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Southern elephant seals north of the Antarctic Polar Front

M. LEWIS[1], C. CAMPAGNA[1,2], M.R. MARIN[1] and T. FERNANDEZ[1]

[1]*Centro Nacional Patagónico (CONICET), Blvd Brown s/n, 9120 Puerto Madryn, Chubut, Argentina*
[2]*Wildlife Conservation Society, 2300 Southern Blvd. Bronx, New York, NY 10460, USA*
lewis@cenpat.edu.ar

Abstract: This paper reports on sightings and dispersion of individual southern elephant seals (*Mirounga leonina*) along the Atlantic and Pacific coasts of South America based on reports of tagged/marked seals from Patagonia and of animals of unknown origin. From 154 sightings, encompassing at least 354 individuals, we found that individuals dispersed to subequatorial latitudes on both sides of the continent, and to more temperate sites, in the Magellanic region of Tierra del Fuego. Nineteen sites were visited by tagged seals from the established colony of Península Valdés (PV, Argentina). PV and the smaller seal population of the Falklands/Malvinas were regularly connected by adults of both sexes. There were more sightings of males than females. No incipient new breeding colonies were found along the Atlantic coast of South America. Some observations coincided with places where elephant seals had been recorded or exploited in the seventeenth and eighteenth centuries. A shortage of suitable habitat for expansion and proximity to predictable food could act as a stabilizing process preventing colonization of new areas from PV. Dispersion data, coherent with population genetics, support a Patagonian elephant seal stock.

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Introduction

Southern elephant seals (*Mirounga leonina* L.) breed and forage mostly in sub-Antarctic waters (Le Boeuf & Laws 1994). A large population exists along the coast of South America, in temperate habitats (Campagna & Lewis 1992, Lewis *et al.* 1998), and smaller colonies occur in the Antarctic (Le Boeuf & Laws 1994, SCAR 2002). The distribution pattern combined with demographic data predicts segregated groups. Foraging seals may travel distances large enough to reunite remote breeding areas (Burton 1985, Bester 1988, Hindell & McMahon 2000). However, connecting colonies would require travelling through unstable physical and oceanographic environments, influencing foraging success (Bornemann *et al.* 2000). Whilst, sub-Antarctic and Antarctic populations may be affected in their movements by sea ice (Burton 1985, Bester 1988) seals in temperate habitats are less restricted by physical barriers (Campagna *et al.* 2000).

We compiled sightings of southern elephant seals in South America to learn about movements and to assess species dispersion north of the Antarctic Polar Front, for the Atlantic and Pacific oceans. An additional objective was to estimate the potential for dispersion in the same geographic area of individuals from Península Valdés (PV; coastal Patagonia, Argentina).

Southern elephant seals often haulout away from their breeding-moulting rookeries (Burton 1985, Bester 1988, 1989, Lewis *et al*. 1996, Hindell & McMahon 2000, Van den Hoff 2001). For our particular geographic area, there are historical records of traditional and non-traditional sites (see Table I and references therein). For the Atlantic coast, the northernmost sighting occurred for Fernando de Noronha Island (3º52'S, 32º28'W, Lodi & Siciliano 1989) during the non-breeding phase of the annual cycle. On the Pacific side, the northernmost sighting has been reported for northern Chile (Caleta Barquito, 26º20'S, 70º38'W, Torres 1981). Both records were of solitary individuals. Sightings also involved small groups and traditionally used haulout places, such as the Magallanes region of Chile (Torres 1981), Isla de Lobos (Uruguay) and Punta Bermeja (northern Patagonia, Argentina; Castello 1984, table 1). Evidence of individuals linking colonies is virtually restricted to PV and the Falklands/Malvinas archipelago (F/M; Scolaro 1976, Castello 1984, Lewis *et al.* 1996, table 5).

Península Valdés (42°04'S, 63°45'W) is the only large breeding colony of southern elephant seals (tens of thousands individuals) in continental South America (Campagna & Lewis 1992, Le Boeuf & Laws 1994, Lewis *et al.* 2004). Seals breed and moult at PV along a 200 km coastline, in the temperate South West Atlantic region. All other colonies for the species are located on islands (Le Boeuf & Laws 1994). The closest, well established breeding place to PV is Sea Lion Island (F/M), at a distance of *c*. 1000 km (Galimberti & Boitani 1999). This small colony encompasses a few hundred births per year. Besides the Sea Lion Island colony, individual seals or small moulting groups are occasionally recorded in remote places of the F/M Archipelago (personal communications: C. Duck 1991, D. Thompson 1995, J. McGhie 1997, F. Galimberti 2004 &

Table I. Categories of information reviewed in this paper. Only the tagged/marked and unknown origin data (shaded columns) were included in results.

Source of data	Historical pre-tagging (before 1990)	Tagged/marked after 1990	Recorded/unknown origin, after 1990	Total
Number of records	52	100	54	206
Published records	52	4	25	81
Number of individuals	102	100	254	456
Tagged/branded at PV	5	42	na	47
Tagged/marked at M-F and PV	na	58	na	58
Rookeries involved	PV, F/M, South Georgia	PV, F/M, South Georgia	PV, F/M	na
Traditional haulout sites	> 11	12	2	na
Non-traditional haulout sites	12 (Fig. 1b)	7	15	na
References	Carrara 1952, Grinwood 1968, Scolaro 1976, Sielfeld 1978, Torres 1981, Castello 1984, Burckardt 1984, Eleta 1985, Aguayo *et al*. 1995	Lewis *et al*. 1996,	Aguayo *et al*. 1995, Lewis *et al*. 1996, Caseca-Santos & Soto 1998, Lorenzani & Lorenzani 2000, Serra *et al*. 2000, Gibbons & Miranda 2001, De Sanctis *et al*. 2002, Silva *et al.* 2002, Magalhaes *et al.* 2003	na

* = Narrative descriptions were not included. na = not applicable.

R. McGill 2004). The next closest breeding places to PV, at *c*. 2–2500 km in a straight line, are the Antarctic Peninsula (Carlini *et al.* 1997, 1999, Bornemann *et al.* 2000) and South Georgia (McCann 1985). Southern elephant seals also breed in islands of the temperate South Atlantic (e.g. Gough; Le Boeuf & Laws 1994, SCAR 2002).

Published information pertinent to this study deals with four topics:

a) fidelity to a birth or breeding site,

b) population genetics studies,

c) satellite tracking data, and

d) other reports on sightings.

Previous studies showed that at least 86% of the adult females return to breed at the PV colony within 0–3 km of tagging locations (Lewis *et al*. 1996). Fidelity to a specific site is common, to the point that mothers, daughters and granddaughters were recorded breeding in the same harem (Lewis & Campagna unpublished data). Genetic studies suggest that PV population stands out as distinct from the pattern of genetic structure of South Georgia in the South Atlantic and Heard and Macquarie populations in the South Indian and South Pacific Ocean (Slade 1998, Hoelzel *et al*. 2001, Fabiani *et al*. 2003). Locations of elephant seals at sea during the pelagic phase of their annual cycle, obtained by geolocations and satellite relay data loggers, have consistently indicated long distance excursions and foraging over deep water by adult females and juveniles (Campagna *et al.* 1998 and unpublished data) and locations on the shelf and along its edge by adult males and juveniles (Campagna *et al.* 1999 and unpublished data). In both sexes, adults from Patagonia feed in the temperate waters of the south-west Atlantic and do not reach Antarctic waters, where seals from South Georgia, South Shetlands and other colonies forage (McConnell *et al.* 1992, Campagna *et al.* 1995, 1998, 1999, McConnell & Fedak 1996, Bornemann *et al.* 2000, Muelbert *et al.* 2004). Previously published information on resights involved 52 records and at least 12 sites along the Atlantic and Pacific coasts of South America (Table I). Sightings were of unmarked animals of uncertain origin (Grimwood 1968, Torres 1981, Castello 1984, Lodi & Siciliano 1989, Aguayo *et al.* 1995).

Methods

The study compiled sightings of elephant seals in the Atlantic and Pacific coasts of continental South America and offshore islands (Table I). Data were obtained from surveying scientists, naturalist, rangers and fishermen (Table I). A record was defined as a sight of a marked, tagged or unidentified elephant seal. To estimate the potential for dispersion of individuals from PV, a record had to involve an animal outside an area of 100 km from the centre of the colony (Fig. 1a). This exclusion zone is justified as follows: the Valdés population breeds along 200 km of the open ocean coast of the Peninsula, and extends 30 km south beyond it (Campagna & Lewis 1992, Lewis *et al*. 1998). Therefore, an area of 100 km from midway distribution range will exclude the latter breeding place. Besides, satellite tracks show that once PV animals leave the rookery they do not haul out close to it (Campagna *et al.* 1995, 1998, 1999). This is consistent with the lack of sightings from breeding beaches in the range of 100 km.

Sightings analysed in this study include records not previously reported and those published in abstracts of regional scientific meetings, newspaper, magazine articles and difficult to access technical reports. Only records after 1990 were included as data. The date coincides with the start of tagging at PV (6836 tagged animals by the end of the 2004 breeding season). Tagging involved the placement of serially numbered plastic tags (Jumbo Rototags, Dalton Supplies, UK) in the inter-digital webbing of the hind flippers of the seals. Animals were also marked with a black dye by stamping an alphanumeric code on a visible part of the body. Most marking involved seals that had been also

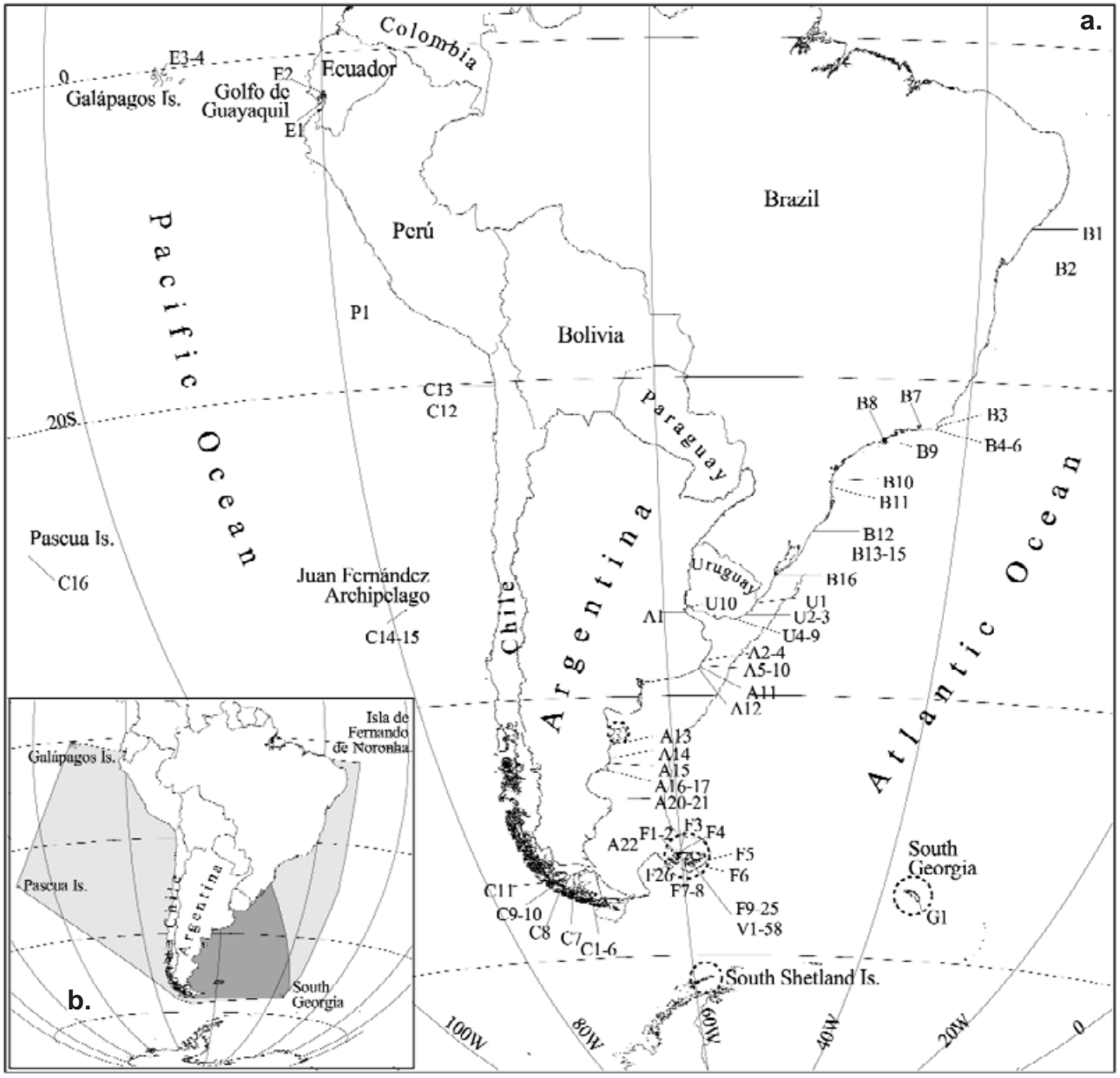

Fig. 1. a. Locations of records of seals tagged, untagged and reported in the grey literature after 1990; *n* = 154. **b.** Polygon connecting the extreme locations from data encompassing the entire database (i.e. tagged, untagged, reported in the literature before and after 1990; *n* = 206). In dark grey is the area connecting only the locations of animals which tags are undoubtedly linked to PV.

tagged, except for 161 animals since 1990 that were only marked.

Sighting records were divided in two categories:

a) animals that were "connected" to PV beyond doubt (seals reported with tags/marks applied at PV during a breeding or a moulting season), and

b) animals that could not be attributed to a specific colony (no tags or mark information accompanied the sighting).

Category (a) included animals tagged/marked only at PV and seals marked at the F/M and resighted at PV (where they were tagged/marked once again). In this paper, both of the latter subcategories were merged as seals linked to PV, because the tagging of an animal that visits two sites often depends on opportunistic aspects. For the same reason, an animal tagged in the F/M and resighted at PV was considered as a confirmed sighting of a PV animal. Six tagged/marked animals were resighted at the F/M but the sex was not reported and the tag number could not be read completely. Therefore, a PV seal was an individual identified with a tag or a PV mark.

We defined, as a record of dispersion, an animal sighted away from its traditional site (Nicholls 1970). Migration

Table II. Individuals sighted since 1990 in each locality by sex and age category. Age category included: Year = weanling, yearlings and underyearling, Juv = non-breeding animals, SA = sub-adult males, Ad = adult females and males, Un = unknown records without category or sex. Travelled distance was estimated from tagged/marked animals in straight line from the PV colony (where more than one individual was sighted we included the range).

Haulout site		Total sighted	Sex			Age category							Travelled distance (km)
			Males	Females	Un	Year	Juv	SA	Ad	Un	Tagged	Marked	
Brazil	10º50'47"S–32º10'44"S	18	11	1	6	0	11	1	0	6	0	1	2000
Uruguay	33º56'15"S–35º01'37"S	36	10	0	26	0	5	9	0	22	7	0	1300–1400
Argentina	34º31'00"S–50º22'00"S	63	17	9	37	9	39	5	8	2	3	0	750–1000
Falklands/Malvinas	51º12'28"S–52º26'51"S	85	72	6	7	1	6	57	14	7	74	11	950–1200
South Georgia	54º49'48"S	1	0	1	0	1	0	0	0	0	1	0	2400
Chile	54º24'28"S–20º13'00"S	146	26	1	119	0	3	23	1	119	2	0	1800
Perú	20º13'00"S	1	1	0	0	0	1	0	0	0	0	0	
Ecuador	0º18'53"S	4	0	0	4	0	2	0	0	2	1	0	8600
Total		354	137	18	199	11	67	95	23	158	88	12	

was a dispersal from the birthplace followed by a return to it (Odum 1959). Movements are records of the same animal in more than one breeding place or traditional haulout place. There is no reliable way of measuring resight effort, thus data only represent opportunistic observations.

Results

A total of 354 seals, involving 100 tagged/marked individuals and 254 unidentified animals (138 belonging to published records), were collected from 1991 to 2005. The 354 animals sighted corresponded to 154 records, as some sightings involved more than one animal.

Table I summarizes the information in the database. Table II shows sightings as a function of sex and age categories.

Sex, age classes, social context and annual cycle

Most sightings involved sexually mature males (67% of 155 individuals categorized and sexed, Table II). Young males represented 25% of the total sample. Reproductive females were rare (4% of the records). Sightings away from rookeries involved solitary individuals more often than groups (37 vs 19). Animals seen during moulting season were more common that breeding individuals (60 vs 40%).

Geographic aspects of dispersion beyond rookeries

Most (65%) of the 69 records of animals sighted at more than 100 km from rookeries involved continental sites. Sightings away (> 100 km) from breeding colonies of seals of known and unknown origin involved 48 different locations along the continental coasts of Brazil, Uruguay, Argentina, Chile, Peru and Ecuador. Records from islands involved Lobos (Uruguay), Galapagos (Ecuador), Juan Fernandez and Pascua (Chile). One sighting that must be of special interest was a male recorded at the Galapagos Island (E3). It involved a young animal with a blue, unread tag, identical in shape and colour to those deployed at PV.

Seventy percent of the records occurred on the Atlantic coast of South America. Elephant seals were recorded in the Atlantic as far north as 10º50'S, in the Brazilian coast (B1 in Table III, Fig. 1a). Dispersion in the Pacific waters reached 2º25'S, in coastal Ecuadorian waters (record E2 in Table III, Fig. 1a).

Traditional haulout areas where seals were found in small groups involved Seno del Almirantazgo and Seno Otway (Chilean side of Tierra del Fuego), Isla de Lobos (Uruguay) and Monte Loayza (coastal Patagonia; Fig. 1a, Table III). Isolated births were reported in Monte Loayza and Mar del Plata, but no new pupping areas occurred along the coast of South America, either on the continent or on islands.

PV as focal site for dispersion

Sightings of animals of known origin involved only seals linked to PV. Valdés seals visited 20% of the total locations reported (Fig. 1a. $n = 50$).

PV seals regularly haulout as part of small groups with individuals of unknown origin at Bahía Ainsworth, Seno del Almirantazgo (Chilean side of Tierra del Fuego), and at Isla de Lobos (Uruguay) (Table II). One adult male that reproduced at PV (records U4, 7 and 9) moulted at Isla de Lobos during at least three consecutive years (2003–05). More opportunistic haulout locations in the Atlantic side and north of PV, involved the coast of Buenos Aires Province (Argentina), Uruguay and Brazil (records A3,7, U4,5,6,12,13,19 and B22; Table III). South of PV, seals were sighted in at least two places along coastal Patagonia (A31 and A32; Fig. 1a. Table III). Isolated sightings from the Pacific coast involved two subadult males that moulted in the south of Chile (C1 and C2, Table III).

PV and F/M as one population

The connection between PV and F/M was reflected by 85 resights (85 individuals), 66 recorded during the last eight years. Seals of both sexes linked these rookeries, although males were more common (72 of 78 sexed individuals; six

Table III. References of the records reported in the figure 1a. Prefixes in capital letters (B, U...) refers to the country of the sighting. Sight shows the number of individuals reported per year and (*) personal communication obtained from survey.

Location in Fig. 1	Record	Year	Reference
B1	1	1998	Serra *et al.* 2000
B2	1	2002	Fonseca, M.* (Puerto Alegre)
B3–B5, B7	4	1994–2002	Magalhães *et al.* 2003
B6	1	2003	Siciliano, S.*
B8	1	2002	Hadel, V.F.*
B9	1	2002	de Sanctis *et al.* 2002
B10, B11	2	1994–97	Caseca-Santos & Soto 1998
B12	1	1997	Ott, P.*
B13	3	1996–98	Silva *et al.* 1998
B14, B15	2	2000	Silva *et al.* 2002
B16	1	2001	Adornes A-Pedraza, S.*
U1	1	2004	Fallabrino, A.*
U2	1	2003	Rodriguez, R.*
U3	1	1993	This paper
U4, U5	24	2003	Iriarte, V.*
U6	4	2003	Katz, H.*
U7, U8	3	2004	Morgades, D.*
U9	1	2005	Franco Trecu, V.*
U10	1	1999	Praderi, R.*
A1	1	1994	Bordino, P.*
A2	1	1999	Lorenzani & Lorenzani 2000
A3	1	1997	Marsili & Lorenzani 1998
A4–A6	3	1993–94, 2003	Lorenzani & Lorenzani*
A7, A8, A11	3	1994–96	Faiella, A.*
A9, A10, A12	3	1999–2002	Giannoccaro *et al.* 2002
A13–A16, A19, A20	33	1991–2004	Reyes, L.*
A17	6	2002	Owen, J.*
A18	1	1995	Borboroglu, P.*
A21	10	1994	Campagna, C.*
A22	1	2004	Crespo, E.*
F1	2	2004	McGill, R.*
F2, F5–F8, F19–F26	13	1995	Thompson, D.*
F3, F9–F11	4	1991	Duck, C.
F4	1	1997	McGhie, J.*
F12–F17	6	1998–2000	Galimberti, F.*
F18	1	1994	Osteck, E.*
G1	1	1999	Boyd, I.*
C1, C2	23	2003	Acevedo Ramirez, J.A.*
C3–C11	119	1998–2001	Gibbons & Miranda 2001
C12, C13	1	1995–99	Sielfeld, W.*
C14	1	2003	Recabarren Green, A.*
C15	1	2003	Gonzales, H.*
C16	1	1995	Aguayo *et al.* 1995
P1	1	1994	Majluf, P.*
E1, E2	2	1998–2002	Alava Saltos, J.J.*
E3, E4	2	2004	Vargas & Steinfurth 2004*
V1–V58	58	1996–2003	This paper

juveniles, 57 subadults and eight adults of 71 males classified). All six females recorded were adults.

Animals connecting these rookeries were mostly males that reproduced at PV and moulted in the F/M (17 adults males tagged in PV and F/M in breeding and moult seasons respectively). At least three juvenile seals that moulted at PV were born at the F/M. No males were reported to reproduce in both sites.

Of the six adult females that showed migration between PV-F/M, four (F8, 22, 26 and V58) reproduced at PV (the first three were also recorded moulting at the F/M). One female (V31) was marked at Sea Lion Island during the breeding season and moulted at PV. One female (V39) reproduced in both colonies. V39 was observed giving birth twice at Sea Lion Island and twice at PV. The animal was first recorded at F/M in 1995, when it was marked, probably as a primiparous female. It was then seen with a pup at Sea Lion Island in 1997. She was then recorded twice at PV (2000 and 2001), each season with a pup.

The PV-F/M population was rarely connected to other colonies. One individual born at PV in 1998 (G1) was sighted, six months later, at South Georgia, > 2400 km distant in a straight line (Table II).

Discussion

Most common dispersion records of southern elephant seals around South America involve non-breeding males. Individuals use few places as moulting locations. Small groups rarely gather away from traditional breeding colonies. Only one location (Seno del Almirantazgo, Chile) is thought to be an incipient pupping area (A. Aguayo, personal communication 2004). Females are rarely sighted away from colonies. Their high dispersion at sea, compared to males, does not have a correlate on land (Campagna *et al.* 1995, 1998, 1999). The large area covered by seals potentially linked to the Patagonian population is in agreement with the lack of physical barriers when travelling in temperate seas.

The dispersion pattern of haulout places for seals of both sexes and different age categories, as well as for different periods of the annual cycle, has been reported by Burton (1985), Bester (1989) and van den Hoff (2001). Seals from Macquarie Island are regularly resighted at Campbell Island, 700 km away (van den Hoff 2001). Likewise, individuals from Marion Island were resighted at Iles de la Possession, *c*. 1200 km away (Bester 1989). These results are similar to our records linking PV with F/M, separated by 1200 km (Lewis *et al*. 1996). Some studies report that most sights correspond to males during the moulting or resting phases or the annual cycle.

Methodological constraints and PV as a source for species dispersion

Most recaptures were opportunistic and involved animals that could not be traced to a known breeding colony. Tagging efforts at PV started about 15 years ago and therefore the potential for sightings increased with time, so most reports were filed during the last eight years. Thus, quantitative measures are precluded for dispersion and connection between breeding places as well as for the estimate of trends and comparisons between seasons.

Could it be that seals sighted away from colonies but of

unknown geographic origin were from PV-F/M? In terms of number of sites, marked/tagged seals from the PV-F/M population show a dispersal range that partially overlaps with the total sample. A polygon drawn as an approximate of the total area potentially used by sighted seals including all samples is much larger than an area encompassing only tagged/marked seals (a surface of 4.7 million km^2).

This is mostly because none of the animals of known origin was recorded at the most extreme sites, such as Pascua, Juan Fernandez and Ecuador. However, distance between sources in breeding colonies and sighting locations, combined with colony size as an indicator of potential for dispersion, suggest that PV is a likely source for some records of unknown animals, at least those in the northern sites along the Atlantic coast of South America. The geographic distribution of breeding/moulting/resting places in the South Atlantic suggests that a seal found along the Atlantic coast of continental South America is likely to be related to the closest colony: first to PV and then to the F/M.

There are five breeding colonies north of the Antarctic Polar Front and close to the Southern Cone: PV, F/M, South Georgia, Gough and Tristan da Cunha islands (Le Boeuf & Laws 1994). PV is located on the continent, and is second in size after South Georgia (14 000 pups born per year vs 113 000; Boyd *et al*. 1996). The F/M colony of Sea Lion Island is relatively close to the Patagonian coast (*c.* 600 km in a straight line) but it is a small colony (about 500 pups born each year; Galimberti & Boitani 1999), thus a less probable source of most sightings. South Georgia, the largest of the southern elephant seal colonies (Le Boeuf & Laws 1994), is located at least 2000 km from the closest continental point in South America, thus many thousands of kilometres from locations in the northern range of the records. Tristán da Cunha and Gough are neglible in size and 3800–4500 km distant from the continent. Therefore the Patagonian colony is, in terms of size and distance, the most likely source for a seals recorded at least along the Atlantic coast of South America.

Sightings and satellite tracks suggest that foraging southern elephant seals may travel in the range of 2000 to 5000 km away from their breeding departing colonies (Campagna *et al.* 1999, Hindell & McMahon 2000). The latter maximum distance is equivalent to linking PV to 10ºS in the coast of Brazil, and to 30ºS in the Pacific, swimming around Tierra del Fuego. This scenario would encompass 84% of the resights of seals of unknown origin. It leaves out the extreme locations, but none of the other colonies would do much better and it would be even more unlikely that seals visited these places from rookeries of the Antarctic Peninsula. In addition, satellite tracks of animals from Antarctic (Bornemann *et al.* 2000) and sub-Antarctic (McConnell *et al.* 1992, McConnell & Fedak 1996) colonies suggest that they rarely travel to temperate waters. Seals from PV seem most likely to disperse in a larger area than indicated by tagged/marked individuals, but extreme locations cannot be easily attributed to any colony. The maximum distance from the colony to an offshore foraging locations that a seal from PV is known to have travelled is 2300 km. However, the same animal travelled total distances of many thousands kilometres during the foraging period (Campagna *et al.* 1998, 1999). Therefore, an elephant seal from PV may reach even the most distant of the sighting places if it is not intending to return to the rookery, following a regular annual cycle.

The tagged seal sighted at the Galapagos Islands (Vargas & Steinfurth 2004) cannot be undisputedly attributed to any rookery and not even to the southern species. From photographs and films, the authors and colleagues (F. Galimberti, S. Sanvito and M. Bester personal communication 2004) are inclined to identify this animal as a young male (five–six years old) southern elephant seal. The animal had a light blue tag, identical in colour and model to the tags deployed at PV. The controversy arises because blue tags had also been used (2003) with northern elephant seals in Guadalupe Island (Mexico; B. Le Boeuf personal communication 2003). Besides phenotypic features, the sighted seal does not match in age to the tagging schedule of northern elephant seals in Guadalupe Island; it was older and larger that any animal tagged in Guadalupe in 2003 could be. However, if the animal had reached Galapagos (0º18'S) from PV, it would have travelled 8000 km, while the Guadalupe–Galápagos trip would only be 4400 km. A young female southern elephant seal was reported north of the Equator, on the central North Arabian Sea coast (Johnson 1990). The closest rookery (Kerguelen, Crozet, Marion) was located about 7500 km away. Compare this to the distance of 5200 km reported by Hindell & McMahon (2000) for a juvenile elephant seal from Macquarie Island.

Historical aspects of distribution and new colonies

Narrative historical records from the 17th and 18th centuries described elephant seals on islands and the subtropical coasts of South America, places similar to the dispersion area based on present records (Fig. 1b), including traditional sites and opportunistic haulout sites (Eleta 1985). In the Pacific, seals were reported for the Galápagos and Juan Fernandez archipelagos (Burckardt 1984). Species identification is not certain for some of the reports, but descriptions and names given to the animals suggest they were elephant seals. In the Atlantic waters, seals entered the Rio de la Plata, and individuals were observed at Rio de Janeiro (22º55'13"S; Eleta 1985).

Along the Patagonian coast and offshore islands, the species identity was more certain because animals were killed at many locations along the coasts of Buenos Aires (Carmen de Patagones) and the Argentine continental Patagonia (San Julian, Puerto Deseado), as well as in the

F/M and Diego Ramirez archipelagos (Arguindeguy 1985, Destefani 1985, Eleta 1985). Surveys of the Patagonian coast, conducted in the mid 20th century (1946–48), described few elephant seals and only at one place in PV (Punta Norte; Carrara 1952). Sixty years later, this breeding colony is the fourth in number of pups born per year of the breeding locations for the species (Le Boeuf & Laws 1994), it increased its size and expanded its distribution at PV and to nearby areas (Scolaro 1976, Campagna & Lewis 1992, Lewis *et al.* 1998). Although a few pups are born on the Uruguayan coast (Castello 1984, table 1), and we reported groups of adults at Lobos Island present over the last twenty years (U4, U9 in Table III), this does not seem to be an expanding rookery. One or two pups are regularly reported for Monte Loayza (Santa Cruz, Argentina; Fig. 1a, A20, A21) or Mar del Plata (Buenos Aires, Argentina; A2), but these occasional occurrences are no indication of being a successful founding event as described for other locations for both species (Antonelis *et al.* 1981, Bester 1989, Hoelzel *et al.* 2001). The exception may be a small breeding group in southern Chile (Tierra del Fuego; A. Aguayo personal communication 2004). A link between PV seals and the Magellanic region of Chile suggests that animals used the latter place for moulting and resting.

The PV-F/M population

There is no conclusive data based on movements and dispersion to suggest that PV and the F/M may function as one genetic population. Studies deploying mtDNA indicate that the PV population stands out as a distinct one from the pattern of genetic structure seen between Macquarie Island, Heard Island and South Georgia (Slade *et al.* 1998, Hoelzel *et al*. 2001), and it is genetically isolated from other populations of the South Atlantic (Hoelzel *et al.* 2001). There is no evidence of an exchange of breeding individuals between the nearest colonies at Falklands Islands/Malvinas; this seems well confirmed by mtDNA data (Fabiani *et al.* 2003).

However, the result of at least one female switching breeding sites suggests that the opportunity for gene flow may not be negligible given the small size of the F/M group. It is unlikely that a breeding animal tagged at PV will not be seen at the F/M, but it is possible that an animal from the latter could be overlooked at PV. There is just one small breeding place in the Archipelago and accurate searching of marked seals have been carried out during the breeding season since 1995 (Galimberti & Boitani 1999). Occasional breeders occur at a few other sites, but this is limited to a few isolated females (F. Galimberti personal communication 2003). Searches conducted at PV are also intense, but for a restricted stretch of coast about 30 km long, in the highest density area (from 200 km used by the seals to reproduce; Campagna & Lewis 1992, Lewis *et al*. 1996).

Why seals disperse and why there are no new colonies

Dispersion to different land sites may reflect segregation of foraging locations that would decrease overlap and competition between sexes and age classes (Burton 1985, Bester 1988, van den Hoff 2001, Field *et al*. 2005). Satellite tracked elephant seals of both species show sexual dimorphism with adult and subadult males foraging along continental shelves, while adult females move to oceanic, open waters (Hindell *et al.* 1991, Campagna *et al*. 1999, Le Boeuf *et al*. 2000). Contrary to adults, juveniles from Macquarie were reported to segregate their foraging areas independent of sex and as a function of age/size classes (Field *et al.* 2005). Juveniles at PV show sex differences in the foraging location (Campagna & Lewis, unpublished data) and haulout at different times and places than adults (Lewis *et al.* 2004).

However, the dispersion of males to more distant locations than females is not consistent with the fact that adult males from PV forage closer to the coast than adult females. Mean maximum travel distance from PV to potential foraging areas is 820 km for males and 1200 km for females (Campagna *et al.* 1998, 1999). Males would leave their terrestrial haulout and disperse to lower latitudes following the productivity of the Malvinas and Brazil Currents (Campagna *et al.* 2000), which may affect their movements to subtropical areas. Post-breeding adult and subadult males spend more weeks at sea than females, who come back to moult one to two months earlier (Lewis *et al*. 2004). This gives males more opportunities to travel long distances. Moreover, foraging closer to the coast may explain why males and juveniles are more frequently resighted, and more likely to move to land to rest.

Why are movements and dispersion not linked to founder effects? Founder effects described for elephant seals are related to dispersion of females (Slade *et al*. 1998, Hoelzel *et al.* 2001). There is no habitat limitation in PV for the seals to reproduce and moult. Besides, proximity of PV to current foraging areas along the shelf or in the Patagonian Basin could be improved only by breeding in the F/M Archipelago, where habitat limitation on land could be more important than for the continent. Finally, predictability of foraging locations and food availability, related to the productive fronts of the SW Atlantic (Bradshaw *et al* 2005, Saraceno *et al*. 2004), would preclude strong pressure to move to alternative, potentially lower quality places on land or at sea.

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References

Aguayo, A., Ibáñez, P., Rauch, M. & Vallejos, V. 1995. Primer registro del elefante marino del sur, *Mirounga leonina*, en la isla de Pascua, Chile. Serie Científica. *Instituto Antártico Chileno (INACH)*, **45**, 123–129.

Antonelis, G.A., Leatherwood, S. & Odell, D.K. 1981. Population growth and censuses of the northern elephant seal, *Mirounga angustirostris*, on the California Channel islands, 1958–1978. *Fishery Bulletin*, **79**, 562–567.

Arguindeguy, P.E. 1985. Las Expediciones españolas a la Patagonia. *In* Destefani, L.A., Arguindeguy, P.E., Muguerza, A.M. & Gonzalez Lonzieme, E., *eds Historia Marítima Argentina*. Departamento de Estudios Históricos Navales. Secretaría General Naval de la Armada Argentina. Buenos Aires, IV, 225–247.

Bester, M.N. 1988. Marking and monitoring studies of the Kerguelen stock of southern elephant seals *Mirounga leonina* and their bearing on biological research in Vestfold Hills. *Hydrobiologia*, **165**, 269–277.

Bester, M.N. 1989. Movements of southern elephant seals and subantarctic fur seals in relation to Marion Island. *Marine Mammal Science*, **5**, 257–265.

Boyd, I.L., Walker, T.R. & Poncet, J. 1996. Status of southern elephant seals at South Georgia. *Antarctic Science*, **8**, 237–244.

Bornemann, H., Kreyscher, M., Ramdohr, S., Martin, T., Carlini, A., Sellmann, L. & Plöz, J. 2000. Southern elephant seal movements and Antarctic sea ice. *Antarctic Science*, **12**, 3–15.

Bradshaw, C.J.A., Hindell, M.A., Sumner, M.D. & Michael, K.J. 2005. Loyalty pays: life-history consequences of fidelity to marine foraging areas by elephant seals. *Animal Behaviour*, **68**, 1349–1360.

Burckardt, G. 1984. Fervor y decaimiento de la caza de focas. *In* Sociedad Anónima Importadora Y Exportadora De La Patagonia. *Argentina Austral Tomo 2.* Selección de los 434 números publicados entre los años 1929–1968. Buenos Aires, 424–434.

Burton, H.R. 1985. Tagging studies of male southern elephant seals (*Mirounga leonina*) in the Vestfold Hills area, Antarctica, and some aspects of their behaviour. *In* Ling, J.K. & Bryden, M.M., *eds. Studies of sea mammals in south latitudes*. Adelaide, Australia: South Australian Museum, 19–30.

Campagna, C. & Lewis, M. 1992. Growth and distribution of a southern elephant seal colony. *Marine Mammal Science*, **8**, 387–396.

Campagna, C., Le Boeuf, B.J., Blackwell, S., Crocker, D.E. & Quintana, F. 1995. Diving behaviour and foraging location of female southern elephant seals from Patagonia. *Journal of Zoology*, **236**, 55–71.

Campagna, C., Quintana, F., Le Boeuf, B.J., Blackwell, S. & Crocker, D.E. 1998. Diving behaviour and foraging ecology of female southern elephant seals from Patagonia. *Aquatic Mammals*, **4**, 1–11.

Campagna, C., Fedak, M.A. & McConnell, B.J. 1999. Post-breeding distribution and diving behaviour of adult male southern elephant seals from Patagonia. *Journal of Mammalogy*, **80**, 1341–1352.

Campagna, C., Rivas, A.L. & Marin, M.R. 2000. Temperature and depth profiles recorded during dives of elephant seals reflect distinct ocean environments. *Journal of Marine Systems*, **24**, 299–312.

Carrara, I.S. 1952. *Lobos marinos*, *pingüinos y guaneras de las costas del litoral marítimo e Islas adyacentes de la República Argentina.* Tesis de Doctorado. Facultad de Ciencias Veterinarias, Universidad Nacional de La Plata, Argentina, 80 pp. [Unpublished].

Carlini, A.R., Daneri, G.A., Marquez, M.E.I., Soave, G.E. & Poljak, S. 1997. Mass transfer from mothers to pups and mass recovery by mothers during the post-breeding foraging period in southern elephant seals (*Mirounga leonina*) at King George Island. *Polar Biology*, **18**, 305–310.

Carlini, A.R., Marquez, M.E.I., Daneri, G.A. & Poljak, S. 1999. Mass changes during their annual cycle in females of southern elephant seals at King George Island. *Polar Biology*, **21**, 234–239.

Caseca-Santos, L.R. & Soto, J.M.R. 1998. Novos Registros de *Lobodon carcinophagus* e *Mirounga leonina* (Pinnipedia, Phocidae) no sul do Brasil. 8ª Reuniao de Trabalho de Especialistas em Mamíferos Aquáticos da América do Sul. 2º Congresso da Sociedade Latinoamericana de Especialistas em Mamíferos Aquáticos (SOLAMAC), Olinda, Brasil, 46.

Castello, H.P. 1984. Registros del elefante marino, *Mirounga leonina* (Carnivora, Phocidade) en las costas del Atlántico S.O. fuera del área de cría. *Revista del Museo Argentino de Ciencias Naturales*, *Zoología*, **24**, 235–243.

De Sanctis, B., Pacheco De Souza, S. & Siqueira Alvarenga, F. 2002. Nova adição â lista de pinípedes do estado de São Paulo, Brasil: ocorrências do elefante-marinho-do-sul *(Mirounga leonina).*10ª Reunión de Trabajo de especialistas en Mamíferos Acuáticos de América del Sur. 4º Congreso de la Sociedad Latinoamericana de Especialistas en Mamíferos Acuáticos (SOLAMAC). Valdivia, Chile, 75–76.

Destefani, L.H. 1985. Colonización Patagónica. *In* Destefani, L.A., Arguindeguy, P.E., Muguerza, A.M. & Gonzalez Lonzieme, E., *eds. Historia Marítima Argentina*. Departamento de Estudios Históricos Navales. Secretaría General Naval de la Armada Argentina, Buenos Aires, IV, 179–223.

Eleta, F. 1985. La gran expedición del Capitán de Navío Don Alejandro Malaspina. *In* Destefani, L.A., Arguindeguy, P.E., Muguerza, A.M. & Gonzalez Lonzieme, E., *eds. Historia Marítima Argentina*. Departamento de Estudios Históricos Navales. Secretaría General Naval de la Armada Argentina. Buenos Aires, IV, 253–285.

Fabiani, A., Hoelzel, A.R., Galimberti, F. & Muelbert, M.M.C. 2003. Long range paternal gene flow in the southern elephant seal. *Science*, **299**, 676.

Field, I.C., Bradshaw, C.J.A., Burton, H.R., Summer, M.D. & Hindell, M.A. 2005. Resourcing partitioning through oceanic segregation of foraging juvenile southern elephant seals (*Mirounga leonina*). *Ocecologia*, **142**, 127–135.

Galimberti, F. & Boitani, L. 1999. Demography and breeding biology of a small, localized population of southern elephant seals *(Mirounga leonina). Marine Mammal Science*, **15**, 159–178.

Giannoccaro, A., Faiella, A., Saubidet, A. & Giangiobbe, A. 2002. Posible caso de tuberculosis en un elefante marino del sur (*Mirounga leonina*). 10ª Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur. 4º Congreso de la sociedad Latinoamericana de Especialistas en Mamíferos Acuáticos (SOLAMAC)Valdivia, Chile, 86.

Gibbons, J. & Miranda, C. 2001. Southern Elephant Seal (*Mirounga leonina)* (Phocidae) at Almirantazgo Sound, Tierra del Fuego. *Anales del Instituto de la Patagonia Serie Ciencias Naturales*, **29**, 157–159.

Grimwood, I. 1968. Endangered mammals in Peru. *Oryx*, **9**, 411–421.

Hindell, M.A., Burton, H.R. & Slip, D.J. 1991. Foraging areas of southern elephant seals, *Mirounga leonina*, as inferred from water temperature data. *Australian Journal of Marine and Freshwater Research*, **42**, 115–128.

Hindell, M.A. & McMahon, C.R. 2000. Long distance movement of a southern elephant seal (*Mirounga leonina*) from Macquarie Island to Peter 1 Øy. *Marine Mammal Science*, **16**, 504–507.

HOELZEL, A.R., CAMPAGNA, C. & ARNBOM, T. 2001. Genetic and morphometric differentiation between island and mainland southern elephant seal populations. *Proceedings of the Royal Society of London*, **B268**, 325–332.

JOHNSON, D.W. 1990. A southern elephant seal (*Mirounga leonina* Linn.) in the Northern Hemisphere (Sultanate of Oman). *Marine Mammal Science*, **6**, 242–243.

LE BOEUF, B.J. & LAWS, R.M. 1994. *Elephant seals: population ecology, behaviour and physiology*. Berkeley, CA: University of California Press, 414 pp.

LE BOEUF, B.J., CROCKER, D.E., COSTA, D.P., BLACKWELL, S.B., WEBB, P.M. & HOUSER, D.S. 2000. Foraging ecology of northern elephant seals. *Ecological Monographs*, **70**, 353–382.

LEWIS, M., CAMPAGNA, C. & QUINTANA, F. 1996. Site fidelity and dispersion of southern elephant seals from Patagonia. *Marine Mammal Science*, **12**, 138–147.

LEWIS, M., CAMPAGNA, C., QUINTANA, F. & FALABELLA, V. 1998. Estado actual y distribución de la población del elefante marino del sur en la Península Valdés, Argentina. *Mastozoología Neotropical*, **5**, 29–40.

LEWIS, M., CAMPAGNA, C. & ZAVATTI, J. 2004. Annual cycle and interannual variation in the haulout pattern of a growing southern elephant seal colony. *Antarctic Science*, **16**, 219–226.

LODI, L. & SICILIANO, S. 1989. A southern elephant seal in Brazil. *Marine Mammal Science*, **5**, 313.

LORENZANI, J.A. & LORENZANI, J.C. 2000. Primer nacimiento de una cría de *Mirounga leonina* en fecha para la provincia de Buenos Aires, Argentina. *9ª Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur. 3º Congreso de la Sociedad Latinoamericana de Mamíferos Acuáticos (SOLAMAC)*. Buenos Aires. 76.

MAGALHAES, F.A., HASSEL, L.B., VENTUROTTI, A.C. & SICILIANO, S. 2003. Southern elephant seals (*Mirounga leonina*) on the coast of Rio de Janeiro State Brazil. *Latin American Journal of Aquatic Mammals*, **2**, 55–56.

MARSILI, L. & LORENZANI, J.A. 1998. Resultados de análisis de metales pesados hallados en un ejemplar de elefante marino *(Mirounga leonina*) en la provincia de Buenos Aires, Argentina. *8ª Reuniao de Trabalho de Especialistas en Mamíferos Aquáticos da América do Sul. 2º Congresso da Sociedade Latinoamericana de Especialistas en Mamíferos Aquáticos* (SOLAMAC). Olinda, Brasil. 123.

MCCANN, T.S. 1985. Size, status and demography of southern elephant seal (*Mirounga leonina*) populations.*In* LING, J.K. & BRYDEN, M.M., *eds. Studies of sea mammals in south latitudes*. Adelaide, Australia: South Australian Museum, 1–17.

MCCONNELL, B.J., CHAMBERS, C. & FEDAK, M.A. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science*, **4**, 393–398.

MCCONNELL, B.J & FEDAK, M.A. 1996. Movements of southern elephant seals. *Canadian Journal of Zoology*, **74**, 485–496.

MUELBERT, M.M.C., ROBALDO, R.B., MARTINÉS, P.E., COLARES, E.P., BIANCHINI, A. & SETZER, A. 2004. Movement of Southern elephant seals (*Mirounga leonina* L.) from Elephant Island, South Shetlands, Antarctica. *Brazilian Archives of Biology and Technology*, **47**, 461–467.

NICHOLLS, D.G. 1970. Dispersal and dispersion in relation to the birthsite of the southern elephant seal, *Mirounga leonina* (L.), of Macquarie Island. *Mammalia*, **34**, 598–616.

ODUM, E.P. 1959. *Fundamentals of ecology*, 2nd ed. Philadelphia, PA: Saunders, 546 pp.

SARACENO, M., PROVOST, C., PIOLA, A.R., BAVA, J. & GAGLIARDINI, D.A. 2004. The Brazil Malvinas Frontal System as seen from nine years of AVHRR data. *Journal of Geophysical Research*, **109**, doi:10.1029/2003JC002127.

SCAR (SCIENTIFIC COMMITTEE FOR ANTARCTIC RESEARCH). 2002. Group of Specialists on Environmental Affairs and Conservation (GOSEAC). *SCAR Report of the GOSEAC XII Meeting*, College Station, TX, USA. No 22, 83 pp.

SCOLARO, J.A. 1976. Censo de elefantes marinos (*Mirounga leonina L.*) en el territorio continental argentino. *Informes técnicos Centro Nacional Patagónico*, **1, 4, 2**, 1–12.

SERRA, S.D., HUBNER, A. & DÓREA-REIS, L.W. 2000. Registros de mamíferos marinhos no litoral do estado de Sergipe. *9ª Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur. 3º Congreso de la Sociedad Latinoamericana de Mamíferos Aquáticos* (SOLAMAC). Buenos Aires, Argentina, 118.

SIELFELD, W. Algunas consideraciones sobre fócidos (Pinnipedia) asociados a las costas de Chile. *Anales del Instituto de la Patagonia (Chile)*, **9**, 153–156.

SILVA, K.G., MESSIAS, L.T. & CARVALHO, R.V. 1998. Status de conservaçao dos pinípedes no litoral do Rio Grande do sul (RS)-Brasil. *8ª Reuniao de Trabalho de Especialistas en Mamíferos Aquáticos da América do Sul. 2º Congresso da Sociedade Latinoamericana de Especialistas en Mamíferos Aquáticos*. (SOLAMAC). Olinda, Brasil, 206.

SILVA, K.G., MESSIAS, L.T. & CARVALHO, R.V. 2002. Status de conservaçao dos pinípedes no litoral do Rio Grande do Sul -Brasil, en 2000 e 2001. *10ª Reunión de Trabajo de especialistas en Mamíferos Acuáticos de América del Sur. 4º Congreso de la Sociedad Latinoamericana de Especialistas en Mamíferos Acuáticos* (SOLAMAC).Valdivia, Chile, 115–116.

SLADE, R.W., MORITZ, C., HOELZEL, A.R. & BURTON, H. 1998. Molecular population genetics of the Southern elephant seal, *Mirounga leonina. Genetics*, **149**, 1945–1957.

TORRES, D. 1981. Notas sobre el elefante marino del sur, *Mirounga leonina* (Linn., 1758) y hallazgo de un ejemplar en Chañaral, III Region, Chile. *(Pinnipedia:Phocidae). Boletín Antártico Chileno*, **1**, 10–14.

VAN DEN HOFF, J. 2001. Dispersal of southern elephant seals (*Mirounga leonina* L.) marked at Macquarie Island. *Wildlife Research*, **28**, 413–418.

VARGAS, H. & STEINFURTH, A. 2004. Primer registro de elefantes marinos en Galápagos. *Informe técnico para la Estación Científica Charles Darwin y Parque Nacional Galápagos*. Archivos ECCD. Isla Santa Cruz, Galápagos.