



Sea lions (*Otaria flavescens*) from the end of the world: insights of a recovery

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Abstract

To understand the recovery process and population dynamics of species that were severely depleted, it is essential to monitor their population size and habitat changes throughout their distribution. The South American sea lion (SASL, *Otaria flavescens*) provides an opportunity to investigate the process of a reduction from sealing and the subsequent recovery in a marine mammal species. Its abundance was depleted throughout its distribution, but the most affected extraction areas were Península Valdés (northern Patagonia) and Tierra del Fuego (Fuegian Archipelago). The aims of this work are to present recent estimates of the population abundance and then analyze changes in social composition, distribution, population size and trend of SASL at their sub-Antarctic distribution. We made an aerial survey of Fuegian Archipelago colonies and compared the results with historical compilation data registered since 1948. In total 49 colonies were surveyed (24 exclusive of SASL, 15 shared with South American fur seals and 10 sites were abandoned). An abundance of 7684 individuals (including 440 pups) was recorded. There was an increase of population abundance, with a change of the social composition and distribution of some colonies through time. The average annual percentage of population changes yields a growth of 8.8%. This value completes the population growth trend data throughout Southwestern Atlantic for SASL, and shows that there is an increasing latitudinal gradient of these rates. We discuss possible explanations related to differences in the beginning of the recovery, or in reactions to local environmental constraints, or migration from Pacific stocks.

Keywords Population recovery · Southern Atlantic · Sea lions · Fuegian archipelago

Introduction

Public awareness about environmental and conservation issues has increased over the last few decades, particularly in relation to marine mammals. However, the relationship between humans and marine mammals has not always been as positive as it is now. Since the 1800s, marine mammals have been used as consumptive resources by humans through sealing. Populations of many pinniped species declined sharply during the nineteenth and twentieth centuries due to overharvesting, and some of them have been reduced to such small sizes that they were thought to be extinct or nearly extinct (Bonner 1982; Gerber and Hilborn 2001; Kovacs et al. 2012). The end of commercial harvesting has resulted in differential levels of recovery for many (but not all) pinniped species through the twentieth century although the period of recovery since the cessation of commercial sealing has varied considerably, some species showing little evidence of recovery for decades (Wickens and York 1997; Gerber and Hilborn 2001; Gentry 2009). South American

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sea lions (SASL, *Otaria flavescens*) are an example of this history: they were sealed for leather, oil, and food from the 19th to the 20th centuries (Godoy 1963) but recovery of this species has been slow since sealing ceased (Carrara 1952; Godoy 1963; Bonner 1982).

The present distribution of SASL in South America is from Torres, Brazil (29°S) to Tierra del Fuego in the Atlantic Ocean and from southern Chile to Zorritos in Peru (4°S) over the Pacific Ocean (Vaz-Ferreira 1976, 1982; King 1983; Sanfelice et al. 1999). The global population size is estimated at least 445,000 individuals between 2008 and 2014 (Cardenas-Alayza et al. 2016). However, in the Atlantic, the current abundance is still well below the estimated pre-exploitation numbers (Crespo et al. 2012; Baylis et al. 2015; Grandi et al. 2015; Romero et al. 2017). Moreover, some SASL populations are still exposed to a range of actual and potential negative impacts linked to the development of coastal human activities (see Crespo et al. 2012 for a review). The post-sealing dynamics of SASL stocks in the Pacific and Atlantic Ocean has shown a remarkable variation

among areas. Stocks from Uruguay and southernmost Chile are declining (Venegas et al. 2002; Franco-Trecu et al. 2015); those from central Chile are stable (Sepúlveda et al. 2011); while the stocks from the Falkland Islands (Malvinas), Peru, northern and southern Chile are slowly recovering (Bartheld et al. 2008; Oliveira and Majluf 2012; Oliva et al. 2012; Contreras et al. 2014; Baylis et al. 2015). Stocks from the southwestern Atlantic coast (with the exception of Uruguay) are rapidly increasing as is described further below.

Along the Argentine coast (Fig. 1a) SASL declined dramatically due to sealing between the 1930s and 1960s (Crespo and Pedraza 1991; Thompson et al. 2005; Baylis et al. 2015; Grandi et al. 2015). Península Valdés (Chubut province) and Tierra del Fuego supported the most heavily exploited stocks (210,000 and 149,000 sea lions killed between 1921–1960 and 1918–1949, respectively). The Falkland Islands (Malvinas) stocks were also decreased (60,723 sea lions killed between 1928 and 1966), while stocks from Buenos Aires, central and southern Patagonia had significantly lower levels of exploitation (34,338, 401

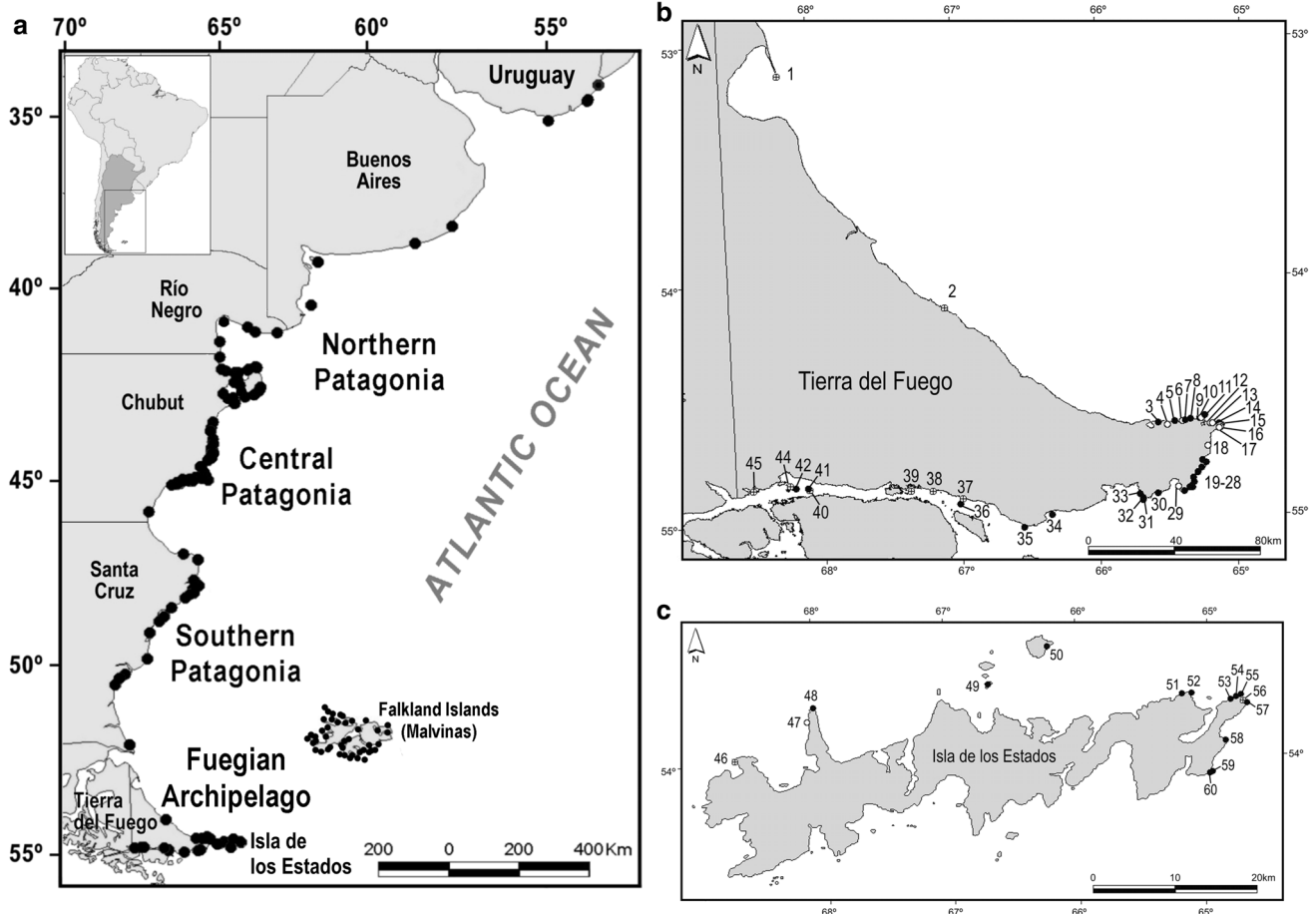


Fig. 1 a Current distribution of *O. flavescens* colonies along Southwestern Atlantic coast, with a detail in Fuegian Archipelago; **b** colonies in Tierra del Fuego; **c** colonies in Isla de los Estados (filled cir-

cle: colony with SASL; open circle: colony without sea lions at the time of the 2012 survey; circled plus: colony not visited during the survey); see text for further explanations

and 39,223 animals killed between 1937–1945, 1918–1940 and 1918–1948, respectively) (Godoy 1963; Crespo 1988; Crespo and Pedraza 1991; Baylis et al. 2015; Grandi et al. 2015). However, all stocks in continental Patagonia, irrespective of the level of exploitation, showed a similar reduction in abundance (~10% of their former values), suggesting a strong demographic linkage by migration of individuals among different stocks of the Patagonian region (Reyes et al. 1999; Dans et al. 2012; Baylis et al. 2015; Grandi et al. 2015).

Along the Argentine Atlantic coast, SASL aggregations are found in more than 120 locations from Buenos Aires to Tierra del Fuego (Crespo et al. 2012). In Patagonia, colonies can be grouped in four areas named: northern Patagonia (Río Negro and northern Chubut provinces), central Patagonia (southern Chubut province), southern Patagonia (Santa Cruz province) and Fuegian Archipelago (FA: Tierra del Fuego and Isla de los Estados) (Fig. 1a). There is an approximate population estimate of ~120,000 individuals for Argentina from terrestrial and aerial surveys conducted between 2004 and 2012. However, the northern rookeries were monitored more frequently than the southern ones (Dans et al. 2012).

The SASL stocks of Patagonia and Fuegian Archipelago encompass around 85% of the total South Atlantic population (Cardenas-Alayza et al. 2016). Along its coast the total population rates of increase are positive (5.6%, 6.0%, and 7.1% in northern, central and southern Patagonia, respectively; Dans et al. 2004; Reyes 2004; Grandi 2010; Grandi et al. 2015). In the Falkland Islands (Malvinas), the population also showed an increase (measured as 8.5% of pups between 2003 and 2014; Baylis et al. 2015). In the Fuegian Archipelago (FA), it was not possible to calculate a population growth rate due to insufficient regular survey effort (e.g. last survey date from 1997; Schiavini et al. 2004). Although the stocks from the Falkland Islands (Malvinas), northern, central and southern Patagonia currently show positive growth, their abundances are still far below those estimated in the past (pre-exploitation) (Baylis et al. 2015; Grandi et al. 2015; Romero et al. 2017).

Recent genetic studies on the population structure of SASL support the hypothesis that the Pacific and Atlantic populations should be considered distinct Evolutionarily Significant Units (Oliveira et al. 2017). There is a low inter-oceanic female gene flow (i.e., strong female philopatry to breeding areas) mediated by male dispersion and migration (Túnez et al. 2007, 2010; Feijoo et al. 2011; Hoffman et al. 2016; Oliveira et al. 2017; Grandi et al. 2018). Moreover, microsatellite analyses indicate that local populations from the Falkland Islands (Malvinas), and in a lesser extent, central and southern Patagonia Argentina, seem to share a genetic component with the Pacific ones (central and southern Chile), which in turn may be related to some gene flow between them (Hoffman et al. 2016; Oliveira et al. 2017).

However, for management purposes it is important to establish boundaries between the two ocean basins analyzing rookeries from southern South America, given the absence of physical barriers between the Atlantic and Pacific ESUs (Cardenas-Alayza et al. 2016) in a region where the gene flow between the Atlantic and Pacific populations potentially takes place (Oliveira et al. 2017).

The information about abundance estimation of southern Atlantic stocks is scarce (Schiavini et al. 2004; Dans et al. 2012). However, historical records allow us to conclude that 30% of the SASL hunted in the Atlantic during sealing activities came from Tierra del Fuego, 12% more came from the Falkland Islands (Malvinas) and 58% from the rest of stocks of Argentina (Godoy 1963). This sealing depleted the southern stocks, and even though the Falkland Islands (Malvinas) stock is actually recovering (Baylis et al. 2015), those at southernmost Chile (Magellanic Region) and Uruguay are still decreasing (Venegas et al. 2001; Franco-Trecu et al. 2015). This differential recovery highlights the need for accurate estimations of the status of SASL stock in the southernmost areas of South America in order to understand the effect that local dynamics have on the recovery of this regional stock. In this context, the aims of the present study are to present recent estimates of the local population abundance and then analyze changes in social composition, distribution of colonies, size and trend of the populations of SASL in Tierra del Fuego and Isla de los Estados (FA). Finally, we also aim at discussing these results in the context of the SALS population recovery in the Southwestern Atlantic.

Materials and methods

Study area and aerial survey design

The Isla Grande de Tierra del Fuego is located at the southern tip of South America (53° 56' S, 68° 32' W; Fig. 1b). Isla de los Estados is formed by a group of islands and islets located to the east of the Isla Grande de Tierra del Fuego (54° 49' S, 64° 29' W) (Fig. 1c). The survey of both islands was carried out by means of a twin-engine high-wing aircraft Cessna Super-Skymaster 337, flying at between 50 and 305 m (500–1000ft) of altitude depending on the cliff height and at a speed of 90 to 120 knots. Pictures were taken with a camera Canon EOS Rebel XT of 8 MP with an 80–200-mm telephoto lens by a photographer. Geo-referencing of pictures was made by synchronizing the camera with an I-GotU GPS logger (from Mobile Action) and georeferencing pictures using the @Trip PC software (https://global.mobileaction.com/download/i-gotU_download1.jsp).

The SALS breeding cycle starts early December with the arrival of adult males at the colonies. Adult females arrive

and establish territories between mid-December and the beginning of January. Mating occurs from mid-December to mid-February and the maximum number of births occurs in mid-January (Campagna 1985; Campagna and Boeuf 1988). In late February, at the end of the breeding season, the breeding structure dissolves slowly: males abandon the colony, and later adult females leave with their pups (up to May) (Campagna 1985). So a single flight took place at mid-day on January 7, 2012, in the middle of the SASL breeding season under good weather conditions (i.e., sunny day, without clouds, and winds less than 10 knots).

Estimate of population abundance and trend

A total of 1090 photographs were taken during the aerial survey and then analyzed in the laboratory to select the best shots based on optimal focus, sharpness, exposure, clarity, coverage and the proximity to the coast. For each colony (defined from previous surveys or discovery in the present survey), an image mosaic was constructed by editing and mounting the best shots. Counts were done by two experienced observers using the OTARIIDAE software (which allows the observer to place different color dots on each category and outputs the total count of the picture analyzed; see Bartheld et al. 2008), recognizing the following age and sex categories: adult males (AM), subadult males (SAM), females (F), pups (P), juveniles of unknown sex (J) and females + juveniles (F+J). This last category includes individuals which could be either F or J due to their close body and color similarity. The categories were based mainly on body size and color pelage, and the location in the rookery and behavioral cues were also taken into account to help to identify adult (territorial and peripheral) and subadult males (Campagna et al. 1988; Campagna and Le Boeuf 1988; Crespo 1988; Crespo and Pedraza 1991; Reyes et al. 1999). Each observer counted each photo once. If there was less than 10% difference between the two counts, the average of the two estimates was used as count for that colony. If there was more than 10% difference between the two counts, then one additional blind count was undertaken. The final estimate was obtained as the mean and standard deviation of all the counts made (Crespo 1988).

The annual rate of population increase (r) was estimated using the formula:

$$r = \frac{\ln N_t - \ln N_0}{t}$$

where N_0 is the number of individuals at time t_0 , N_t is the total number of individuals at time t , and t is the time elapsed between counts (Caughley 1977). Two rates were calculated taking into account the number of sea lions registered in the previous available abundance count in 1997 (N_0 ;

total and non-pups) and the sea lion counted in this work in the breeding season (N_t ; total and non-pups). The finite rate of increase (λ) is related to r by $\lambda = e^r$ (Caughley 1977), and this rate can be expressed as a mean annual percentage of population change in order to facilitate between-year and between-population comparisons. The conversion is done by subtracting 1 from λ and then multiplying this value by 100 (Caughley 1977).

Analyses of the social structure of the colonies

Colonies were classified as breeding, with a high proportion of pups (> 20% of all individuals in the colony) and traditional structure of harems (defined by Campagna 1985), non-breeding or haul-out colonies (without pups) and mixed (those that present important amount of juveniles, sub-adults and a small proportion of pups, < 20%) (Crespo 1988; Dans et al. 2004; Grandi et al. 2008, 2015).

To analyze if there had been changes in social composition and pup production of colonies through time, we compared the 2012 survey with available data (Schiavini et al. 1999, 2004). In 1997 SASL breeding season, an aerial census was carried out on January 29 and February 27, using high wing twin-engine airplanes ARAVA and CASA-212 under good weather conditions (i.e. sunny day, without clouds, and winds less than 10 knots). Flight altitude was maintained between 150 and 200 m (~ 650ft) whenever the topographic conditions and wind allowed it. Then, comparisons were made taking into account data from social structure from 1997 and 2012. Therefore, the proportion of pups and non-pups (raw survey) between 1997 and 2012, were compared using a normal approximation of the Chi-square test (Zar 1996).

Results

Population abundance

A total of 900 km were surveyed, during 5 flight hours. A total of 49 sites were covered (24 exclusive of SASL, 15 shared with South American fur seals and 10 that were surveyed but where no individuals were found). The survey yielded a total of 7684 ± 1651 individuals of SASL, located in 39 colonies (Table 1). The total number of non-pups recorded for the Fuegian Archipelago in 2012 was 7244 (including 866 AM, 845 SAM, 436 F, 458J and 4639 F+J). We counted 440 pups in twelve rookeries, but not all of the colonies presented a traditional breeding social structure. Only the rookeries Las Piedras, Las Chapas, Cabo Hall north and Islas Becasses (8, 9, 33 and 36, Table 1, Figs. 1, 2) presented a breeding social structure and the highest number of pups.

Table 1 South American sea lion colonies of Fuegian Archipelago, comparing sites previously recorded with the ones of the present study

Location	Summer 1948 ^a		Summer 1997 ^b		Summer 2012		Type of colony
	Non-pups	Pups	Non-pups	Pups	Non-pups	Pups	
<i>Isla Grande de Tierra del Fuego</i>							
1	1940	140	+				–
2	NR		221				–
3	4875	600	223	17	920	16	936 ± 40.5
4	2625	300	116	D	0	0	0
5	400 Dnbs		+		22	0	22 ± 0.7
6	1800		+		0	0	0
7	NR		NR		35	0	35 ± 2.3
8	2366	100	217	85	757	189	946 ± 19
9	2933	400	178	111	580	120	700 ± 12
10	2500	350	+		0	0	0
11	1600	250	+		179	2	181 ± 9
12	2333	300	+		0	0	0
13	3000	500	127	3	0	0	0
14	160 Dnbs		+		57	0	57 ± 0
15	1575	150	114	19	443	33	476 ± 29
16	630 Dnbs		+		0	0	0
17	2166	100	+		0	0	0
18	1266	70	+		0	0	0
19	2500	200	+		567	10	577 ± 18
20	1500	90	+		187	0	187 ± 1.4
21	166	15	+		73	0	73 ± 5
22	NR		NR		349	2	351 ± 26.5
23*	NR		NR		21	1	22 ± 1.4
24*	43 Dnbs		+		375	0	375 ± 7.5
25	NR		NR		47	0	47 ± 3.2
26*	NR		NR		21	0	21 ± 2.1
27	NR		NR		194	0	194 ± 3.2
28	66	6	+		91	0	91 ± 6.4
29	266	40	+		0	0	0
30	NR		D		378	0	378 ± 33
31	NR		3		81	0	81 ± 2.1
32	133	50	3		259	0	259 ± 7
33	NR		NR		100	20	120 ± 1.4
34	90	17	50	D	189	7	196 ± 7.5
35	NR		NR		140	0	140 ± 14.3
36*	126	20	59	179	200	30	230 ± 9.6
37	NR		D				–
38	NR		D				–
39	55		+				–

Table 1 (continued)

Location	Summer 1948 ^a		Summer 1997 ^b		Summer 2012		Type of colony
	Non-pups	Pups	Non-pups	Pups	Non-pups	Pups	
40	NR	NR	4	–	–	–	–
41*	NR	54.87°S, 68.10°W	105	5	9	0	9 ± 1.7
42*	NR	54.87°S, 68.10°W	32	–	88	0	88 ± 2.1
43	600	Not specific	+	–	–	–	–
44	NR	54.86°S, 68.22°W	17	–	–	–	–
45	NR	54.87°S, 68.50°W	20	–	–	–	–
<i>Isla de los Estados</i>							
46	500	54.79°S, 64.69°W	+	50	–	–	–
47	1500	54.79°S, 64.55°W	51	20	0	0	0
48	300	54.73°S, 64.54°W	+	–	129	0	129 ± 0
49	NR	54.70°S, 64.24°W	50	D	155	10	165 ± 4
50	NR	54.65°S, 64.12°W	100+	–	509	0	509 ± 31.5
51*	NR	54.72°S, 63.90°W	NR	–	16	0	16 ± 5
52*	NR	54.72°S, 63.89°W	NR	–	23	0	23 ± 8.5
53*	NR	54.72°S, 63.83°W	NR	–	3	0	3 ± 1.4
54*	NR	54.72°S, 63.82°W	20	–	9	0	9 ± 1.4
55*	NR	54.72°S, 63.81°W	NR	–	11	0	11 ± 1.4
56	NR	54.73°S, 63.81°W	17	–	–	–	–
57*	NR	54.73°S, 63.80°W	NR	–	4	0	4 ± 5
58*	NR	54.75°S, 63.80°W	NR	–	11	0	11 ± 1.4
59*	NR	54.79°S, 63.84°W	NR	–	7	0	7 ± 6
60*	NR	54.79°S, 63.85°W	10	–	5	0	5 ± 3
GRAND TOTAL	3998	38,624	1734	7244	440	7684 ± 1651	

Numbers on the left refer to position in Figs. 1 and 2. Census data grouped as pups and non-pups and Total (mean ± SD)

[*] colonies with the presence of *Arctocephalus australis* in 2012; [#] new location recorded for SASL; D: sea lions detected but not counted; Dnbs: sea lions counted in non-breeding season, not included in the grand total; [+] colony not found during the survey; [–] colony not visited during the survey; NR: not reported by previous surveys

^aData from Carrara (1952)

^bData from Schiavini et al. (2004)

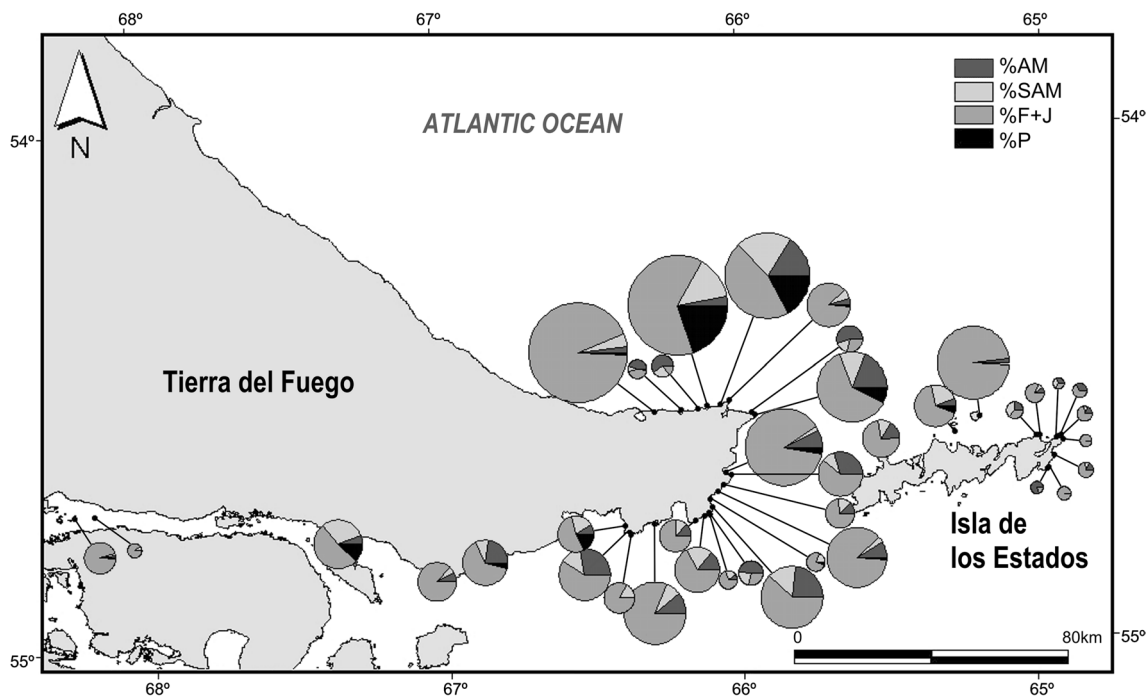


Fig. 2 Distribution of SASL colonies in Fuegian Archipelago in 2012. Each colony with presence of sea lions is shown by a pie diagram, where colony size (maximum number 2012) is indicated by circle area and social composition is indicated by the pie slice

When comparing the survey conducted in 2012 with that of 1997 (Schiavini et al. 2004), there is an evident increase in the number of individuals in almost all registered colonies. Only three colonies presented a decrease in the number of individuals compared to the previous survey: Islotes Les Esclaireus west ($N_{1997} = 110$), Cabo San Juan, ($N_{1997} = 20$) and Punta Fallows ($N_{1997} = 10$) (colonies 41, 54 and 60, Table 1, Figs. 1, 2). The decrease in these colonies may be due to the fact that they are haul-out colonies in which the number of sea lions is variable (Grandi et al. 2017).

Population trend

The population of *O. flavescens* in Tierra del Fuego and Isla de los Estados increased from 2173 in the year 1997 (Schiavini et al. 2004) to 7684 individuals in the year 2012. Population trend calculated using total individual count yields an intrinsic rate of increase $r = 0.084$ and the finite population growth rate $\lambda = 1.087$ between 1997 and 2012. Then, the average annual percentage of population change yields a growth of 8.8%. Considering the non-pups individuals, the intrinsic rate of increase was $r = 0.095$ and the finite growth rate $\lambda = 1.10$ between 1997 and 2012, with an average annual percentage of population change of 10%.

Changes in the social composition of colonies through time

Thirty-nine colonies were registered in 2012, from which 4 were confirmed as breeding colonies, 28 as haul-out sites and 7 as mixed (Table 1, Fig. 2).

The comparison of the 1997 and 2012 surveys revealed a change in the proportion of pups and non-pups in five colonies (Table 2). For these colonies, changes in the social structure can be related to an increase in the proportion of non-pups. However, Caleta Policarpo West maintained the production of pups, while Las Piedras, Las Chapas and Cabo San Diego increased the production of pups. Islas Becasses on the contrary diminished the pup production compared to 1997.

The social composition of Fuegian Archipelago as a whole could be described as a reservoir area of non-reproductive age classes, with small breeding groups located mainly at the Isla Grande de Tierra del Fuego (Fig. 2). Isla de los Estados has few individuals (11.6% of the total) distributed in 12 sites, most of them colonies of South American fur seal *Arctocephalus australis* (Milano et al. 2020).

Changes in the spatial distribution

The comparison of the present SASL locations with published records in the past reveals changes in the spatial

Table 2 Percentage of non-pups and pups of South American sea lion from some colonies of Fuegian Archipelago, and the results of the normal approximation of the Chi-square test

Location		Summer 1997		Summer 2012		Z_c	p
		Non-pups	Pups	Non-pups	Pups		
3	Caleta Policarpo west (Rancho Donata)	92.92	7.08	98.29	1.71	4.46	0.000029
8	Las Piedras	71.85	28.15	80.02	19.98	4.49	0.000008
9	Las Chapas	61.59	38.41	82.86	17.14	8.50	0
15	Cabo San Diego	85.71	14.29	93.07	6.93	2.89	0.003296
36	Islas Becasses	24.79	75.21	86.96	13.04	14.25	0

Numbers on the left refer to position in Figs. 1 and 2

distribution of colonies. There were nine colonies that were recolonized after 64 years (i.e., sites that were present in 1948 but not found during the 1997 survey): Sin Nombre 1, Cabo San Vicente, Caleta Chica (east), Bahía Buen Suceso north and south, Ensenada Patagones north and south and Cabo San Antonio (colonies number 5, 11, 14, 19, 20, 21, 24, 28, 48, Table 1 and Fig. 1a, b). There were 10 sites that are now abandoned (i.e., colonies where sea lions were present in 1948 and/or 1997 but without sea lions in the 2012 survey). Finally, 15 new SASL locations are described (i.e. colonies not registered in the 1948 and 1997 surveys, holding individuals in the 2012 survey), which represent 16.4% of the total abundance of sea lions in the zone. Of these, we report one new breeding colony (colony 33 in Table 1, Figs. 1, 2), two mixed colonies (colonies 22, 23 in Table 1, Figs. 1a, 2), and 12 haul-out colonies (Table 1, Fig. 2). Most of these last locations could be considered as occasional, due to the low abundance of individuals (< 50) or because the sites were occupied by South American fur seals, *Arctocephalus australis* (Crespo et al. 2015; Milano et al. 2020).

Discussion

The 2012 survey gives an abundance estimate after 15 years without surveys, evidencing an increase since 1997 for the Fuegian Archipelago (Tierra del Fuego e Isla de los Estados). The total abundance is lower than 64 years ago (when sealing ends), but represents a positive sign of population recovery. However, our results should be considered as a minimum abundance estimate for two reasons. First, due to weather conditions, the survey was made a week before the peak of births (Campagna 1985), so pups could be underestimated because we did not count some pups to be born. Second, it should also be considered that at the time of the survey there was a proportion of animals of the stock that was in the water (Crespo 1988; Reyes et al. 1999; Dans et al. 2004; Schiavini et al. 2004). When studying the population abundance of marine mammals that inhabit places of difficult access or throughout a vast territory, the only really feasible way to undertake population estimate is to perform

aerial surveys, which provide a permanent record of the distribution and the number of individuals (Mathews et al. 2011).

Tierra del Fuego was one of the three main regions of the Atlantic in which sea lions were severely reduced, the other being Península Valdés and the Falkland Islands (Malvinas). The Fuegian Archipelago declines from 38,624 individuals estimated in the 1946–1949 survey (Carrara 1952), to 2182 individuals (estimated in the 1990s), 5.65% of the abundance with regard to Carrara's counts (Schiavini et al. 2004). The number of SASL surveyed in 2012 shows an increase compared to the previous survey. However, the figures are still lower than those previous to the commercial sealing activities. In spite of this, the total rate of increase from FA (8.8%) is the largest reported for sea lions all along the SW Atlantic (see below). The total population growth rate found is similar (i.e., in the same order of magnitude) to that reported for other recovering populations of otariids, such as the Steller's (Eberhardt et al. 1979; Maniscalco et al. 2015) and California sea lions (Barlow et al. 1995), but it is lower compared to the population rate for several *Arctocephalus* species in recovery (Guinet et al. 1994; Hucke-Gaete et al. 2004; Wege et al. 2016). This discrepancy is expected, taking into account the differences in body size of the sea lion compared to the fur seal, which would have implications for physiology and reproductive output (Costa 1991; Costa et al. 2004; Arnould and Costa 2006), age at sexual maturity (Riedman 1990), and foraging strategies between fur seals and sea lions (Costa et al. 2004; Gentry 2009). These are the reasons why worldwide fur seal populations increase faster than sea lion populations and outnumber them by an order of magnitude (Gentry 2009).

It is very interesting that the rate of an increase in SASL from Patagonia increases with latitude (i.e. from north to south). In northern Patagonia, the population grows at a rate of 5.7% (Dans et al. 2004, 2012), in central Patagonia the rate is 6% (Reyes 2004), in southern Patagonia is 7.10% (Grandi et al. 2015), while in Falkland Islands (Malvinas) is 8.5% (Baylis et al. 2015) and in Fuegian Archipelago is 8.8%. The observed gradient along the coast could be due to the fact that the beginning of the recovery of the different

stocks occurred at different times, causing a delay. Then, areas where the recovery process started later present higher rates of increase while areas where the recovery process started earlier present lower rates of increase now. Alternatively, if the recovery process started at the same time in all the areas, this gradient could be explained because each area responded in a different way to local environmental constraints. The different level of productivity at the sea adjacent to the colonies in each region may be related to differences in the availability and variety of food resources, which influence vital rates (Hastings and Testa 1998; Pistorius et al. 1999, 2004; Reid and Forcada 2005; Hofmeyr et al. 2007). So far, there are not enough data from all the areas to allow us to determine the strategy used by the sea lions along the Southern Atlantic coast.

In spite of the available information about the different stocks throughout their distribution, the causes of the delay between the cease of sealing (1948–60, Godoy 1963) and the SASL stock's recovery (between 1990 and 1995) are not clear (Dans et al. 2004; Schiavini et al. 2004; Thompson et al. 2005; Otley 2008). First it was interpreted as a consequence of fishery development (Crespo and Pedraza 1991). Nevertheless, for northern Patagonia stock it was demonstrated that sea lion increase was independent of both fishery development and hake decline by fishery overexploitation (Drago et al. 2009). As an alternative, the delay was also attributed to changes in environmental conditions (e.g., carrying capacity) (Crespo and Pedraza 1991; Dans et al. 2004; Koen-Alonso and Yodzis 2005). The extreme reduction in the Atlantic sea lion populations led to a severe reorganization of the whole marine ecosystem (Koen-Alonso and Yodzis 2005), reaching a new trophic rearrangement and even equilibrium, with species such as small cetaceans, elephant seals and marine birds occupying trophic and spatial niches left by sea lions along the Atlantic coast (Grandi et al. 2015). Also, the fishing activity modified the structure of the ecosystem and reduced the quality of the preys (Trites and Donnelly 2003; Drago et al. 2009). So, differences observed in the rate of population growth along the entire Patagonian coast could be the consequence of the inertia of the whole marine ecosystem, both at a population and at a community level of recovery. Other possible causes proposed could be the effect of epidemic diseases, toxic algal blooms, accidental bycatch, predation, competition with fisheries, and oceanographic fluctuations/climate change (Otley 2008; Baylis et al. 2015). In the case of the FA sea lion stock, evidence supporting or rejecting some of these hypothesis is still pending.

This work shows a growth in SASL abundance together with an increase in the number of colonies and a change in the social composition of some of them. The process of SASL population recovery was accompanied by changes in social composition and spatial distribution, with

recolonization and/or colonization of new sites (Reyes et al. 1999; Thompson et al. 2005; Grandi et al. 2008, 2015). The change in the social composition found in some colonies from FA was similar to the recovery process observed in northern and southern Patagonia, with the transformation of haul-out sites into mixed colonies and the increase in pup production for some rookeries (Crespo 1988; Grandi et al. 2008, 2015). These changes in the social structure in FA were expected, due to juveniles being dominant in colonies in the 90's (Schiavini et al. 2004), age-class which seems to be essential both for the recolonization process and for population recovery (Grandi et al. 2008).

Population increase can be explained due to the intrinsic growth of the population (births outnumbering deaths) and also due to positive net balance of migration (final incorporation of individuals from other areas) (Begon et al. 2006). In the case of SASL from the Fuegian Archipelago, we can almost rule out that births had a major contribution in the population increase rate, because the 2012 pup production was similar to that from 1997 (Table 1). Moreover, the rate of increase in non-pup age classes was higher than the total rate of increase in the stock. So the population increase can be mainly explained by migration of non-pups age classes from closer areas. Analyzing some areas along the southern continent, we can see that there is a declining trend in the Magallanes Region (Region XII of Chile), which from 6912 SASLs counted in 1976–1978 dropped to 2606 individuals (Venegas et al. 2001, 2002). On the contrary, the Falkland Islands (Malvinas) and southern Patagonia have high and positive trends (Baylis et al. 2015; Grandi et al. 2015). The evidence for migration from the Falklands Islands (Malvinas) to Argentina is weak (Baylis et al. 2015, 2017). So we do not rule out the possibility of a flow of individuals from XII Region of Chile and southern Patagonia, which would generate the increase in the number of non-pups individuals found in Fuegian Archipelago. Genetic studies verify some exchange of individuals among colonies from the Pacific and the Atlantic (Weinberger 2013; Hoffman et al. 2016; Oliveira et al. 2017). Moreover, there is evidence in the Pacific that Peruvian stock is recovering as a consequence of both the availability of food resources and migration of SASL from northern Chile (Dans et al. 2012). The large and fragmented distribution of most otariid species may help to buffer some anthropogenic and climatic disturbances and stocks can be rebuilt from repeated migration events from other stocks within the range (Raum-Suryan et al. 2002; Lancaster et al. 2010; Pinsky et al. 2010).

The potential for “rescue effects” among local populations or stocks (Hanski 1982) shows the importance of considering spatial dynamics in the persistence of SASL in South America and highlights the importance of maintaining long-term and detailed monitoring studies of marine populations after an extreme reduction, in order to fully understand

the effect of local dynamics on the recovery of a depleted population.

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Author contributions EAC and ACMS Design the field work were done by CEA and SACM Aerial survey were done by SACM Material preparation and data analysis, and first draft of the manuscript were performed by MVN and GMF. All authors discussed the results and contributed to the final manuscript.

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Data availability All data and materials included in the present work is available.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Informed consent Informed consent was obtained from all individual participants included in the study.

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