supplementary data

Table S1. Records of *Mirounga leonina* along the eastern South Pacific of South America from 1944 to 2014.

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