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The recovery process of a population is not always the same: The case of *Otaria flavescens*

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Abstract
Populations of the South American sea lion (*Otaria flavescens*) were decimated throughout its range along the Atlantic coast. Responses to this decline have been different in different parts of the species' distribution range. Some stocks are still decreasing, some remain stable, and some are recovering slowly. In the Southwestern Atlantic, sea lion populations are now increasing. However, 50 years after the cessation of hunting these populations have not recovered to the levels they had before exploitation, with the recovery process occurring at the same time as increasing development of human coastal activities. The aims of this study were to present recent information on abundance and trends in the southern Patagonian population of sea lions and to test the hypothesis of population expansion with a particular recolonization process. Results showed that there was an increase in the number of sea lions in all colonies and a change in the social composition of nine colonies, but no new breeding colonies were found. The population trajectory of *O. flavescens* from southern Patagonia was similar to that observed in the rest of the South Atlantic populations, but the recovery and recolonization processes are still in progress. Here we discuss possible explanations of which factors could have delayed the recovery within the Southwestern Atlantic stocks.

Key words: *Abundance, recolonization process, South American sea lion, Southwestern Atlantic, trends*

Introduction

Historically, human interaction with marine ecosystems has caused a great impact on marine populations. Pinniped species have been heavily exploited worldwide, resulting in the reduction of different populations during the nineteenth and twentieth centuries (Bonner 1982). Several populations have been reduced to such small sizes that they were thought to be extinct or nearly extinct (Gerber & Hilborn 2001; Kovacs et al. 2012). Responses to these dramatic changes were different, depending on the species and populations. Some stocks have recovered throughout the twentieth century to different degrees, but mainly after a long time lag (Wickens & York 1997; Gerber & Hilborn 2001; Gentry 2009). However, because of the differences in diet and foraging strategies between fur seals and sea lions, it is thought that worldwide fur seal populations increased faster than sea lion populations and outnumber them by an order of magnitude (Gentry 2009).

At present, South American sea lions (*Otaria flavescens* Shaw, 1800) are distributed from Torres (29.33°S, 49.71°W), southern Brazil, in the Atlantic Ocean (Rosas et al. 1994) to Zorritos (4°S), northern Peru in the Pacific Ocean (Cappozzo & Perrin 2009). This species was one of the most exploited species along the South American coast, and populations were decimated during the early twentieth century (Crespo & Pedraza 1991; Páez 2006). Responses to reductions in abundance varied according to geographical area. Some stocks are still decreasing, such as the Uruguayan and austral Chilean populations (Venegas et al. 2001; Páez 2006), those from central and southern Chile are stable (Oliva et al. 2008; Sepúlveda et al. 2011) and

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some are recovering slowly, such as Peruvian and northern Chilean (Bartheld et al. 2008; Oliveira & Majluf 2012).

Particularly along the Southwestern Atlantic coast (Figure 1a), rough estimations of the populations of *O. flavescens* were carried out in the late 1930s (Hamilton 1934, 1939; Godoy 1963) and in the late 1940s, when the harvesting activity was declining (Carrara 1952; Strange 1979). Based on these data, South Atlantic sea lion stocks appeared to have dropped drastically in a few years (Figure 1b). Despite the fact that marine mammal harvesting in Argentina was prohibited by a National Decree in 1974, the population recovery occurred at the same time as increasing development of human coastal activities: oil and gas exploration and exploitation, fisheries, tourism, and the coastal establishment of industries.

Even though historic data suggest that sea lion abundance was higher in southern Patagonia (Santa Cruz province) and the Malvinas (Falkland) Islands (Figure 1b), the harvesting operations for leather and oil between 1920 and 1960 had occurred mostly along the Valdés Peninsula (northern Patagonia) and Tierra del Fuego (210,000 and 149,000 sea lions hunted, respectively), while stocks from central and southern Patagonia remained almost unexploited (401 and 39,000 animals hunted, respectively; Godoy 1963; Crespo 1988; Crespo & Pedraza 1991). However, both exploited and unexploited stocks showed a similar reduction in size (~10% of their former values; Figure 1b), suggesting a strong demographic interrelation in the Patagonian region (Reyes et al. 1999; Dans et al. 2012). Although the stocks from

the Malvinas Islands, northern and central Patagonia currently show positive growth, their numbers are still below those estimated in the past (Figure 1b; Reyes et al. 1999; Dans et al. 2004, 2012; Thompson et al. 2005; Grandi et al. 2008).

The status and trend of South American sea lions along the Argentine coast are mainly known from the northern Patagonia stock (Río Negro and northern Chubut provinces; Figure 1a). This stock fell to its lowest level during the 1960s (Koen-Alonso & Yodzis 2005; Grandi 2010) and is now growing at an intrinsic rate of increase of 0.057 (Dans et al. 2004; Grandi 2010). Along with this growth, there was a recolonization of new areas following a particular recovery process, in which many colonies exhibited changes in spatial distribution and social composition (Grandi et al. 2008). In this recolonization process, the new breeding sites are not located at random but are next to dense, established rookeries (i.e. traditional colonies; Grandi et al. 2008). Once a new site is occupied, the social composition of the colony changes through time. The process of this change begins with the establishment of juveniles followed by adult and sub-adult males, which yields mixed composition colonies with a rapid increase of pup production that ultimately results in traditional breeding sites (Crespo 1988; Dans et al. 2004; Grandi et al. 2008). These results highlight the importance of juveniles and adjacent areas to colonies in the establishment of new colonies and the population recovery.

Contrary to the observations in the north, information from the southern Patagonia stock is scarce and fragmentary. Historical data show that
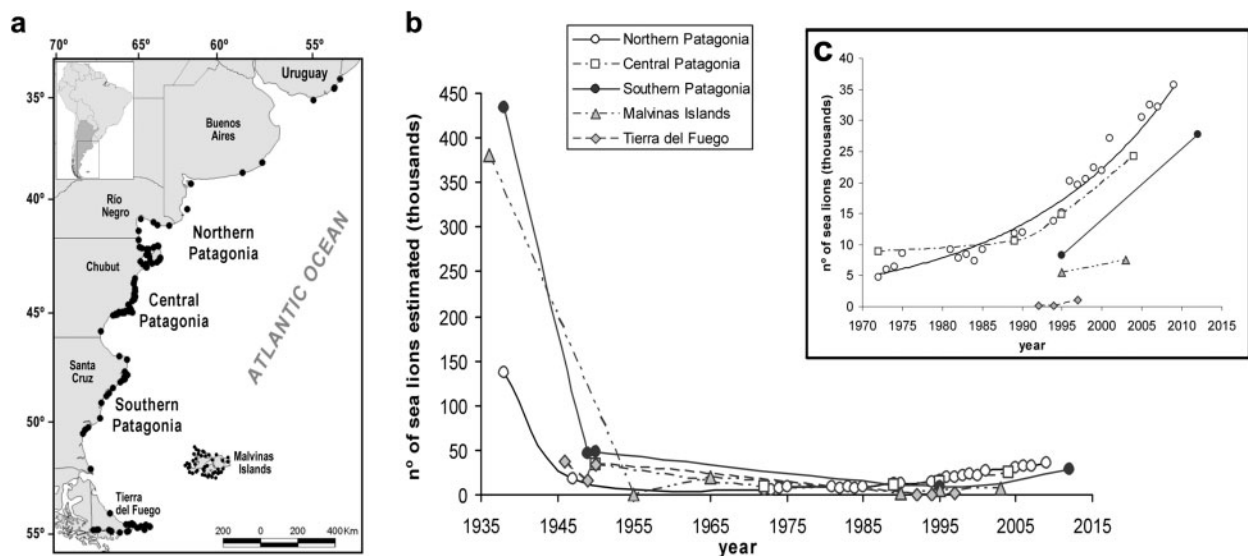

Figure 1. (a) Current distribution of *Otaria flavescens* colonies along the Southwestern Atlantic coast. (b) Number of South American sea lions (in thousands) estimated by region after the beginning and posterior to commercial harvest activities. (c) Detail of the last 45 years showing recent population abundances and trends of South American sea lions from the Southwestern Atlantic.

this stock was the most abundant among South-western Atlantic ones (Figure 1a). Sealing operations in southern Patagonia were restricted to very few colonies and isolated harvest periods (Godoy 1963). Nevertheless, the sea lion population also fell severely. Colonies in this region were last surveyed in 1995; however, there were not enough long-term data to estimate a population trend (Schiavini et al. 2004). These authors noted that juvenile age-classes were predominant in the social structure of these colonies, and showed that there was no change in the spatial distribution of colonies between 1950 and 1995. The scarce information about southern populations (Túnez et al. 2008; Dans et al. 2012) highlighted the need for accurate estimations of the size, status and distribution of these populations in order to understand the effect that local dynamics have on the recovery of this regional stock.

In this context, in which the rest of the south-western Atlantic stocks are recovering and rookeries present a specific recolonization dynamic and a possible interconnection between areas, we could therefore assume that the southern Patagonia sea lion stock has maintained a positive growth rate. Additionally, taking into account the high percentage of juveniles in this area, the aim of this study was to test the hypothesis that there was a population expansion in southern Patagonia with the particular recolonization process established in the north. If this hypothesis is true, we would expect to find more colonies in the area, with a high probability of them appearing close to the traditional rookeries. With this hypothesis, we also would expect to record a change in social composition of some colonies through time and a larger number of breeding colonies. To test this hypothesis, we first present recent estimates of the population abundance and trend of South American sea lions in southern Patagonia, then we analyse and describe changes in the social composition and spatial distribution of colonies through time, and finally we discuss these results in the context of sea lion population recovery in the Southwestern Atlantic.

Materials and methods

Study area and aerial survey design

The whole coast of Santa Cruz province (southern Patagonia), between Monte Loayza (47.08°S, 66.27°W) and Cabo Vírgenes (52.33°S, 68.34°W) (Figure 1a), was surveyed by low-wing single-engine aircraft (Piper Turbo Lance) in order to document the presence of animals ashore. The South American sea lion breeding season occurs from the second half of December to mid February, but it is expected that during the last week of January most of the individuals are present at the rookeries for reproduction and almost all of the pups were born (Campagna 1985; Crespo 1988). Therefore, the whole coast (~890 km) was surveyed on two different days, 24 and 25 January 2012, flying from north to south. The average speed of the aircraft remained fairly constant at around 166 km/h and at an altitude of about 150 m. Three people travelled on each flight: the pilot, located on the left side and looking offshore, one observer/recorder, located on the right side and looking at the coastline and forwards searching for sea lion colonies, and a second observer/photographer, also located on the right side and behind the first observer in charge of taking pictures of each group of sea lions detected. Each colony was photographed using a Nikon D80 digital camera of 10.2 MP equipped with a 80–200 mm telephoto lens.

Counting methodology

More than 1400 photographs were taken during the aerial survey which were then analysed in the laboratory. A mosaic was constructed for each colony by editing and mounting a selection of the best shots. A census was undertaken using OTARI-IDAE software (Bartheld et al. 2008) by an experienced observer (MFG). Individuals were counted separately by age-class and sex: adult males (AM, territorial and peripheral), sub-adult males (SAM), pups (P, born during the season of the census), and females + juveniles (F + J, both sexes pooled together). This last category is mainly composed of juvenile and adult females in established breeding rookeries, while in the non-breeding or haul-out sites it is impossible to assign age and sex to individuals due to their high similarity. These categories were based on body shape and colour, location in the rookery, and behavioural cues (Crespo 1988; Crespo & Pedraza 1991; Reyes et al. 1999).

Pups are the age-class most commonly under-estimated in aerial surveys (see Reyes et al. 1999; Schiavini et al. 2004; Bartheld et al. 2008). Fortunately, Schiavini et al. (2004) developed a correction factor in the 1995 census by means of a linear regression between the number of pups and non-pups counted in rookeries with a well-defined breeding structure. With the results of the 2012 raw census, we know that many of the colonies have a mixed social structure (i.e. small breeding areas with a large number of juveniles or non-reproductive animals in close proximity); thus, we corrected pups' counts (applying the formula *pups* = 48.05 + (0.83 × *non-pups*), extracted from Schiavini et al. 2004) only on groups with a breeding structure within each colony.

Analysis of changes in social composition of colonies through time

To analyse if there had been changes in the social composition and pup production for some colonies through time, we used the present raw census and looked for available data from detailed population surveys for the period 1990–2004 (Sutton 1990; Reyes & Crespo 1991; Szapkievich 1992; Pérez & Crespo 1994; Vila & Pérez 1996; Crespo et al. 2004; Schiavini et al. 2004). Most colonies had only one past census during the breeding season. So, in order to compare the proportion of pups and non-pups from the total number of individuals between 1995 and 2012, we used a normal approximation of the chi-square test (Zar 1996). For those colonies with available data for more than two years, the annual rate of change of the colony was estimated by a linear regression between $\log_e$ numbers of individuals (the total and pups) and the year of census.

Population trend

The annual rate of increase or exponential rate of population change (r) was determined using the following formula:

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

where N_0 is the number of sea lions at time t_0, N_t is the total number of sea lions at time t, and t is the time elapsed between counts (Caughley 1977). This population rate was calculated using both raw and corrected censuses from the 1995 and 2012 breeding seasons.

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).

Results

Distribution and census of colonies

A total of 17 colonies were observed during this study, all having been previously recorded (Carrara 1952; Szapkievich 1992; Schiavini et al. 2004), while 14 colonies described in previous surveys were absent from the present study and three colonies were not surveyed (Table I; Figure 2). The methodology of a census based on photographs provides a more accurate picture than a direct census by observers counting sea lions (Bartheld et al. 2008; Sepúlveda et al. 2011). Our results can therefore be considered to provide minimum abundance estimates, as a census based on a single observer provides no estimate of error. The results of the census are shown in Table I. The corrected number of pups is presented only for the global counts and thus values presented in Table I are not corrected.

The total number of non-pups recorded for southern Patagonia in 2012 was 23,123 (including 1638 AM, 1437 SAM, and 20,048 F + J). Pup numbers estimated by direct count from photos was 4651 and after applying the correction factor gave a pup production of 8469 pups. This last estimate leads to a total population estimate of 31,592 sea lions for the coast of southern Patagonia. Monte Loayza, Isla Lobos and Cerro Bayo (colony numbers 2, 10 and 29, Figure 2) were the colonies with both the highest number of sea lions and pup production.

The 2012 census confirmed the presence of pups in 10 colonies. Compared with the last aerial census from the 1995 breeding season (Schiavini et al. 2004), we detected that the distribution of some colonies had changed. Three sites (colony numbers 21, 24 and 25, Figure 2) recorded sea lions in 1995 but were absent in the present survey. There was a record of one sea lion in Isla Rasa Chica (48.36°S, 66.32°W), which could probably be an occasional resting site as it was not registered in previous censuses.

Changes in abundance and social composition of colonies through time

Compared to the last aerial census performed in the 1995 breeding season (Schiavini et al. 2004), there was an increase in the number of sea lions in all colonies registered, except for colonies 16 and 18 that maintained a similar size. Together with this growth, there was a change in the social composition of nine colonies, in which the proportion of pups and non-pups was significantly different between 1995 and 2012 ($Z_c > 1.96$; d.f. = 1; $p < 0.05$). Changes differed among colonies, but they could be explained as follows. On one hand, there were colonies showing an increase in pup production; thus, the proportion of pups in their social structure had changed significantly (colony numbers 2, 10, 11, 18 and 29, Figure 2). On the other hand, the most significant changes occurred at colonies described as haul-out sites in the 1995 breeding season (Schiavini et al. 2004), which have now turned into breeding colonies with a mixed structure of small breeding areas with groups of non-reproductive animals in close proximity (colony numbers 6, 15, 22 and 33, Figure 2). There were eight colonies that did not show a significant change in social composition between 1995 and 2012 (colony numbers 3, 5, 7, 13, 16, 28, 32 and 34, Figure 2). These colonies

Table I. South American sea lion colonies of southern Patagonia, comparing sites previously recorded with those of the present study. Preliminary raw census data (without correction factors) are presented with the percentage of pups in parentheses. Numbers on the left refer to position in Figure 2.

Location		Summer 1949[a] Total	Spring 1992[b] Total	Summer 1995[c] Non-pups	Summer 1995[c] Pups	Summer 2012 Non-pups	Summer 2012 Pups	Summer 2012 Total
1	Punta Casamayor	46.92°S, 66.89°W	375	+	+				−
2	Monte Loayza	47.08°S, 66.27°W	2940	1112	1727	245 (12.42%)	6777	1415 (17.27%)	8192
3	Cabo Blanco	47.20°S, 65.74°W	450	+	36	0	146	0	146
4	Roca Foca	47.75°S, 65.84°W	−	152	+				−
5	Islote Lobos	47.75°S, 65.95°W	−	+	25	0	60	1 (1.64%)	61
6	Isla Blanca	47.91°S, 65.73°W	4500	+	521	0	1676	31 (1.82%)	1707
7	Isla Pingüino	47.91°S, 65.71°W	2900	190	207	0	591	0	591
8	Islas Gemelas	47.92°S, 65.74°W	4500	+	+		0	0	WS
9	Punta Pozos	47.95°S, 65.77°W	850	40	+				−
10	Isla Lobos	47.96°S, 65.87°′W	6000	+	769	175 (18.54%)	2360	1126 (32.30%)	3486
11	Islet front of Pta. Médano Negro	48.01°S, 65.92°W	−	+	30	4 (11.76%)	880	442 (33.43%)	1322
12	Islote Liebres	48.10°S, 65.90°W	1000	+	+		0	0	WS
13	Isla Shag	48.11°S, 65.89°W	−	312	744	0	2036	0	2036
14	Islote Burgos	48.11°S, 65.96°W	3500	+	+		0	0	WS
15	Islote Puntudo	48.13°S, 66.04°W	5000	426	302	0	785	225 (22.28%)	1010
16	Islote Cabo	48.25°S, 66.22°W	400	586	52	0	40	0	40
17	Punta Mercedes	48.46°S, 66.69°W	115	+	+		0	0	WS
18	Islet front of Cerro Ordoñez	48.50°S, 66.76°W	−	156	622	51 (7.58%)	523	131 (20.03%)	654
19	Cerro Ordoñez	48.50°S, 66.77°W	−	220	+		0	0	WS
20	Islet front of Cabo Vigía	48.61°S, 66.89°W	3000	+	+		0	0	WS
21	Islet N of Islote Chato	48.69°S, 67.08°W	−	+	31	0	0	0	WS
22	Islote Chato	48.75°S, 67.06°W	7000	50	509	0	1512	257 (14.53%)	1769
23	Cabo Dañoso	48.84°S, 67.22°W	−	600	+		0	0	WS
24	Islet S of Cabo Dañoso	48.86°S, 67.24°W	−	+	147	0	0	0	WS
25	La Mina	49.16°S, 67.62°W	−	+	72	1 (1.37%)	0	0	WS
26	Cabo Curioso	49.18°S, 67.61°W	95	50	+		0	0	WS
27	San Francisco de Paula	49.74°S, 67.72°W	−	90	+		0	0	WS
28	Makenke	49.84°S, 67.77°W	−	+	626	0	1732	0	1732
29	Cerro Bayo	50.25°S, 68.63°W	1600	57	763	135 (15.03%)	2463	974 (28.34%)	3437
30	South of Rincón del Buque	50.28°S, 68.73°W	−	28	WS		0	0	WS
31	Punta Observación	50.35°S, 68.88°W	−	270	+		0	0	WS
32	Cerro Monte León	50.36°S, 68.88°W	725	45	7	0	100	0	100
33	Punta Cuevas	50.53°S, 69.05°W	−	90	461	0	1145	49 (4.10%)	1194
34	Cañadón Gapp	52.09°S, 68.60°W	1140	+	60	0	296	0	296
	GRAND TOTAL				7651	611	23,123	4651	27,774

[a]Data from Carrara (1952); [b]data from Szapkievich (1992); [c]data from Schiavini et al. (2004); [+] colony not found during the survey; [−] colony not visited during the survey; [WS] colony or rookery without sea lions at the moment of the survey.

were described as haul-out sites in the 1995 breeding season (Schiavini et al. 2004) and have maintained the same social structure of non-reproductive age-classes (i.e. without pup production).

Analysing all the available past data, we found seven colonies that had more than two censuses. However, four of them did not show a significant change in social composition (colony numbers 3, 7, 28 and 32, Figure 2). Nevertheless, we could describe and analyse the social composition of three colonies through time.

In Monte Loayza (colony number 2, Figure 2), the number of individuals increased, with a rate $r = 0.064$ ($r^2 = 0.91$; $n = 6$). Pup production also increased, with a higher rate $r = 0.11$ ($r^2 = 0.95$; $n = 5$; Figure 3a, left panel). This colony was previously described as having a social composition of 90% juveniles with the presence of a small breeding area with some pups (Schiavini et al. 2004). The growth of this colony was accompanied by a change in its social composition, with a large proportion of pups (Figure 3a, right panel).
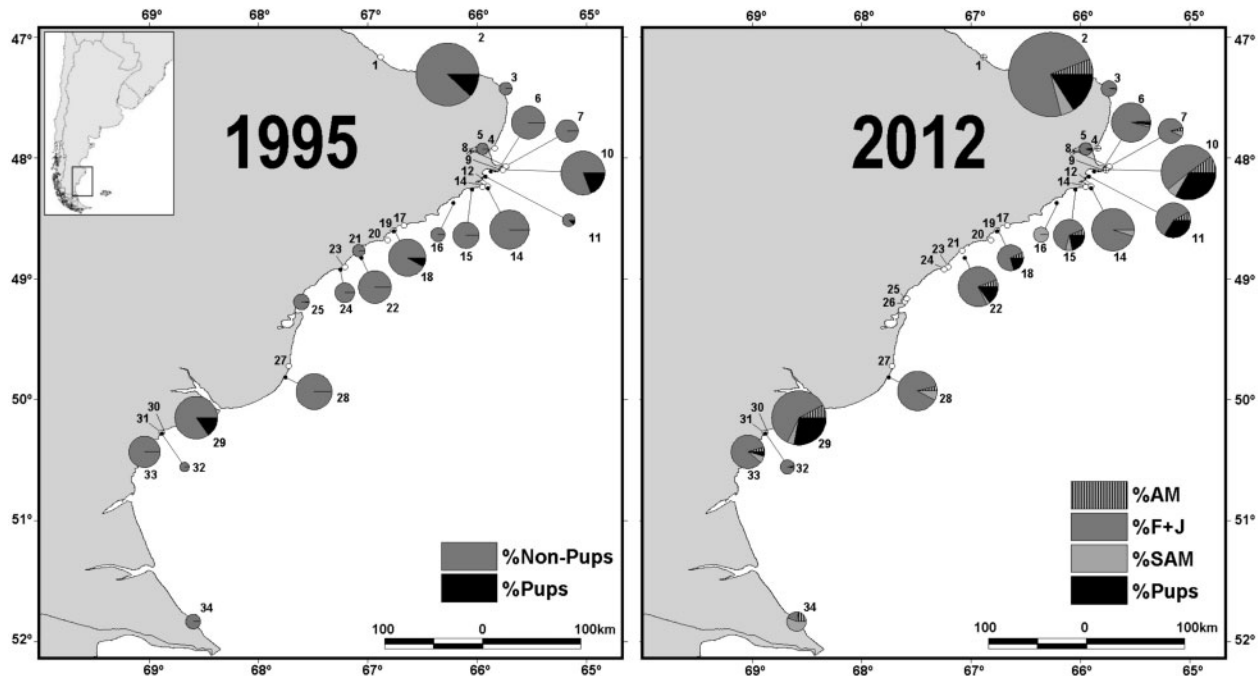
Figure 2. Distribution of South American sea lion colonies of southern Patagonia in 1995 and 2012. Each colony with presence of sea lions is shown by a pie diagram, where colony size (maximum number in 1995 or 2012) is indicated by circle area and social composition is indicated by the pie slice (○: colony without sea lions at the time of the survey; ⊕: colony not visited during the survey); see text for further explanations.

Cerro Bayo (colony number 29, Figure 2) was previously described as a typical breeding rookery (Schiavini et al. 2004). This colony also showed growth in the number of individuals, with a rate $r = 0.079$ ($r^2 = 0.95$; $n = 4$) and pup production also increased with a higher rate $r = 0.085$ ($r^2 = 0.6$; $n = 4$; Figure 3b, left panel). In spite of the increase in the number of individuals of all age-classes, Cerro Bayo did not change its social structure (Figure 3b, right panel), maintaining it as an important breeding colony in southern Patagonia.

Finally, Punta Cuevas (colony number 33, Figure 2) showed an increase in the number of individuals, with a rate $r = 0.057$ ($r^2 = 0.65$; $n = 3$). Pup production also increased, with a higher rate $r = 0.23$ ($r^2 = 0.87$; $n = 3$; Figure 3c, left panel). This colony was previously described as a haul-out site in 1995 (Schiavini et al. 2004) and in 2004 a breeding group was registered in the northern side of the colony, while the southern groups remained with non-reproductive age-classes, mostly juveniles (Figure 3c, right panel).

Population trend

The South American sea lion population in southern Patagonia increased from 8262 animals counted in 1995 (including 611 pups; Schiavini et al. 2004) to 27,774 estimated in 2012 (including 4651 pups). This raw census leads to an intrinsic rate of increase $r = 0.071$ between 1995 and 2012. Taking into account the population estimate including the correction of the pup numbers, the intrinsic rate of increase was $r = 0.069$. These population trends correspond to a mean annual percentage of population change of 7.39% and 7.10% (raw and corrected censuses, respectively).

Discussion

The 2012 South American sea lion population showed an increase in the number of pups and non-pups in all the breeding colonies, being 3.2 times higher than during the 1995 population census. However, we could not confirm the hypothesis that there was the same recolonization process observed in the northern Patagonia stock. Contrary to what was expected, we were able to confirm that there were no new breeding colonies along the coast. Since 1949 there was almost the same number of colonies, but there was a change in the number of sites where breeding occurred. In 1949, 18 breeding colonies were recorded, in 1995 only six of 20 colonies produced pups and in 2012 breeding activity took place in 10 (of 18) colonies. However, none of these sites were new locations; thus, there was no colonization of new areas. This was different from northern and central Patagonia and the Malvinas Islands stocks, where the positive growth was accompanied by an increase in the number of colonies
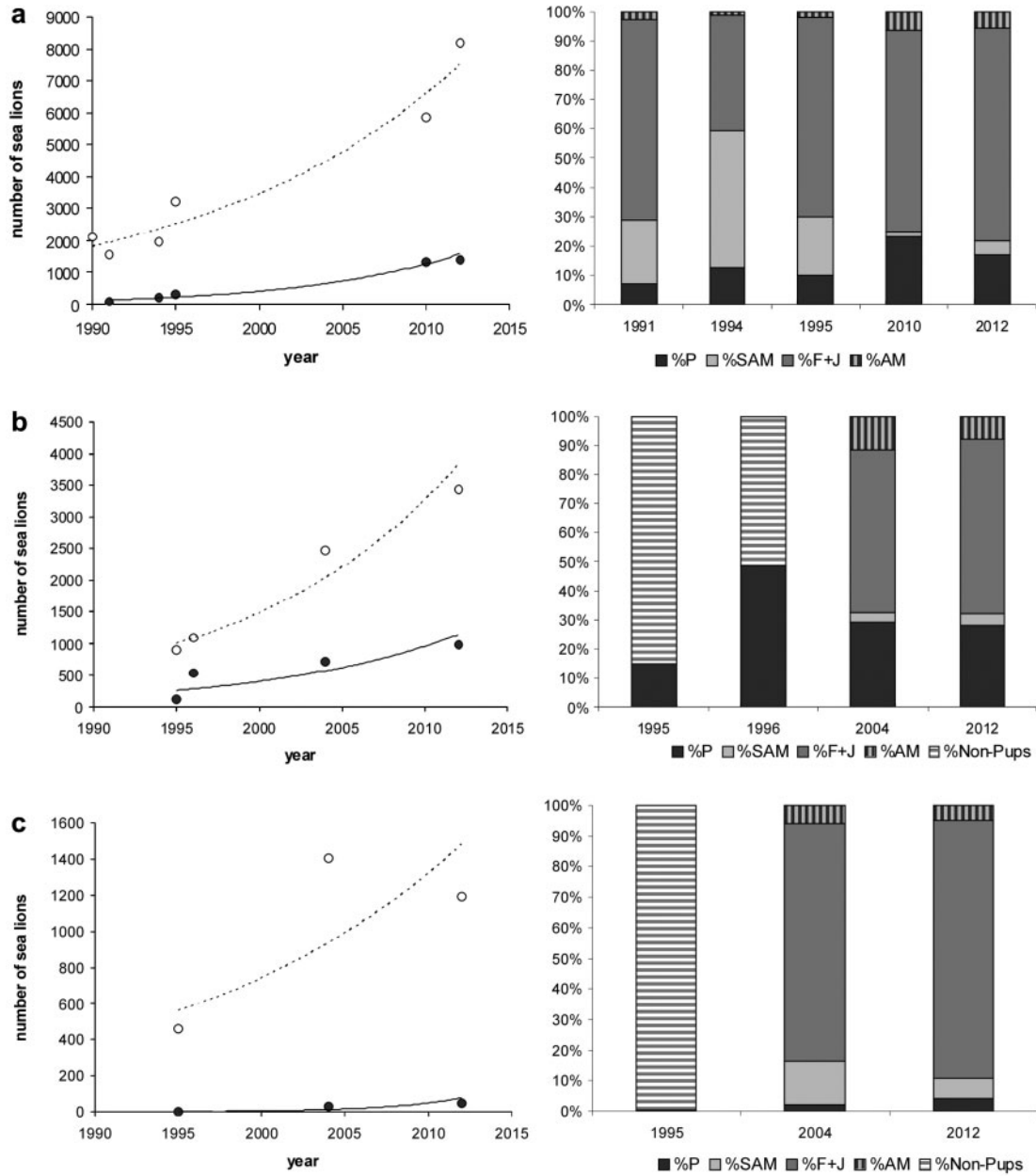
Figure 3. Left panels: counts and trend of South American sea lions (white: total, black: pups); right panels: proportion of South American sea lion individuals by age-classes; (a) Monte Loayza colony, (b) Cerro Bayo colony, (c) Punta Cuevas colony; see text for further explanations.

(Reyes et al. 1999; Thompson et al. 2005; Grandi et al. 2008). Túnez et al. (2008) suggested that the small number of sea lion breeding colonies in southern Patagonia could be explained by the effects of the high tidal range on the Atlantic coast. However, the differences in total abundance of sea lions and the regional concentration of colonies are probably more related to the vicinity of marine tidal fronts of high primary and secondary productivity in summer (Acha et al. 2004; Gagliardini et al. 2004; Palma et al. 2004; Rivas 2006; Rivas et al. 2006; Romero et al. 2006; Rivas & Pisoni 2010). Examples

of this are the high concentrations of sea lions close to the Valdés Peninsula (northeast of Chubut province), and on the northern coast of San Jorge Gulf (southeast of Chubut province), northern Santa Cruz, Tierra del Fuego and Isla de los Estados (Figure 1a).

In concordance with what we expected, we could record a change in the social composition of some colonies through time, although there was no population expansion in southern Patagonia. This change in the social composition of colonies was similar to the recovery process observed in northern Patagonia,

with the transformation of haul-out sites into breeding colonies with a mixed structure and the increase in pup production for some rookeries. Changes in the social structure in southern Patagonia was expected due to juveniles being dominant in colonies in 1995 (Schiavini et al. 2004) and this age-class seems to be essential both in the recolonization process and in population recovery (Grandi et al. 2008).

The population trajectory of *Otaria flavescens* from southern Patagonia is similar to that observed in the rest of the South Atlantic stocks during the second half of the twentieth century (Figure 1b). It showed a drastic decline between 1940 and 1980 and the most likely explanation for the depletion reported was the strong sealing operations performed mainly at the Valdés Peninsula (northern Patagonia) and at Tierra del Fuego (Schiavini et al. 2004). The southern Patagonia total population of *O. flavescens* recovered by a mean annual value of 7.10% between 1995 and 2012. This value is in the same order of magnitude as that reported for northern and central Patagonia stocks (5.87% and 6.18%, respectively; Dans et al. 2004; Reyes 2004) and higher than the 3.8% reported for the Malvinas Islands stock (Thompson et al. 2005; Figure 1c). The similarity in the population trajectories (the decline and the recovery) from northern, central and southern Patagonia could be explained by a strong connection and interchange of individuals among breeding areas that could function as a metapopulation along the Atlantic coast. Genetic population analyses of South American sea lions suggest that gene flow is mediated by male dispersal and migration along the Atlantic coast while females have a strong philopatry to breeding areas (Szapkievich et al. 1999; Freilich 2004; Túnez et al. 2007, 2010; Gehara 2009; Feijoo et al. 2011).

Roux (1987) identified four successive stages in the recovery of fur seal populations: (1) 'survival' that extends from the cessation of human exploitation to the initiation of breeding activities (i.e. individuals surviving exploitation ensure a remnant population for breeding); (2) 'establishment', which is the period when breeding is restricted to a few founding colonies; (3) 'recolonization', during which numbers increase and new colonies arise rapidly in response to a shortage of space in the founding colonies; and (4) the 'maturity' stage is initiated by a decline in the rate of increase caused by density-dependent factors. Taking into account these stages, we could see that Southwestern Atlantic sea lion populations are passing through different phases of the recolonization process. The Southern Patagonia population is still in the establishment phase, while Malvinas, northern and central Patagonia stocks may have reached the

recolonization stage, with some breeding colonies close to the maturity stage (Grandi et al. 2008).

The southern Patagonia sea lion population estimate presented here represents approximately 7.28% of the original estimated population abundance for the late 1930s (at the beginning of commercial exploitation). It should be noted that the historical data could be biased. The earliest estimates correspond to the period of commercial exploitation (López Arregui & González Regalado 1940; Carrara 1952; Godoy 1963). The estimate from 1938 was calculated from terrestrial census data (López Arregui & González Regalado 1940; Godoy 1963), and could be overestimated (Crespo & Pedraza 1991) because the ultimate goal was to evaluate quantitatively the faunal resources to be exploited by factories. The estimate from 1947–1949 was calculated from both aerial and terrestrial surveys (Carrara 1952), but could be slightly underestimated because the final number corresponds to a mean of several censuses before, during and after the breeding season among different years (Crespo & Pedraza 1991). However, recent population models developed for the northern Patagonia population (one of the stocks that has the longest data set available for the species) describe the population trajectory from 1900 to 2015 and, without using these two historic data to fit the models, the abundance estimates surprisingly agreed with the population census from 1938 and 1947–1949 (Koen-Alonso & Yodzis 2005; Grandi 2010). This suggests that biases from the earlier data may be small.

Sealing in southern Patagonia occurred at only six rookeries between 1920 and 1949, but the exploitation was not as important as that carried out in other regions (Godoy 1963; Crespo & Pedraza 1991). The relatively slow increase and the delay in the recovery were first interpreted as a consequence of fishery development (Crespo & Pedraza 1991). Nevertheless, it was demonstrated recently that, at least for northern Patagonia, sea lion population increase was independent of both fishery development and hake decline by fishery overexploitation (Drago et al. 2009).

As an alternative, the delay between the cessation of sealing and the population's recovery was also attributed to changes in environmental conditions (e.g. carrying capacity) (Crespo & Pedraza 1991; Dans et al. 2004; Koen-Alonso & Yodzis 2005). The extreme reduction in the Atlantic sea lion populations led to a severe reorganization of the whole marine ecosystem (Koen-Alonso & Yodzis 2005), in which it reached a new trophic 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. Evidence of

such changes were the increase of other predators, like the Magellanic penguin *Spheniscus magellanicus* (Forster, 1781) (Carribero et al. 1995; Schiavini et al. 2005) and Southern elephant seal *Mirounga leonina* (Linnaeus, 1758) (Lewis et al. 1998), as well as several shifts in the diet of some former hake predators, like the spiny dogfish *Squalus acanthias* (Linnaeus, 1758) (Koen Alonso et al. 2002). Consequently, the ecosystem which collapsed populations are expected to re-occupy may no longer have the same properties favourable for recovery as when the populations were larger.

While the decline in abundance of other over-hunted sea lion species is well documented (e.g. *Eumetopias jubatus* (Schreber, 1776), Atkinson et al. 2008; *Phocarctos hookeri* (Gray, 1844), Robertson & Chilvers 2011), the threats that are presently limiting recovery are more difficult to assess (Kovacs et al. 2012). However, there is a consensus that fishery interaction is recognized as the dominant current threat (Kovacs et al. 2012). Moreover, for Steller and New Zealand sea lions, nutritional stress due to fisheries competition and fisheries-related by-catch are possible factors delaying population recovery (Robertson et al. 2006; Atkinson et al. 2008; Robertson & Chilvers 2011). In the case of the southern Patagonia sea lion population, evidence supporting or rejecting this hypothesis is still pending.

In conclusion, the South Atlantic *O. flavescens* populations are growing, but the recovery and recolonization process are still in progress. Nevertheless, it is worth pointing out that, although this species is now classified as 'Least concern' by the IUCN Red List (Campagna 2008), it has not recovered to the levels it had before exploitation (Kovacs et al. 2012). Thus, it is important to consider that even though population trends are positive, they are not equivalent to full population recovery, but only an indicator of movement towards recovery. Moreover, in the rest of the species' range the abundance and trend of stocks are dissimilar and some of them continue to decrease (Dans et al. 2012; Grandi et al. 2012). This highlights the importance of the maintenance of long-term and detailed monitoring studies of marine populations after an extreme reduction, in order to assess the causes and factors influencing the recovery process. The results obtained here provide a better understanding of the status of South American sea lions along the Atlantic coast and make possible further investigations on the connectivity among areas and the effect of local dynamics on the recovery of a depleted population. Lastly, the information attained will constitute an essential tool for the management and conservation of this species and also for any other recovering population of pinnipeds.

References

Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J. 2004. Marine fronts at the continental shelves of austral South America: Physical and ecological processes. Journal of Marine Systems 44:83–105.

Atkinson S, DeMaster DP, Calkins DG. 2008. Anthropogenic causes of the western Steller sea lion *Eumetopias jubatus* population decline and their threat to recovery. Mammal Review 38:1–18.

Bartheld JL, Pavés H, Vera C, Manque C, Miranda D. 2008. Cuantificación poblacional de lobos marinos en el litoral de la I a IV Región, Chile. Informe Técnico Fondo de Investigación Pesquera IP-IT/2006-50. 124 pages. http://www.fip.cl/prog_x_year/2006/2006-50.htm (accessed July 2011).

Bonner WN. 1982. Seals and Man. A Study of Interactions. Seattle: University of Washington Press. 170 pages.

Campagna C. 1985. The breeding cycle of the southern sea lion, *Otaria byronia*. Marine Mammal Science 1:210–18.

Campagna C. 2008. *Otaria flavescens*. In: IUCN 2011. IUCN Red List of Threatened *Species*. Version 2013.2. http://www.iucn-redlist.org/ (accessed June 2014).

Cappozzo HL, Perrin WF. 2009. South American Sea Lion, *Otaria flavescens*. In: Perrin WF, Würsig B, Thewissen JCM, editors. Encyclopedia of Marine Mammals, 2nd edition. London: Academic Press, p 1076–79.

Carrara IS. 1952. Lobos marinos, pingüinos y guaneras de las costas del litoral marítimo e islas adyacentes de la República Argentina. Facultad de Ciencias Veterinarias. Buenos Aires: Universidad Nacional de La Plata. 191 pages.

Carribero A, Pérez D, Yorio P. 1995. Actualización del estado poblacional del pingüino patagónico *Spheniscus magellanicus* en Península Valdés, Chubut, Argentina. El Hornero 14:33–37.

Caughley G. 1977. Analysis of Vertebrate Populations. London: John Wiley & Sons. 234 pages.

Crespo EA. 1988. Dinámica Poblacional del Lobo Marino del Sur *Otaria flavescens* (Shaw, 1800), en el Norte del Litoral Patagónico. PhD Thesis. Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Buenos Aires. 298 pages.

Crespo EA, Pedraza SN. 1991. Estado actual y tendencia de la población de lobos marinos de un pelo (*Otaria flavescens*) en el litoral norpatagónico. Ecología Austral 1:87–95.

Crespo EA, Dans SL, García NA, Pedraza SN, Coscarella MA, Berón Vera B, et al. 2004. Estudio de línea de base y plan de monitoreo de mamíferos marinos del futuro Parque Nacional Monte León. Informe Final. 57 pages.

Dans SL, Crespo EA, Pedraza SN, Koen Alonso M. 2004. Recovery of the South American sea lion population in northern Patagonia. Canadian Journal of Fisheries and Aquatic Sciences 61:1681–90.

Dans SL, Sielfeld W, Aguayo A, Giardino G, Mandiola MA. 2012. Estado y tendencia de las poblaciones. In: Crespo E, Oliva D, Dans S, Sepúlveda M, editors. Estado de Situación del Lobo Marino Común en su Área de Distribución. Valparaíso: Universidad de Valparaíso, p 18–35.

Drago M, Crespo EA, Aguilar A, Cardona L, García NA, Dans SL, et al. 2009. Historic change of the diet of the South American sea lion in Patagonia as revealed by isotopic analysis. Marine Ecology Progress Series 384:273–86.

Feijoo M, Lessa EP, Loizaga de Castro R, Crespo EA. 2011. Mitochondrial and microsatellite assessment of population structure of South American sea lion (*Otaria flavescens*) in the Southwestern Atlantic Ocean. Marine Biology 158:1857–67.

Freilich SY. 2004. Genetic Diversity and Population Genetic Structure in the South American Sea Lion (*Otaria flavescens*) from Argentina and the Falkland Islands. PhD Thesis. University of Durham, UK. 100 pages.

Gagliardini DA, Amoroso RO, Dell'Arciprete OP, Yorio P, Orensanz JM. 2004. Detection of small-scale coastal oceanographic processes through Landsat-TM/ETM+ images: Implications for the study of biological processes along the Patagonian coasts of Argentina. Gayana 68(2):194–200.

Gehara MCM. 2009. Filogeografia do Leão-marinho-do-sul, *Otaria flavescens* Shaw, 1800. Grade Thesis. Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil. 51 pages.

Gentry RL. 2009. Eared Seals, Otariidae. In: Perrin WF, Würsig B, Thewissen JCM, editors. Encyclopedia of Marine Mammals, 2nd edition. London: Academic Press, p 339–41.

Gerber LR, Hilborn R. 2001. Catastrophic events and recovery from low densities in populations of otariids: Implications for risk of extinction. Mammal Review 31:131–50.

Godoy JC. 1963. Evaluación de los Recursos Naturales de la Argentina (Primera Etapa), volume VIII. Fauna Silvestre, volume 1. Argentina: Consejo Federal de Inversiones. 527 pages.

Grandi MF. 2010. Dinámica Poblacional y Cambios Estructurales en una Población en Crecimiento de Lobo Marino Común, *Otaria flavescens*, del Litoral Norpatagónico. PhD Thesis. Universidad Nacional del Comahue, Bariloche, Argentina. 182 pages.

Grandi MF, Dans SL, Crespo EA. 2008. Social composition and spatial distribution of colonies in an expanding population of South American sea lions. Journal of Mammalogy 89:1218–28.

Grandi MF, Oliveira LR, Dans SL, Crespo EA. 2012. A hunted population in recovery: Effective population size for South American sea lions from Patagonia. Animal Biology 62:433–50.

Hamilton JE. 1934. The southern sea lion (*Otaria byronia*) (de Blainville). Discovery Reports 8:269–318.

Hamilton JE. 1939. A second report on the southern sea lion (*Otaria byronia*) (de Blainville). Discovery Reports 19:121–64.

Koen Alonso M, Crespo EA, García NA, Pedraza SN, Mariotti PA, Mora NJ. 2002. Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. Environmental Biology of Fishes 63:193–202.

Koen-Alonso M, Yodzis P. 2005. Multispecies modelling of some components of the marine community of northern and central Patagonia, Argentina. Canadian Journal of Fisheries and Aquatic Sciences 62:1490–512.

Kovacs KM, Aguilar A, Aurioles D, Burkanov V, Campagna C, Gales N, et al. 2012. Global threats to pinnipeds. Marine Mammal Science 28:414–36.

Lewis MN, 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.

López Arregui E, González Regalado T. 1940. Lobos marinos en la Argentina. Su aprovechamiento integral. Boletín de Fomento Ganadero, Ministerio de Agricultura de la Nación No. 18. Buenos Aires. 19 pages.

Oliva D, Sielfeld W, Buscaglia M, Matamala M, Moraga R, Pavés H, et al. 2008. Plan de acción para disminuir y mitigar los efectos de las interacciones del lobo marino común (*Otaria flavescens*) con las actividades de pesca y acuicultura de la X y XI Región, Chile. Informe Técnico Fondo de Investigación Pesquera IP-IT/2006-34. 435 pages. http://www.fip.cl/FIP/Archivos/pdf/informes/inffinal 2006-34.pdf (accessed October 2014).

Oliveira LR, Majluf P. 2012. WP1. Recuperación de la población de lobos de un pelo después del más fuerte evento de El Niño en la historia. In: Crespo E, Oliva D, Dans S, Sepúlveda M, editors. Estado de Situación del Lobo Marino Común en su Área de Distribución. Valparaíso: Sello Editorial Universidad de Valparaíso, p 18–19.

Páez E. 2006. Situación de la administración del recurso lobos y leones marinos en Uruguay. In: Menafra R, Rodríguez-Gallego L, Scarabino F, Conde D, editors. Bases para la Conservación y el Manejo de la Costa Uruguaya. Montevideo: Vida Silvestre, Sociedad Uruguaya para la Conservación de la Naturaleza, p 577–583.

Palma ED, Matano RP, Piola AR. 2004. A numerical study of the Southwestern Atlantic Shelf circulation: Barotropic response to tidal and wind forcing. Journal of Geophysical Research 109: C08014. 17 pages.

Pérez F, Crespo EA. 1994. Relevamiento de las loberías de Monte Loayza, Cabo Blanco y Makenke en la Provincia de Santa Cruz. Anexo 3 del Cuarto Informe del PMIZCP, GEF/PNUD/FPN. 8 pages.

Reyes L. 2004. Estado actual y tendencia de la población de lobos marinos de un pelo del centro de Patagonia. In: XIX Jornadas Argentinas de Mastozoología. Puerto Madryn, Argentina, p 92.

Reyes L, Crespo EA. 1991. Relevamiento del apostadero de lobos marinos de un pelo de Monte Loayza, en el norte de Santa Cruz. Informe No. 9 enviado a la Dirección de Fauna de la Provincia de Santa Cruz. 10 pages.

Reyes LM, Crespo EA, Szapkievich V. 1999. Distribution and population size of the southern sea lion (*Otaria flavescens*) in central and southern Chubut, Argentina. Marine Mammal Science 15:478–93.

Rivas AL. 2006. Quantitative estimation of the influence of surface thermal fronts over chlorophyll concentration at the Patagonian shelf. Journal of Marine Systems 63:183–90.

Rivas AL, Pisoni JP. 2010. Identification, characteristics and seasonal evolution of surface thermal fronts in the Argentinean Continental Shelf. Journal of Marine Systems 79(1–2):134–43.

Rivas AL, Dogliotti AI, Gagliardini DA. 2006. Seasonal variability in satellite-measured surface chlorophyll in the Patagonian Shelf. Continental Shelf Research 26:703–20.

Robertson BC, Chilvers BL. 2011. The population decline of the New Zealand sea lion *Phocarctos hookeri*: A review of possible causes. Mammal Review 41:253–75.

Robertson BC, Chilvers BL, Duignan PJ, Wilkinson IS, Gemmell NJ. 2006. Dispersal of breeding, adult male *Phocarctos hookeri*: Implications for disease transmission, population management and species recovery. Biological Conservation 127:227–36.

Romero SI, Piola AR, Charo M, Eiras Garcia CA. 2006. Chlorophyll-a variability off Patagonia based on SeaWiFS data. Journal of Geophysical Research 111: C05021. 11 pages.

Rosas FCW, Pinedo MC, Marmontel M, Haimovici M. 1994. Seasonal movements of the South American sea lion (*Otaria flavescens*, Shaw) off the Rio Grande do Sul coast, Brazil. Mammalia 58:51–59.

Roux JP. 1987. Recolonization processes in the subantarctic fur seal, *Arctocephalus tropicalis*, on Amsterdam Island. In: Croxall JP, Gentry RL, editors. Status, Biology, and Ecology of Fur Seals. National Marine Fisheries Service, Cambridge, UK, National Oceanic and Atmospheric Administration Technical Report NMFS 51:189–94.

Schiavini ACM, Crespo EA, Szapkievich V. 2004. Status of the population of South American sea lion (*Otaria flavescens*) in Santa Cruz and Tierra del Fuego Provinces, Argentina. Mammalian Biology 69:108–18.

Schiavini A, Yorio P, Gandini P, Raya Rey A, Boersma D. 2005. Los pingüinos de las costas argentinas: Estado poblacional y conservación. El Hornero 20:5–23.

Sepúlveda M, Oliva D, Urra A, Pérez-Álvarez MJ, Moraga R, Schrader D, et al. 2011. Distribution and abundance of the South American sea lion *Otaria flavescens* (Carnivora: Otariidae) along the central coast off Chile. Revista Chilena de Historia Natural 84:97–106.

Strange I. 1979. Sea lion survey in the Falklands. Oryx 15:175–84.

Sutton PE. 1990. Nuevos aportes sobre los apostaderos de pinnípedos en las costas de la Provincia de Santa Cruz, Argentina. In: IV Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur. Valdivia, Chile, p 69.

Szapkievich V. 1992. Estimación de la Población del Lobo Marino de un Pelo *Otaria flavescens* (Shaw, 1800) en el Litoral Patagónico mediante Fotografías Obtenidas en Relevamientos Aéreos. Graduate Thesis. Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Buenos Aires. 89 pages.

Szapkievich VB, Cappozzo HL, Crespo EA, Bernabeu RO, Comas C, Mudry M. 1999. Genetic relatedness in two Southern sea lion (*Otaria flavescens*) rookeries in Southwestern Atlantic. International Journal of Mammalian Biology 64:1–5.

Thompson D, Strange I, Riddy M, Duck CD. 2005. The size and status of the population of southern sea lions *Otaria flavescens* in the Falkland Islands. Biological Conservation 121:357–67.

Túnez JI, Centrón D, Cappozzo HL, Cassini MH. 2007. Geographic distribution and diversity of mitochondrial DNA haplotypes in South American sea lions (*Otaria flavescens*) and fur seals (*Arctocephalus australis*). Mammalian Biology 72:193–203.

Túnez JI, Cappozzo HL, Cassini MH. 2008. Natural and anthropogenic factors associated with the distribution of South American sea lion along the Atlantic coast. Hydrobiology 598:191–202.

Túnez JI, Cappozzo HL, Nardelli M, Cassini MH. 2010. Population genetic structure and historical population dynamics of the South American sea lion, *Otaria flavescens*, in north-central Patagonia. Genetica 138:831–41.

Venegas C, Gibbons J, Aguayo A, Sielfeld W, Acevedo J, Amado N, et al. 2001. Cuantificación poblacional de lobos marinos en la XII Región, Chile. Informe Técnico Fondo de Investigación Pesquera IP-IT/2000-22. 91 pages. http://www.fip.cl/prog_x_year/2000/2000-22.htm (accessed June 2014).

Vila AR, Pérez F. 1996. Apostaderos de aves y mamíferos marinos de Monte Loayza, Santa Cruz. Informe Técnico no. 15. Plan de Manejo Integrado de la Zona Costera Patagónica GEF/PNUD/WCS/FPN. 40 pages. http://www.patagonianatural.org/publicaciones/archivos/informes-tecnicos/item/1162-pmzcp-1-informe-tecnico-n-15 (accessed October 2014).

Wickens P, York AE. 1997. Comparative population dynamics of fur seals. Marine Mammal Science 13:241–92.

Zar JH. 1996. Biostatistical Analysis. 3rd edition. Upper Saddle River, NJ: Prentice Hall. 662 pages.

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