

Improvement in Survivorship: The Key for Population Recovery?

María Florencia Grandi^{1,*}, Silvana L. Dans^{1,2}, and Enrique A. Crespo^{1,2}

¹Laboratorio de Mamíferos Marinos, Centro Nacional Patagónico-CONICET, Bvd. Brown 2915, 9120 Puerto Madryn, Chubut, Argentina

²Universidad Nacional de la Patagonia San Juan Bosco, Bvd. Brown 3051, 9120 Puerto Madryn, Chubut, Argentina.

E-mail: dans@cenpat-conicet.gob.ar, kike@cenpat-conicet.gob.ar

(Received May 15, 2014; Accepted October 13, 2015)

María Florencia Grandi, Silvana L. Dans, and Enrique A. Crespo (2016) In northern Patagonia, commercial harvesting of South American sea lions, *Otaria flavescens*, from 1920 to 1960, decimated its population abundance. Population recovery was not immediate after hunting ceased in 1962. The population was stable until 1989, and since then has grown at an annual rate of increase of 5.7%. Along with this growth there was an increase of the juvenile fraction and changes in the social composition of colonies, which could be related to changes in some population vital rates. The aim of this study was to analyze changes in the survivorship pattern of *Otaria flavescens* through time. The ultimate goal was to contribute to a better understanding of changes that could have operated on the ecosystem after the decline and recovery of one of the main marine top-predators in the southern South Atlantic Ocean. The comparisons of survivorship curves of males and females, obtained from the life tables of two periods with different population trends: 1981-1987 (stationary) and 2000-2008 (recovering), showed that there were differences in survivorship between sexes, where recent female age-specific survival was higher than that of males at any age. The comparison of survivorship between periods showed differences in both sexes. Both juveniles and adults, both male and female, from the recent period showed higher survival than those of the 1980's decade. This improvement in survivorship could be one of the essential factors that drove population recovery in the last decades. Here we discuss the possible hypotheses of which factors could have changed in the ecosystem to favour juvenile and adult survivorship, such as an increase in the availability of food resources, a decrease of exogenous mortality causes, or a combination of both factors.

Key words: Life table, *Otaria flavescens*, South American sea lion, Survivorship, Population recovery, Northern Patagonia.

BACKGROUND

Most natural populations experience fluctuations in their abundance through time. These fluctuations could be due to the intrinsic characteristics of a species (*i.e.* life history traits), or because of the influence of external factors (such as prey availability, competition, exploitation, habitat degradation, disease, etc.). Understanding the factors and mechanisms causing these fluctuations is a key subject in ecological studies, especially for the conservation of populations that have suffered dramatic declines. Age- and sex-specific survival and reproductive rates are

essential for understanding the dynamics of animal populations. However, these vital rates are rarely available for long-lived mammals because the long-term data sets and large sample sizes required for these analyses are difficult to obtain from wildlife populations (Eberhardt 1985).

South American sea lions (*Otaria flavescens*) are distributed along the South American coast from Torres (29.33°S; 49.71°W), southern Brazil, on the Atlantic Ocean (Rosas et al. 1994) to Zorritos (4°S), northern Peru on the Pacific Ocean (Cappozzo and Perrin 2009). This species was one of the seals most exploited along the South American coast, and populations were decimated

*Correspondence: Tel: +054-280-4883184 int. 1272. Fax: +054-280-4883543. E-mail: grandi@cenpat-conicet.gob.ar

during the early 20th century (Crespo and Pedraza 1991; Páez 2006). This dramatic decline leads to the present great dissimilarities in abundance and population trends observed throughout their range (Crespo et al. 2012). Populations from Uruguay and austral Chile (XII Region) are decreasing (Venegas et al. 2001; Páez 2006), while those from central and southern Chile (V-IX and X-XI Regions, respectively) are stable (Oliva et al. 2008; Sepúlveda et al. 2011). Populations from the Malvinas (Falkland) Islands, Peru and northern Chile are slowly recovering (Thompson et al. 2005; Bartheld et al. 2008; Crespo et al. 2012), and those of Patagonia (Argentina) are steadily recovering (Reyes et al. 1999; Dans et al. 2004; Schiavini et al. 2004; Grandi et al. 2015).

In Argentina, harvesting operations occurred between 1920 and 1960, mostly on northern Patagonia and Tierra del Fuego stocks, while stocks from central and southern Patagonia remained almost unexploited (Godoy 1963; Crespo 1988; Crespo and Pedraza 1991; Grandi et al.

2015). However, both exploited and unexploited stocks showed similar trajectories (reduction in abundance and posterior recovery), suggesting a strong interconnection in the Patagonian region (Reyes et al. 1999; Dans et al. 2004; Grandi et al. 2015). The population of South American sea lions in northern Patagonia (Fig. 1) has been monitored almost continuously since 1972, resulting in a data set that comprises 40 years of census data. Based on historical data, it is known that the population declined from an estimated 137,500 individuals in 1938 (Godoy 1963) to 18,396 in 1946 (Carrara 1952). It has been estimated that the population reached its lowest numbers (~ 5000 individuals) in the 1960s (Koen-Alonso and Yodzis 2005; Grandi 2010). Although hunting ceased in 1962, signs of population recovery were not detected until 1990 (Crespo and Pedraza 1991). Fortunately, the northern Patagonian stock is recovering and at present is growing at an annual rate of increase of 5.7% (Dans et al. 2004; Grandi 2010).

As a result of the population recovery, the

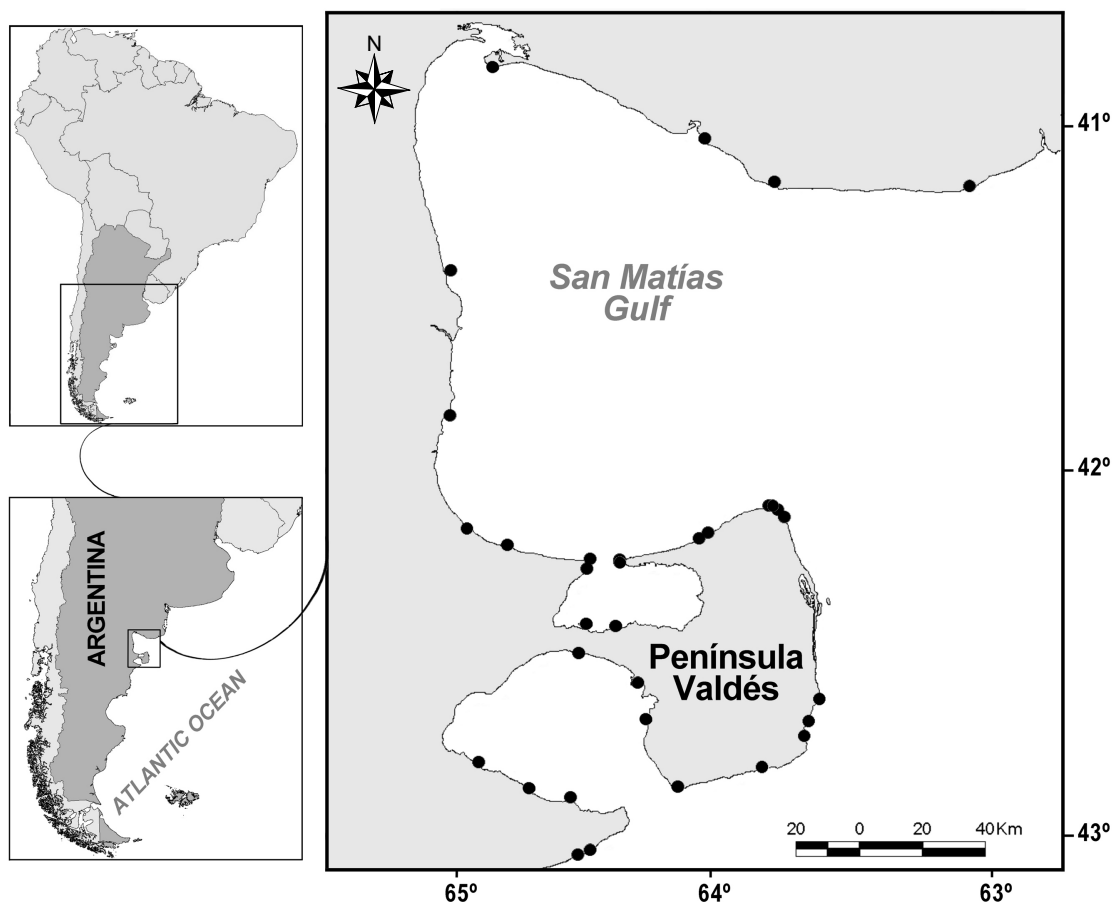


Fig. 1. Detailed study area with the current distribution of *Otaria flavescens* colonies at northern Patagonia

social composition and spatial distribution of certain northern Patagonian colonies changed through time (Crespo 1988; Dans et al. 2004; Grandi et al. 2008). The process of this change began with the establishment of juveniles of both sexes in new and small breeding areas near larger rookeries or within haul-out sites, followed by the arrival of adult males, subadult males, or both. This process yields mixed-composition colonies with higher rates of pup production in comparison to the dense established breeding sites. Consequently, new areas were colonized and colonies turned from haul-outs to rookeries (Crespo 1988; Dans et al. 2004; Grandi et al. 2008).

It was hypothesized that all these changes that accompanied the population recovery could be related directly or indirectly to changes of vital rates through time, such as age specific survivorship and/or fecundity (Dans et al. 2004; Grandi et al. 2008). This could be supported by a positive rate of increase of pups in all colonies (Dans et al. 2004; Grandi et al. 2008), higher rates of pup production in new sites (Grandi et al. 2008), and an increase in the juvenile fraction of the population since among non-pups, juveniles were the age-class that had the highest intrinsic rate of increase in recent times (Dans et al. 2004).

Age-specific survival (or mortality) rates are one of the most useful demographic parameters used to interpret and understand animal population dynamics, because they enable estimations of how natural mortality affects different age classes and the intensity of those interactions (Caughley 1977). Accurate estimates of age- and sex-specific survival rates are essential to develop population models to be used in conservation and management (Caswell 2001). In practice, accurate measurements of age-specific survival are difficult to obtain in the field because they require long-term longitudinal monitoring of known-aged individuals (Lebreton et al. 1992). Traditionally, two approaches have been used to estimate age-specific demographic rates. The first approach includes long-term mark-recapture studies, which does not require assumptions about the dynamics of the population, but has a number of assumptions about the probability of individual capture and tag loss (e.g. Boyd et al. 1995; Beauplet et al. 2006; Pendleton et al. 2006; Hernández-Camacho et al. 2008; Pistorius et al. 2004, 2008; McMahon and White 2009). On the other hand these studies are extremely costly in terms of effort and money. The second approach corresponds to the generation of life tables, and provides indirect estimates from

age frequency distributions of a sample, but this requires some assumptions about population dynamics (i.e. random sampling, age structure stability, Caughley 1977). Even so, life tables provide a useful summary to describe mortality patterns operating on a population. The age- and sex-specific survival rates they describe can also be an essential tool for evaluating the status of a population, and are very effective in the conservation area when they are associated with models that assess the susceptibility of different age classes to anthropogenic factors (e.g. Crouse et al. 1987; Doak et al. 1994; Winship and Trites 2006). Moreover, life tables can be used for the design of conservation and management strategies, mainly because there is evidence that variations in juvenile and adult survival rates of pinnipeds have an important effect on the rate of population increase (York 1994; Holmes and York 2003; Pendleton et al. 2006).

There are a small number of published examples of life tables for marine mammals in general (Barlow and Boveng 1991), but only a few have been developed for sea lions (York 1994; Hernández-Camacho 2001; McIntosh 2007). When considering South American sea lions, Crespo (1988) developed vertical life tables for the northern Patagonian stock from the period 1981-1987, when the population was stationary. These data, together with the present knowledge about this population provide a unique opportunity to understand its recovery process. The aim of this study was to analyze changes in the survivorship pattern of *Otaria flavescens* through time. To do this we compare survivorship curves of males and females obtained from life tables from two periods of different population trend: 1981-1987 (stationary) and 2000-2008 (recovering). The ultimate goal was to contribute to a better understanding of how the ecosystem could have reorganized after the decline and recovery of one of the main marine top-predators in the Atlantic Ocean.

MATERIALS AND METHODS

Collection of specimens and age estimation

The study area includes sea lion colonies that conform the northern Patagonia population (Fig. 1). During the period 2000-2008 the coastline of the study area as well as sea lion colonies were surveyed seasonally, looking for dead animals. All accessible sites were walked (322 km) and the

effort was equally distributed both spatial (both provinces) and temporally (all seasons in each year). Skulls of sea lions were collected, and then cleaned by dermestid beetles, boiled to eliminate the remaining fat and flesh, washed with water and soap, and finally stored dry. All specimens were deposited in the scientific collection of Marine Mammals at CENPAT (Puerto Madryn, Argentina). Individual ages were estimated by two methods: a) for pups (*i.e.* newborns to individuals of less than 1 year), ages were estimated according to the teeth eruption schedule defined by E. A. Crespo (1988: 76-79). He established four age-classes for pups: category A (0 to 1.5 months); B (from 1.5 to 5 months); C (from 5 to 8 months); and D (from 8 to 12 months) (see description in Fig. 2); b) for individuals of one or more years old, age was estimated from counts of incremental growth layers of tooth sections (Crespo et al. 1994). The tooth preparation and age reading techniques used were described by Crespo (1988) and are also detailed in Grandi et al. (2010).

Frequency distribution of age at death

The sample collected represents the age distribution at death. However it may be biased from the true distribution due to several factors. Therefore, age frequencies were corrected by three adjustments previous to the construction of life tables.

a) Adjustment of first-year mortality

Among pups, it is more likely to find dead

newborn pups (0 to 1.5 months of life) because they do not swim and are more probable to die on the beach, than pups of other age-classes. Thus the number of individuals younger than one year in the sample was corrected by considering data on pup mortality estimated in other sources and the number of pups born in one year in the whole population.

First-year mortality of pups (q_0) - defined as the proportion of newborn that die before their first birthday (Caughley 1977) - was estimated in two steps. First, mortality from 0 to 1.5 months, that is the mortality of pups from age-class category A (M_A), was estimated from available information in the literature (Campagna et al. 1992; Soto et al. 2004; Svendsen 2005; Svendsen et al. 2012). Fourteen different mortality estimates were available, which were averaged. Then, the mortality of the categories B, C and D were estimated as a proportion of the estimated mortality in category A (*i.e.* relative mortality for each category, MR_i), as follows:

$$MR_i = \frac{\hat{f}'_i}{\hat{f}'_A} \times M_A$$

where \hat{f}'_i is the expected number of dead pups in age-class category i , \hat{f}'_A is the expected number of dead pups in age-class category A, and M_A is the mortality of pups from age-class category A (Crespo 1988). The expected number of dead pups corresponds to the observed number in the sample when the sex ratio did not differ from 1:1. In the case that the sex ratio was different, the expected number of dead pups was estimated from the observed ratio.

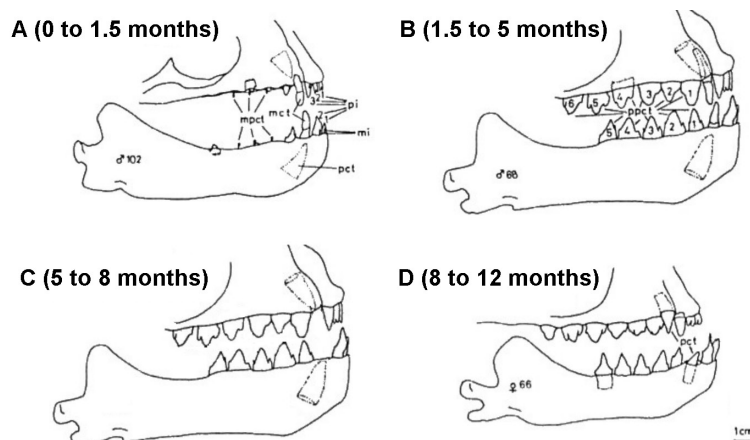


Fig. 2. Lateral view of the teeth eruption schedule of *O. flavescens* pups (extracted from Crespo 1988). Category A: milk and permanent teeth present (mi: milk incisor; mpct: milk postcanine teeth; mct: milk canine teet; pi: permanent incisor h) and the permanent canine teeth (pct) inside the alveolus; Category B: mct, pi and permanent postcanine teeth (ppct) present; Category C: mct are lost and pct remain inside the alveolus; Category D: pct erupt through the gum and become visible.

The expected number of female and male dead pups in the population were then reconstructed applying the relative mortality for each category (MR_i) to a cohort of 10940 individuals (that correspond to the mean pups born in the study area in the period 2005-2008; Grandi 2010). Subsequently, first-year mortality (q_0) was estimated for each sex as the ratio between the sum of the expected number of dead pups in each category i and the size of the cohort considered.

b) Adjustment for known rate of population growth

The frequency distribution of deaths (f'_x) from age-class $x = 1$ to the last age-class were adjusted for population growth by multiplying by the correction factor e^{rx} (Caughley 1977), where r is the exponential growth rate estimated from censuses from the period 1982-2007 ($r = 0.0581$ from Grandi 2010). Second, this adjusted frequency distribution (F'_x) was smoothed by a log-polynomial regression (Caughley 1977).

c) Adjustment of pup frequency

It is more probable to find dead pups than dead animals of other age classes. Thus after applying the previous adjustments, the frequency for the age-class 0 (F'_0) was adjusted. This was first calculated for females by iterations of the F'_0 values until q_0 was equal to the estimates calculated in the first step, using the Solver function in Microsoft Excel (Microsoft Corp.). Then r values were estimated from the resolution of the Lotka's equation ($\sum l_x e^{-rx} m_x = 1$, Caughley 1977). The fit was repeated considering the mean, minimum and maximum values of q_0 until obtaining a value of r that was inside the CI of the exponential growth rate estimated from censuses ($0.055 \geq r \leq 0.061$, Grandi 2010). Age-specific fecundity rates (m_x , Table 2) were considered as 1/2 of age-specific pregnancy rates (b_x) calculated in previous studies from the examination of reproductive tracts, mammary glands and the presence and development of corpora lutea and corpora albicantia in the ovaries, $n = 76$ (Grandi 2010; Grandi et al. 2010). Considering that the average age at sexual maturity for female South American sea lions was estimated at 4.8 ± 0.5 years old (Grandi et al. 2010), fecundity rates were applied to mature age-classes ($x = 4$ and older).

Survival estimates for the period 2000-2008

Survival (l_x) is defined as the probability at birth of surviving to the age x (Caughley 1977). Here l_x was estimated, for male and female South American sea lions, constructing life tables from age distribution at death considering natural mortality factors (Caughley 1977; Krebs 1999) and applying the former adjustments. Life table calculations were based on the assumptions that the probability of finding a carcass was independent of the age and sex of South American sea lions from northern Patagonia, reproductive and mortality rates remained constant throughout the study period and there was no emigration or immigration or they were balanced (Caughley 1977; Rabinovich 1980; Krebs 1985).

Survival estimates for the period 1981-1987

Crespo (1988) developed several life tables using stranded sea lions collected from northern Patagonia between 1981 and 1987 ($n = 140$; females = 57, males = 83). Eighteen models of life table were constructed considering different adjustments of the age frequency distribution at death and three ages of development of sexual maturity. Each life table was projected to obtain population growth rates (Crespo 1988). Here we select, from those eighteen life tables, the mean survivorship values (l_x) of those models (3 for females and 2 for males) that correspond to a stationary population trajectory during the period 1981-1987 (Crespo 1988), as representative of the mortality pattern of male and female South American sea lions from that period.

Comparison of survivorship curves

Survivorship values obtained from all life tables were adjusted by Siler's competing risk model (Siler 1979). Siler's curve was designed to fit three general stages of life -a juvenile stage with increasing survival, an adult stage with stable survival, and a late stage with decreasing survival. So this model considers the total risk of mortality at a given age x as the product of three competing risks: $l(x) = l_j(x) \times l_c(x) \times l_s(x)$, an exponentially decreasing risk due to juvenile mortality factors $l_j(x) = \exp[-(a_1/b_1)] \times \{1 - \exp(-b_1 \times x/\Omega)\}$, a constant risk experience by all age classes $l_c(x) = \exp(-a_2 \times x/\Omega)$, and an exponentially increasing risk due mortality factors associated with senescence $l_s(x) = \exp[(a_3/b_3) \times \{1 - \exp(b_3 \times x/\Omega)\}]$.

To be able to compare survivorship patterns from different periods age was re-expressed as a fraction of longevity, Ω (Barlow and Boveng 1991), defining this parameter as the 99th percentile of the age distribution of the sample. The transformation of age as a fraction of longevity proved to be less dependent on sample size than is a definition based on the maximum age observed (Barlow and Boveng 1991).

The five parameters of the survivorship model (a_1 , a_2 , a_3 , b_1 and b_3) are constants that allow considerable flexibility in the shape of this function and were fit using a maximum likelihood approach. The likelihood function L is given by:

$$L(Y|\Theta) = \prod_{i=0}^w p(l_i)$$

where each l_i is an observation of the variable Y , p is the probability density function, and Θ is the vector of parameters (Hilborn and Mangel 1997).

A likelihood ratio test (LRT) was used to compare the full model where all parameters could vary with models that constrained some of them to test the following hypothesis:

H₀₁: survivorship curves have a similar constant risk of mortality experience by all age classes (*i.e.* $a_2 = a_2'$).

H₀₂: survivorship curves have a similar risk of

juvenile mortality (*i.e.* $a_1 = a_1'$; $b_1 = b_1'$).

H₀₃: survivorship curves have a similar risk of senescent mortality (*i.e.* $a_3 = a_3'$; $b_3 = b_3'$)

H₀₄: survivorship curves have similar risks of mortality (*i.e.* $a_1 = a_1'$; $b_1 = b_1'$; $a_2 = a_2'$; $a_3 = a_3'$; $b_3 = b_3'$)

where Θ and Θ' are parameters of each different data sets used to test each hypothesis (*i.e.* females vs. males, recent vs. past, etc.). Survivorship models of male and female sea lions within and between periods were compared by LRT , considering $\alpha = 0.15$ to increase test power due to small sample size (Buckland et al. 2001).

RESULTS

Age frequency distribution of deaths

A total of 424 dead sea lions were found from 2000 to 2008. Of these, 210 were female and 214 male (Fig. 3). Ages ranged from newborn pups to 19 year-old males and 22 year-old females. This sample showed a pronounced mode in the age-class 0, a high frequency of juveniles of age-class 1 and 2, and an increase of frequency of adult age-classes (> 6 years) for both males and females. We consider juvenile South American sea lions,

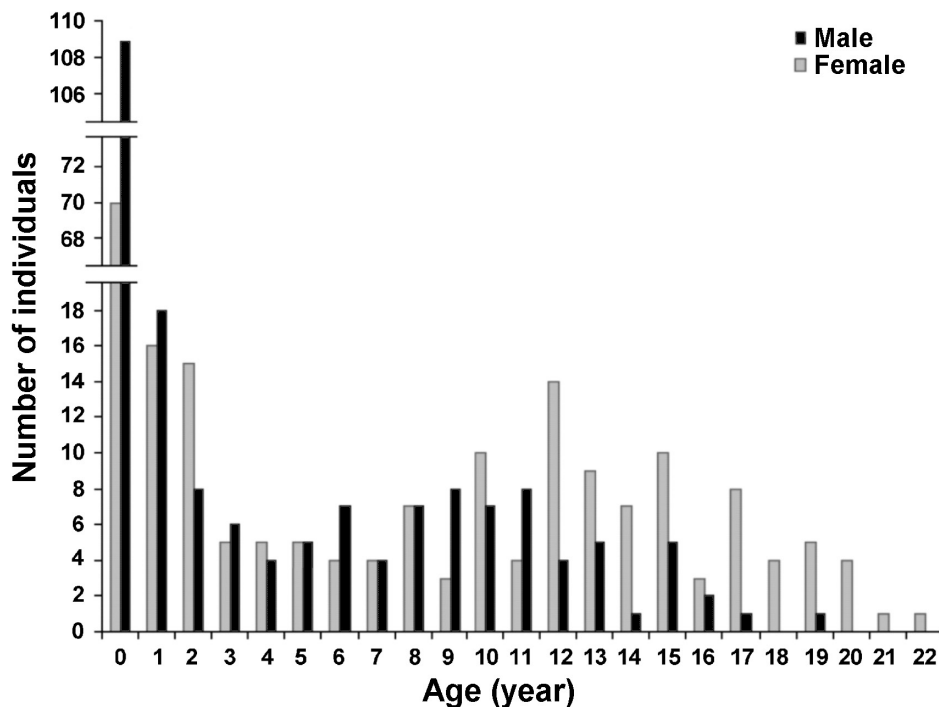


Fig. 3. Age-frequency distribution of female ($n = 210$) and male ($n = 214$) South American sea lions from northern Patagonia collected between 2000-2008.

both females and males, from age 1 to 4 (Grandi et al. 2010). Ages were estimated with an error of -0.084 ± 0.79 years (mean \pm SD), and there were no differences among readers (Kruskal-Wallis test, $H_{2,724} = 0.778$; $p = 0.677$).

The age-class frequency distribution of the pups collected is shown in figure 4. There were significant differences between sex ratio only in the age-class category B ($G = 7.883$; $d.f. = 1$; $p = 0.0049$), with male pups being more represented than female pups.

Mortality estimation of the first year

Mean mortality of pups from age-class category A was 0.0585 ± 0.0428 (mean \pm SD; $n = 14$). The relative mortality proportions for the rest

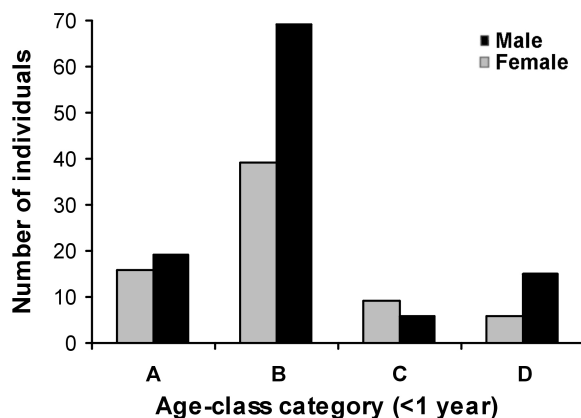


Fig. 4. Age-frequency distribution of female ($n = 70$) and male ($n = 109$) pups by age-class category from northern Patagonia collected between 2000-2008.

of the categories were calculated using the former estimate (Table 1). Considering a cohort of 5470 individuals born per sex in the area (Grandi 2010), and equal sex ratio at birth (Lewis and Ximénez 1983; Crespo 1988), females had a lower mortality rate than males for the first year (Table 1). The strong difference found between male and female age-class B mortality (Fig. 4) explains the resultant disparity in mortality of the first year.

Life tables

From the resolution of Lotka's equation, the female pup mortality estimation (q_0) that best fitted into the CI of the observed population exponential growth rate was the maximum value obtained. Therefore life tables were calculated considering $q_0 = 0.29$ for females and $q_0 = 0.39$ for males (Table 1). Tables 2 and 3 show age frequency in the sample, the adjusted age frequency and parameter values of life tables for female and male South American sea lions.

Comparison of survivorship curves

The maximum likelihood fit of the full Siler model to the age-frequency distribution for male and female sea lions is shown in Figure 5. The parameter values which resulted in the best fit are given in table 4. Comparison between present male and female survivorship risks showed that there was significant difference in juvenile mortality factors (H_{02} : $LRT = 42.103$; $d.f. = 2$; $p < 0.001$), in senescent mortality factors (H_{03} : $LRT = 35.357$; $d.f. = 2$; $p < 0.001$) and in all mortality factors together

Table 1. Relative mortality estimated, and expected frequency of death by age class category and sex calculated from a cohort of 5470 per sex. Pup mortality estimate (q_0) from the total. Minimum and maximum values are in brackets

Age-class category	Females		Males	
	MR_i	f'_i	MR_i	f'_i
A	0.0585 (0.0157-0.1013)	320 (86-554)	0.0585 (0.0157-0.1013)	320 (86-554)
B	0.1304	713	0.2307	1262
C	0.0251	137	0.0251	137
D	0.0351	192	0.0351	192
Total		1363 (1129-1597)		1911 (1677-2145)
q_0		0.25 (0.21-0.29)		0.35 (0.31-0.39)

Table 2. Life table for female South American sea lions based on stranded animals from 2000 to 2008 ($n = 214$)

Age	Sample frequency	Corrected frequency	Smoothed frequency	Fecundity rate	Life table			
x	f'_x	$f'_x e^{rx}$	F'_x	m_x	d_x	l_x	q_x	p_x
0	70	70	119	0	0.290	1.000	0.290	0.710
1	16	17	35	0	0.085	0.710	0.120	0.880
2	15	17	22	0	0.054	0.625	0.086	0.914
3	5	6	14	0	0.034	0.571	0.060	0.940
4	5	6	8	0.099	0.020	0.537	0.036	0.964
5	5	7	5	0.171	0.012	0.517	0.024	0.976
6	4	6	3	0.248	0.007	0.505	0.014	0.986
7	4	6	2	0.323	0.005	0.498	0.010	0.990
8	7	11	3	0.389	0.007	0.493	0.015	0.985
9	3	5	5	0.441	0.012	0.486	0.025	0.975
10	10	18	8	0.470	0.020	0.473	0.041	0.959
11	4	8	12	0.470	0.029	0.454	0.065	0.935
12	14	28	16	0.433	0.039	0.425	0.092	0.908
13	9	19	20	0.354	0.049	0.385	0.127	0.873
14	7	16	22	0.177	0.054	0.337	0.159	0.841
15	10	24	23	0.177	0.056	0.283	0.198	0.802
16	3	8	23	0.177	0.056	0.227	0.247	0.753
17	8	21	20	0.177	0.049	0.171	0.286	0.714
18	4	11	17	0.177	0.041	0.122	0.340	0.660
19	5	15	13	0.177	0.032	0.081	0.394	0.606
20	4	13	9	0.177	0.022	0.049	0.450	0.550
21	1	3	5	0.177	0.012	0.027	0.455	0.545
22	1	4	6	0.000	0.015	0.015	1.000	0.000

Table 3. Life table for male South American sea lions from 2000 to 2008 ($n = 210$)

Age	Sample frequency	Corrected frequency	Smoothed frequency	Life table			
x	f'_x	$f'_x e^{rx}$	F'_x	d_x	l_x	q_x	p_x
0	109	109	104	0.390	1.000	0.390	0.610
1	18	19	21	0.079	0.610	0.130	0.870
2	8	9	12	0.045	0.531	0.085	0.915
3	6	7	7	0.026	0.486	0.054	0.946
4	4	5	5	0.019	0.459	0.041	0.959
5	5	7	5	0.019	0.441	0.043	0.957
6	7	10	5	0.019	0.422	0.045	0.955
7	4	6	8	0.030	0.403	0.075	0.925
8	7	11	9	0.034	0.373	0.091	0.909
9	8	13	12	0.045	0.339	0.133	0.867
10	7	13	12	0.045	0.294	0.154	0.846
11	8	15	13	0.049	0.249	0.197	0.803
12	4	8	12	0.045	0.200	0.226	0.774
13	5	11	11	0.041	0.154	0.268	0.732
14	1	2	9	0.034	0.113	0.300	0.700
15	5	12	7	0.026	0.079	0.333	0.667
16	2	5	4	0.015	0.053	0.286	0.714
17	1	3	4	0.015	0.038	0.400	0.600
18	0	0	2	0.008	0.023	0.333	0.667
19	1	3	4	0.015	0.015	1.000	0.000

(H_04 : $LRT = 151.012$; $d.f. = 5$; $p < 0.001$) (Table 4). Additionally there was no significant difference in constant risk of mortality experienced by all age classes (H_01 : $LRT = 0.248$; $d.f. = 1$; $p = 0.618$) (Table 4). Females had higher survival (l_x and p_x) in juvenile and adult age classes than males (Fig. 5; Tables 2 and 3).

When we compared each sex separated in two time periods (2000-2008 vs. 1981-1987); the pattern was similar to the later (Tables 5 and 6). There was no significant difference in female constant risk of mortality experienced by all age classes (H_01 : $LRT = 1.159$; $d.f. = 1$; $p = 0.282$). However, there was significant difference in female juvenile mortality factors (H_02 : $LRT = 17.478$; $d.f. = 2$; $p < 0.001$), in female senescent mortality factors (H_03 : $LRT = 24.551$; $d.f. = 2$; $p < 0.001$), and in all mortality factors together (H_04 : $LRT = 148.061$; $d.f. = 5$; $p < 0.001$). These could indicate

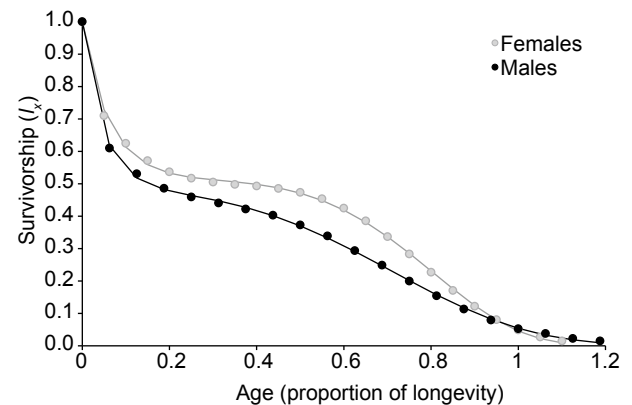


Fig. 5. Survivorship curves for male (black) and female (grey) sea lions from 2000-2008. Parameter values for the full model are given in table 4. Age is expressed as proportion of longevity, Ω .

Table 4. Likelihood estimates of the survivorship models (full and constrained) adjusted to the data for males and females from 2000-2008

Sex	Model	Siler parameters				
		a_1	a_2	a_3	b_1	b_3
Female	full	8.905	-0.651	0.155	11.212	4.454
	H_01	8.905	-0.720	0.170	10.987	4.356
	H_02	10.249	-0.567	0.164	13.856	4.349
	H_03	9.138	-0.690	0.211	11.877	3.997
	H_04	10.742	-0.845	0.371	13.507	3.330
Male	full	12.543	-1.150	0.820	15.830	2.337
	H_01	12.684	-0.720	0.580	16.896	2.663
	H_02	10.249	-0.226	0.288	13.856	3.417
	H_03	11.942	-0.225	0.211	15.757	3.997
	H_04	10.742	-0.845	0.371	13.507	3.330

Table 5. Likelihood estimates of the survivorship models (full and constrained) adjusted to the data for females from different periods

Period	Model	Siler parameters				
		a_1	a_2	a_3	b_1	b_3
2000-2008	full	8.908	-0.651	0.155	11.212	4.457
	H_01	8.920	-0.541	0.132	11.611	4.632
	H_02	9.818	0.432	0.013	19.503	7.177
	H_03	10.266	0.527	0.009	20.977	7.368
	H_04	19.732	-17.453	17.988	47.196	0.169
1981-1987	full	25.640	1.347	0.198	85.048	3.108
	H_01	27.776	-0.541	1.789	84.404	1.004
	H_02	9.818	-35.167	35.508	19.503	0.115
	H_03	24.764	1.711	0.009	86.288	7.368
	H_04	19.732	-17.453	17.988	47.196	0.169

that survivorship of female from period 2000–2008 was slightly higher in early juvenile age classes (< 2 years) than survivorship of females from period 1981–1987 (Fig. 6). Adult survival was higher in females from period 2000–2008 than females from period 1981–1987, but survivorship were similar in senescent ages (Fig. 6).

Similar results were obtained when we compared males from different periods: there was no significant difference in male constant risk of mortality experienced by all age classes (H_01 : $LRT = 0.022$; $d.f. = 1$; $p = 0.883$). There was significant difference in male juvenile mortality factors (H_02 : $LRT = 12.622$; $d.f. = 2$; $p = 0.002$), in male senescent mortality factors (H_03 : $LRT = 8.505$; $d.f. = 2$; $p = 0.014$), and in all mortality factors together (H_04 : $LRT = 127.944$; $d.f. = 5$; $p < 0.001$). Therefore, survivorship of males from the period 2000–2008 was higher in early juvenile, adult

and senescent age classes than those from the period 1981–1987 (Table 6, Fig. 7). It is remarkable that there were no significant differences in both females and males constant risk of mortality experienced by all age classes between periods.

DISCUSSION

The present study demonstrates that in the course of these 20 years there was an increase in the survivorship of both juvenile and adult *Otaria flavescens*. This improvement in the survivorship could be one of the essential factors that drove population recovery and expansion. Here we discuss the possible hypotheses of which factors could have changed in the ecosystem to favour juvenile and adult survivorship.

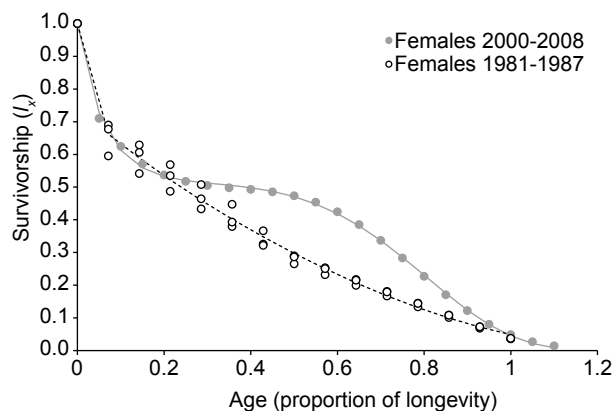


Fig. 6. Survivorship curves for recent (grey) and past (white) female sea lions. Parameter values for the full model are given in table 5. Age is expressed as proportion of longevity, Ω .

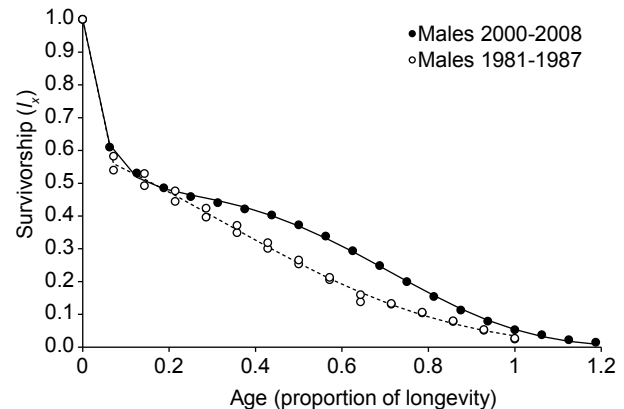


Fig. 7. Survivorship curves for recent (black) and past (white) male sea lions. Parameter values for the full model are given in table 6. Age is expressed as proportion of longevity, Ω .

Table 6. Likelihood estimates of the survivorship models (full and constrained) adjusted to the data for males from different periods

Period	Model	Siler parameters				
		a_1	a_2	a_3	b_1	b_3
2000–2008	full	12.609	-1.004	0.738	16.216	2.432
	H01	12.596	-1.075	0.779	16.071	2.381
	H02	16.187	0.211	0.203	26.432	3.677
	H03	13.181	-0.446	0.513	18.983	2.668
	H04	42.342	0.953	0.195	87.619	3.493
1981–1987	full	79.006	-1.392	2.320	155.619	1.111
	H01	78.741	-1.075	2.028	155.753	1.212
	H02	16.187	-14.233	14.560	26.432	0.302
	H03	77.145	0.632	0.513	156.565	2.668
	H04	42.342	0.953	0.195	87.619	3.493

Pup mortality

South American sea lion pups enter the water for the first time when they are one month old (Campagna 1985) and pups between two and four months old move at sea swimming with their mothers between rookeries (Ximénez 1975; Lewis and Ximénez 1983). The lactation period usually lasts between 8 and 12 months (Crespo 1988), but little is known about the exact time of weaning, or when pups start mixing milk with solid prey. We found different levels of mortality between the sexes for the first year that probably come from the higher mortality of males from category B (from 1.5 to 5 months). This could indicate that male pups take greater risks than females when they start swimming or could also be related to an earlier weaning (Crespo 1988). In sexually dimorphic, polygynous mammals, male pups are larger and with higher food demands than females. So males are expected to be more susceptible than females at birth, when a newborn has to adjust to a sudden, complete change in environment, and again at weaning when offspring begin to depend entirely on independent food acquisition (Kraus et al. 2013).

First year mortality from the recent period was relatively low (29% for females and 39% for males, Tables 2 and 3) compared to other sea lion species. For example, pup mortality has been reported at 40-70% for Australian sea lions, *Neophoca cinerea* (McIntosh et al. 2012); 1-45% for California sea lion, *Zalophus californianus* (Hernández-Camacho et al. 2008); 44% for Galapagos sea lions, *Z. wolfebaeki* (Kraus et al. 2013); 20-28% for west stock of Steller sea lion, *Eumetopias jubatus* (York 1994; Pendleton et al. 2006) and 27-33% for females and 39-47% for males from the growing east stock (Pendleton et al. 2006); and 28% for New Zealand sea lions, *Phocarctos hookeri* (Chilvers 2012). However this comparison should be taken with caution because these estimates are for populations in different conditions (harvested, stationary or declining), or are indirect estimations from mark-recapture individuals, or an average of the mortality for the first years.

It can be expected that pups of poor quality, or with poor-quality mothers, die prior to weaning. Therefore weaning high-quality pups is likely to lead to high post-weaning survival (McIntosh 2007). Thus, pup mortality could be mainly related to the condition of the mother, associated with changes in prey availability due to environmental

conditions. This relationship has been proven in several Otariid species (Guinet et al. 1994; Beauplet et al. 2005; Lea et al. 2006; McIntosh et al. 2013), as well as in *O. flavescens* from Peru where environmental fluctuations are extreme (Soto et al. 2004, 2006). In the Atlantic Ocean such natural fluctuations are not as great, but human activities during the 20th century (such as sea lion harvest and the development of industrial fisheries) caused an impact in the marine ecosystem, leading to changes in the food-web structure (Koen-Alonso and Yodzis 2005). However, using multispecies trophodynamic models of the marine community of Patagonia, that include South American sea lions and their primary prey items (hake, squid and anchovy), Koen-Alonso and Yodzis (2005) concluded that sea lion population trend do not seem to depend on the fluctuations of one specific prey. Taking all these arguments into account, the high rate of population increase and the low pup mortality found here suggest that both food availability and the quality of prey are good (Svendsen et al. 2012) and that the population is still well below the carrying capacity (Grandi 2010).

Life tables and mortality pattern

Cross-sectional studies, such as accessing carcasses from populations, provide instantaneous information and are based on the assumption that the individuals provide a random sample of all age groups in the population and require a reliable method of ageing individuals (Caughley 1966; Caughley 1977). However, there are some factors that may influence the analysis of the age structure of a population. First, sampling bias is one of the potential factors that can affect the age structure of the sample based on dead animals, which is the starting point for the construction of life tables. Even though pups are more available to be sampled (because they are all ashore to be fed and their mortality is higher than other age classes), some pup carcasses may be lost (because of their small size they could be washed away in tides, or squashed and broken down easily). Additionally older age classes may die at sea and carcasses not arrive onshore to be collected, leading to under-representation of the sample. Nevertheless, for the present study we can assume that all age classes sampled are representative of the population because we surveyed systematically all types of colonies (rookeries and haul-outs), as well as all accessible beaches within the study area to collect skulls. Moreover, the possible bias between

age frequencies was corrected by the applied adjustments. Second, variability among cohorts (*i.e.* observed annual variation in births) may also influence the stable age distribution (Chapman 1964). To smooth this bias we did not analyze age distribution by following individual cohorts through time but instead we pooled age distributions over a small period (2000–2008) with similar population rates that reflect the mean conditions of several cohorts within a population (*i.e.* similar demographic conditions). A third factor that can affect the age frequency of the sample is the effect of errors in age determination. Nevertheless, the methodology used has been repeatedly proven for the species (Crespo 1988; Rosas et al. 1993; Grau and Acuña 1998; Drago et al. 2009a, 2010a; Grandi et al. 2010) and the estimated error was negligible and thus should not bias the results. Finally, the fourth factor that can bias a life table analysis is migration (Caughley 1977). However, for the northern Patagonia population it is assumed that the observed recovery was due to changes in survival and reproduction, without immigration from other sites, since all possible sources were also reduced and are still recovering (Reyes et al. 1999; Dans et al. 2004; Grandi et al. 2015).

We found that female longevity was longer than that of males, which agrees with estimates from other otariid species (Boyd and Roberts 1993; Wickens 1993; Lima and Páez 1997). This could be related to the polygynic social structure of Otariid species (Riedman 1990), as well as physiologic and metabolic differences between sexes that led to a higher mortality in males. Maximum ages in our sample were 22 years for females and 19 years for males, which were older than *Otaria* from Brazil (Rosas et al. 1993), Chile (Grau and Acuña 1998) and other studies from Patagonia (Crespo 1988; Grandi et al. 2010).

Survivorship pattern

The survival pattern found is similar to most wild animal populations (Caughley 1977) and follows the typical pattern of pinnipeds, where there is a sudden drop in juvenile survival, especially during the first year of life (Harwood and Prime 1979; Lander 1982; York 1994), then once this stage ends, survival decreases slightly with age and after 14 years of life the decline is accentuated which could be related to senescence.

For polygynous, sexually dimorphic mammals, survival rates often differ between offspring and adults and between adult males

and females (Caughley 1966; Ralls et al. 1980). Survivorship curves by sex for *O. flavescens* from the 2000–2008 period show that females have higher survivorships than males at any age, with the highest differences between the 11 and 15 years of life (Tables 2 and 3). This fact reflects differences in mortality rates by sex, with higher mortality in males. Sexual selection on males favours morphological traits and behaviours that confer short-term reproductive advantages (Selander 1965). However, this investment in reproductive success may play a disadvantage for males: increase of mortality because of their higher growth rates and metabolic activity, leading to increased susceptibility to nutritional stress and diseases; also intrasexual competition for mates or resources increases risk of death by infections and diseases provoked by physical debilitation (Clinton and Le Boeuf 1993; Ralls et al. 1980).

Survival rates of pinnipeds are mainly dependent on two factors: population density and environmental changes (Hastings and Testa 1998; Pistorius et al. 1999; Reid and Forcada 2005; Hofmeyr et al. 2007; Drago et al. 2011). Density of a population affects survival when space becomes limited in the breeding colony or by competition for resources. Environmental effects on survival are related to changes in prey densities that vary the availability of food resources to maintain body condition. In the present study, survivorship comparison between periods shows that in the course of these 20 years there was an increase in the survival of early juveniles and adults of both sexes. Possible hypothesis for the improvement in juvenile and adult survivorship could be: an increase in the availability of food resources, a decrease of mortality causes, or a combination of both factors. The reduction in South American sea lion abundance caused by their harvest in the last century was followed by a decrease of its primary prey: Argentine hake *Merluccius hubbsi* (Koen Alonso et al. 2000; Koen-Alonso and Yodzis 2005). During the 1990s Argentine hake stocks were depleted as a result of the huge impact of high-sea fisheries (Crespo et al. 2000; Pérez 2000; Dans et al. 2003; Cordo 2004). These changes led to a severe reorganization of the whole ecosystem off northern Patagonia (Crespo and Pedraza 1991; Drago et al. 2009b, 2010a). However, through retrospective analysis of stable isotopes in the skull bones of male and female South American sea lions, an increased *per capita* consumption of pelagic prey (like Argentine hake) was found at a time when both the sea lion population was

recovering and the hake population was declining (Drago et al. 2009b). This increase in the *per capita* consumption of pelagic prey was explained by a density-dependent mechanism: while the sea lion population was growing there was an increased intraspecific competition at the benthic foraging grounds near colonies, leading to an increased exploitation of pelagic feeding grounds (Drago et al. 2009b, 2010a). This scenario is consistent with the hypothesis that an increase in the availability of food resources could have improved sea lion survivorship.

A decrease of natural mortality causes between periods could be expected if there were an improvement of body health and condition. Pelagic potential prey had on average a higher energy density and lipid content than benthic prey, thus leading to a higher nutritional value of the potential pelagic offshore prey (Eder and Lewis 2005; Drago et al. 2009b, 2010b). So the increase of pelagic prey in the diet of South American sea lion females (Drago et al. 2009b), may have improved female fitness, increasing their own survival and also the production and maintenance of their pups. Pup growth is strongly influenced by their mother's diet; and it has been found that *O. flavescens* pups of females that rely mostly on pelagic offshore prey grew faster than those of females that feed on benthic coastal prey (Drago et al. 2010b). Typically, populations of pelagic foragers tend to recover quickly and benthic foragers fail to recover, possibly because they often operate near their physiological diving capability and, for this reason, have a lower capacity to increase their foraging effort in response to the reduction in food availability caused by fishing (Costa et al. 2004, 2006). An improvement in the female fitness could be translated directly to a increase in her survival and indirectly to a reduction of pup mortality due to maternal care, which will ultimately increase recruitment in the subsequent age classes. In the present study we demonstrate for *O. flavescens* that in the course of these 20 years there was an increase in the survivorship of both juveniles and adults. Due to the fact that both survival and fecundity of adult females were high, more pups were being produced and fed back into this cycle. Consequently, the improvement in survivorship could be one of the key factors that led to population growth in recent decades.

Additionally, it might be hypothesized that due to the increase in the number of individuals in the rookeries (Dans et al. 2004; Grandi et al. 2008), there could be a positive interaction effect between

female groups, not only in the care of the pups but also in helping primiparous females. Natal site fidelity is common in several pinniped species, and it was studied for some female sea lion species (Maldonado et al. 1995; Hoffman et al. 2006; Wolf and Trillmich 2007; Campbell et al. 2008; Chilvers and Wilkinson 2008). So philopatry could be considered as a learned behaviour that increases female reproductive success (*i.e.* pup survival) (Parker et al. 2008). Long-term maintenance of female social structure may convey direct benefits minimizing agonistic interactions that cause early pup mortality (Wolf and Trillmich 2007) and could favor kinship structures and matrilineal groups (Greenwood 1980). It was demonstrated that *O. flavescens* pup survival is higher in dense and big rookeries than in isolated or marginal breeding areas (Campagna et al. 1992; Drago et al. 2011; Svendsen et al. 2012; Franco-Trecu et al. 2015). Also there is some degree of philopatry and site fidelity driving the recolonization process observed in the last 40 years (Grandi et al. 2008). Therefore we could accept the hypothesis that there was a decrease of external causes of death, while future studies may prove the existence of a level of kinship between individuals within a rookery.

For long-lived mammals survivorship among younger age classes contributes significantly to population growth (Eberhardt and Siniff 1977; DeMaster et al. 1980) and it is often used as an indicator of population status (Eberhardt 1985; Beauplet et al. 2005). Even though for several pinniped species population growth is influenced by the magnitude of adult survival and fecundity (Pascual and Adkison 1994; York 1994; Wickens and York 1997; Pistorius et al. 1999; Goldsworthy et al. 2003; Holmes and York 2003; Winship and Trites 2006; Holmes et al. 2007; Gibbens and Arnould 2009), there are other studies that demonstrate that juvenile survival rates are equally if not more influential on population growth (York 1994; Holmes and York 2003; Pendleton et al. 2006). The present study demonstrates that in the course of these 20 years there was an increase in the survivorship of both juvenile and adult *O. flavescens*.

In large mammal populations, the contribution of different age classes on population growth is different, and that is why it would be better to analyze the dynamics using methods that explicitly characterize each class (Caswell 2001). Therefore, for the purpose of increasing the knowledge of a pinniped population recovery, the next step is to model *O. flavescens* population dynamics applying

matrix population models to prove the sensitivity of the growth rate to changes of vital rates, and to determine how important the increase in survival of the different age classes was for population expansion and colonization. In this context, the results reported in the present study may serve as a baseline for developing such analysis.

Acknowledgments: The authors would like to express their gratitude to all those people who were involved in the fieldwork and collections of specimens throughout 40 years on which this paper is based, especially to G. Svendsen, A. Romero (Instituto A. Storni), and N. García (CENPAT-CONICET). We also thank to all the persons and the personnel of private and state organizations who report the presence of carcasses on the different beaches of the area. The authors would like to thanks to N. Bustos for the histological preparations. Thanks are also due to R. Natalie P. Goodall for her assistance with the English and two anonymous reviewers for their helpful suggestions on the manuscript. Natalie passed away on 25 May 2015, while this paper was in press. As scientists and good friends of her, we will all miss her knowledge and her unbounded generosity. This study was supported by GEF/PNUD (1992-1996), BBVA Foundation (BIOCON 04), Scientific Cooperation Program of Spain (1996-1999), Fundación Vida Silvestre Argentina, National Agency for the Promotion of Science and Technology of Argentina and The University of Patagonia. This research also received logistic and institutional support from Centro Nacional Patagónico-CONICET and financial support of the Zoo d'Amneville. We thank the Government agencies from the provinces of Río Negro and Chubut for providing the permit to work.

REFERENCES

- Barlow J, Boveng PL. 1991. Modeling age-specific mortality for marine mammals population. *Mar Mam Sci* 7:50-65.
- Barthled 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. Available via DIALOG. http://www.fip.cl/prog_x_year/2006/2006-50.htm. Accessed July 2011.
- Beauplet G, Barbraud C, Chambellant M, Guinet C. 2005. Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: Influence of pup sex, growth rate and oceanographic conditions. *J Anim Ecol* 74:1160-1172.
- Beauplet G, Barbraud C, Dabin W, Küssener C, Guinet C. 2006. Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos* 112:430-441.
- Boyd IL, Croxall JP, Lunn NJ, Reid K. 1995. Population Demography of Antarctic Fur Seals: The Costs of Reproduction and Implications for Life-Histories. *J Anim Ecol* 64(4):505-518.
- Boyd IL, Roberts JP. 1993. Tooth growth in male Antarctic fur seals (*Arctocephalus gazella*) from South Georgia: an indicator of long-term growth history. *J Zool Lon* 229:177-190.
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L. 2001. Introduction to Distance Sampling. Oxford University Press, Oxford.
- Campagna C. 1985. The breeding cycle of the southern sea lion, *Otaria byronia*. *Mar Mam Sci* 1:210-218.
- Campagna C, Bisioli C, Quintana F, Perez F, Vila A. 1992. Group breeding in sea lions: pups survive better in colonies. *Anim Behav* 43:541-548.
- Campbell RA, Gales NJ, Lento GM, Baker CS. 2008. Islands in the sea: extreme female natal site fidelity in the Australian sea lion, *Neophoca cinerea*. *Biol Lett* 4:139-142.
- Cappozzo HL, Perrin WF. 2009. South American sea lion (*Otaria flavescens*). In: Perrin WF, Würsing B, Thewissen JGM (eds) Encyclopedia of marine mammals, 2nd edn. San Diego: Academic Press.
- 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, Universidad Nacional de La Plata.
- Caswell H. 2001. Matrix population models. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- Caughley G. 1966. Mortality patterns in mammals. *Ecology* 47:906-918.
- Caughley G. 1977. Analysis of Vertebrate Populations. John Wiley & Sons, Chichester, New York, Brisbane, Toronto.
- Chapman DG. 1964. A critical study of Pribilof fur seal population estimates. *Fish Bull* 63:657-669.
- Chilvers BL. 2012. Using Life-History Traits of New Zealand Sea Lions, Auckland Islands to Clarify Potential Causes of Decline. *J Zool* 287(4):240-49.
- Chilvers BL, Wilkinson IS. 2008. Philopatry and site fidelity of New Zealand sea lions (*Phocarctos hookeri*). *Wildl Res* 35:463-470.
- Clinton WL, Le Boeuf BJ. 1993. Sexual selection's effects on male life history and the pattern of male mortality. *Ecology* 74:1884-1892.
- Cordo HD. 2004. Evaluación del estado del efectivo sur de 41°S de la merluza (*Merluccius hubbsi*) y estimación de la captura biológicamente aceptable correspondiente al año 2004. Informe Técnico Interno N°17-04, INIDEP.
- Costa DP, Kuhna CE, Weisea MJ, Shaffer SA, Arnould JPY. 2004. When does physiology limit the foraging behaviour of freely diving mammals? *Int Congr Ser* 1275:359-366.
- Costa DP, Weise MJ, Arnould JPY. 2006. Potential influences of whaling on the status and trends of pinniped populations. In: Estes JA, Demaster DP, Doak DF, Williams TM, Brownell RL (eds) Whales, whaling and ocean ecosystems. University of California Press, Berkeley.
- Crespo EA. 1988. Dinámica poblacional del lobo marino del sur *Otaria flavescens* (Shaw, 1800), en el norte del litoral patagónico. PhD dissertation, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Buenos Aires, Argentina.

- Crespo EA, Koen Alonso M, Dans SL, García NA, Pedraza SN, Coscarella MA, González R. 2000. Incidental catch of dolphins in mid-water trawls for southern anchovy off Patagonia. *J Cetac Res Manag* **2**(1):11-16.
- Crespo E, Oliva D, Dans S, Sepúlveda M. 2012. Estado de situación del lobo marino común en su área de distribución. Editorial Universidad de Valparaíso, Valparaíso, Chile.
- Crespo EA, Pedraza SN. 1991. Estado actual y tendencia de la población de lobos marinos de un pelo (*Otaria flavescens*) en el litoral norpatagónico. *Ecol Austr* **1**:87-95.
- Crespo EA, Schiavini A, Perez Macri G, Reyes L, Dans S. 1994. Estudio sobre la determinación de edades en mamíferos marinos del Atlántico Sudoccidental. In: Oporto JA (ed) *Anales IV Reunión de Trabajo de Especialistas en Mamíferos Marinos de América del Sur*. Valdivia, Chile, 1994.
- Crouse DT, Crowder LB, Caswell H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* **68**:1412-1423.
- Dans SL, Koen Alonso M, Crespo EA, Pedraza SN, García NA. 2003. Interactions between marine mammals and high seas fisheries in Patagonia: an integrated approach. In: Gales N, Hindell M, Kirkwood R (eds) *Marine Mammals: Fisheries, Tourism and Management Issues*. CSIRO Publishing, Collingwood.
- Dans SL, Crespo EA, Pedraza SN, Koen Alonso M. 2004. Recovery of the South American sea lion population in northern Patagonia. *Can J Fish Aquat Sci* **61**:1681-1690.
- DeMaster DP, Thomas JA, Stone S, Andriashek D. 1980. Biological studies of seals in pack ice habitat. *Antarct J US* **14**:179-180.
- Doak DF, Kareiva PM, Klepetka B. 1994. Modelling population viability for the desert tortoise in the western Mojave Desert. *Ecol Appl* **3**:446-460.
- Drago M, Cardona L, Aguilar A, Crespo EA, Ameghino S, García N. 2010b. Diet of lactating South American sea lions, as inferred from stable isotopes, influences pup growth. *Mar Mam Sci* **26**(2):309-323.
- Drago M, Cardona L, Crespo EA, Aguilar A. 2009a. Ontogenic dietary changes in South American sea lions. *J Zool* **279**:251-261.
- Drago M, Cardona L, Crespo EA, Grandi MF. 2010a. Reduction of skull size in South American sea lions reveals density-dependent growth during population recovery. *Mar Ecol Progr Ser* **420**:253-261.
- Drago M, Cardona L, García N, Ameghino S, Aguilar A. 2011. Influence of colony size on pup fitness and survival in South American sea lions. *Mar Mam Sci* **27**(1):167-181.
- Drago M, Crespo EA, Aguilar A, Cardona L, García N, Dans SL, Goodall N. 2009b. Historic diet change of the South American sea lion in Patagonia as revealed by isotopic analysis. *Mar Ecol Progr Ser* **384**:273-286.
- Eder EB, Lewis MN. 2005. Proximate composition and energetic value of demersal and pelagic prey species from the SW Atlantic Ocean. *Mar Ecol Progr Ser* **291**:43-52.
- Eberhardt LL. 1985. Assessing the dynamic of wild populations. *J Wildl Manage* **49**:997-1012.
- Eberhardt LL, Siniff DB. 1977. Population dynamics and marine mammal management policies. *J Fish Res Board Can* **34**:183-90.
- Franco-Trecu V, Drago M, Baladán C, García-Olazábal MD, Crespo EA, Cardona L, Inchausti P. 2015. Postharvesting population dynamics of the South American sea lion (*Otaria byronia*) in the southwestern Atlantic. *Mar Mam Sci* **31**:963-978.
- Gibbens J, Arnould JPY. 2009. Age-specific growth, survival, and population dynamics of female Australian fur seals. *Can J Zool* **87**:902-911.
- Godoy JC. 1963. Evaluación de los Recursos Naturales de la Argentina (Primera Etapa) Tomo VIII. Fauna Silvestre. Vol 1. Consejo Federal de Inversiones.
- Goldsworthy SD, Bulman C, He X, Larcombe J, Littnan C. 2003. Trophic interactions between marine mammals and Australian fisheries: an ecosystem approach. In: Gales NJ, Hindell MA, Kirkwood R (eds) *Marine Mammals: Fisheries, Tourism and Management Issues*.
- Grandi MF. 2010. Dinámica poblacional y cambios estructurales en una población en crecimiento de lobo marino común, *Otaria flavescens*, del litoral norpatagónico. PhD dissertation, Universidad Nacional del Comahue, Argentina.
- Grandi MF, Dans SL, Crespo EA. 2008. Social composition and spatial distribution of colonies in an expanding population of South American sea lions. *J Mam* **89**(5):1218-1228.
- Grandi MF, Dans SL, Crespo EA. 2015. The recovery process of a population is not always the same: The case of *Otaria flavescens*. *Mar Biol Res* **11**(3):225-235.
- Grandi MF, Dans SL, García NA, Crespo EA. 2010. Growth and age at sexual maturity of South American sea lions. *Mam Biol* **75**:427-436.
- Grau R, Acuña E. 1998. Determinación de la edad y crecimiento en el lobo marino común *Otaria flavescens* (Shaw, 1800), a través del análisis de estructuras dentales por corte, en la zona norte de Chile. Paper presented at the XVII Congreso de Ciencias del Mar, Santiago, Chile, 13-16 May 1998.
- Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* **28**:1140-1162.
- Guinet C, Jouventin P, Georges J-Y. 1994. Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St. Paul and Amsterdam) islands and their possible relationship to El Niño southern oscillation. *Antarct Sci* **6**:473-478.
- Harwood J, Prime JH. 1979. Some factors affecting the size of British grey seal population. *J Appl Ecol* **15**:401-411.
- Hastings KK, Testa JW. 1998. Maternal and birth colony effects on survival of Weddell seal offspring from McMurdo Sound, Antarctica. *J Anim Ecol* **67**:722-740.
- Hernández-Camacho CJ. 2001. Tabla de vida del lobo marino de California *Zalophus californianus californianus* en la lopera Los Islotes, B.C.S. Mexico. MS thesis, Centro Interdisciplinario de Ciencias Marinas-Instituto Politécnico Nacional, Mexico.
- Hernández-Camacho CJ, Aurióles-Gamboa D, Laake D, Gerber LR. 2008. Survival rates of the California sea lion, *Zalophus californianus*, in Mexico. *J Mamm* **89**(4):1059-1066.
- Hilborn R, Mangel M. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, New Jersey.
- Hoffman JI, Matson C, Amos W, Loughlin TR, Bickham JW. 2006. Deep genetic subdivision within a continuously distributed and highly vagile marine mammal, the Steller's sea lion *Eumetopias jubatus*. *Mol Ecol* **15**:2821-2832.
- Hofmeyr GJG, Bester MN, Pistorius PA, Mulaudzi TW, De Bruyn PJN, Ramunasi JA, Tshithabane HN, McIntyre T,

- Radzilani PM. 2007. Median pupping date, pup mortality and sex ratio of fur seals at Marion Island. *S Afr J Wildl Res* **37**:1-8.
- Holmes EE, York AE. 2003. Using age structure to detect impacts on threatened populations: a case study with Steller sea lions. *Conserv Biol* **17**(6):1794-1806.
- Holmes EE, Fritz LW, York AE, Sweeney K. 2007. Fecundity declines in Steller sea lion birth rate in the Gulf of Alaska suggests new conservation and research priorities. *Ecol Appl* **17**:2214-2232.
- Koen-Alonso M, Yodzis P. 2005. Multispecies modelling of some components of the marine community of northern and central Patagonia, Argentina. *Canadian J Fish Aquat Sci* **62**:1490-1512.
- Koen Alonso M, Crespo EA, Pedraza SN, García NA, Coscarella MA. 2000. Food habits of the South American sea lion *Otaria flavescens*, off Patagonia, Argentina. *Fish Bull* **98**:250-263.
- Kraus C, Mueller B, Meise K, Piedrahita P, Pörschmann U, Trillmich F. 2013. Mama's boy: sex differences in juvenile survival in a highly dimorphic large mammal, the Galapagos sea lion. *Oecologia* **171**:893-903.
- Krebs CJ. 1985. Ecology. The experimental analysis of distribution and abundance. Harper & Row Publishers, New York.
- Krebs CJ. 1999. Ecological Methodology. 2nd edn. Benjamin/Cummings.
- Lander RH. 1982. A life table and biomass estimate for the Alaskan fur seals. *Fish Res* **1**(1981/1982):55-70.
- Lea M-A, Guinet C, Cherel Y, Duhamel G, Dubroca L, Pruvost P, Hindell M. 2006. Impacts of climatic anomalies on provisioning strategies of a Southern Ocean predator. *Mar Ecol Prog Ser* **310**:77-94.
- Lebreton JD, Burnham KP, Clobert J, Anderson DR. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* **62**:67-118.
- Lewis MN, Ximénez I. 1983. Dinámica de la población de *Otaria flavescens* (Shaw) en el área de Península Valdés y zonas adyacentes (Segunda parte). Contrib N° 79 Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina.
- Lima M, Páez E. 1997. Demography and Population Dynamics of South American Fur Seals. *J Mamm* **78**:914-920.
- Maldonado JE, Orta DF, Stewart BS, Geffen E. 1995. Intraspecific genetic differentiation in California sea lions (*Zalophus californianus*) from southern California and the Gulf of California. *Mar Mam Sci* **11**:46-58.
- McIntosh RR. 2007. Life history and population demographics of the Australian sea lion. PhD dissertation, La Trobe University, Melbourne, Australia.
- McIntosh RR, Goldsworthy SD, Shaughnessy PD, Kennedy CW, Burch P. 2012. Estimating pup production in a mammal with an extended and aseasonal breeding season, the Australian sea lion (*Neophoca cinerea*). *Wildl Res* **39**:137-48.
- McIntosh RR, Arthur AD, Dennis T, Berris M, Goldsworthy SD, Shaughnessy PD, Teixeira CEP. 2013. Survival estimates for the Australian sea lion: Negative correlation of sea surface temperature with cohort survival to weaning. *Mar Mam Sci* **29**(1):84-108.
- McMahon CR, White GC. 2009. Tag loss probabilities are not independent: Assessing and quantifying the assumption of independent tag transition probabilities from direct observations. *J Exp Mar Biol Ecol* **372**:36-42.
- Oliva D, Sielfeld W, Buscaglia M, Matamala M, Moraga R, Pavés H, Pérez MJ, Schrader D, Sepúlveda M, Urrea A. 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. Available via DIALOG. http://www.fip.cl/prog_x_year/2006/2006-34.htm. Accessed July 2011.
- Páez E. 2006. Situación de la administración del recurso lobos y leones marinos en Uruguay. In: Menafrá R, Rodríguez-Gallego L, Scarabino F, Conde D (eds) Bases para la conservación y el manejo de la costa uruguaya. Vida Silvestre, Sociedad Uruguaya para la Conservación de la Naturaleza.
- Parker P, Harvey JT, Maniscalco JM, Atkinson S. 2008. Pupping-site fidelity among individual Steller sea lions (*Eumetopias jubatus*) at Chiswell Island, Alaska. *Can J Zool* **86**:826-833.
- Pascual MA, Adkison MD. 1994. The decline of the Steller sea lion in the northeast Pacific: demography, harvest or environment? *Ecol Appl* **4**:393-403.
- Pendleton GW, Pitcher KW, Fritz LW, York AE, Raum-Suryan KL, Loughlin TR, Calkins DG, Hastings KK, Gelatt TS. 2006. Survival of Steller sea lions in Alaska: a comparison of increasing and decreasing populations. *Can J Zool* **84**:1163-1172.
- Pérez M. 2000. Resumen del estado del efectivo y de explotación (año 2000) de la merluza (*Merluccius hubbsi*) al sur de 41°S. Informe Técnico Interno N°21-00, INIDEP.
- Pistorius PA, Bester MN, Hofmeyer GJG, Kirkman SP, Taylor FE. 2008. Seasonal survival and the relative cost of first reproduction in adult female Southern elephant seals. *J Mamm* **89**(3):567-574.
- Pistorius PA, Bester MN, Kirkman SP. 1999. Survivorship of a declining population of southern elephant seals, *Mirounga leonina*, in relation to age, sex and cohort. *Oecologia* **121**:201-211.
- Pistorius PA, Bester MN, Lewis MN, Taylor FE, Campagna C, Kirkman SP. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). *J Zool Lon* **263**:107-119.
- Rabinovich J. 1980. Introducción a la ecología de poblaciones animales. Compañía Editorial Continental SA, México.
- Ralls K, Brownell RL, Ballou J. 1980. Differential mortality by sex and age in mammals with specific reference to the sperm whale. *Rep Int Whal Comm, Special Issue* **2**:233-243.
- Reid K, Forcada J. 2005. Causes of offspring mortality in the Antarctic fur seal, *Arctocephalus Gazella*: the interaction of density dependence and ecosystem variability. *Can J Zool* **83**:604-609.
- Reyes LM, Crespo EA, Szapkievich V. 1999. Distribution and population size of the southern sea lion (*Otaria flavescens*) in central and southern Chubut, Argentina. *Mar Mam Sc* **15**(2):478-493.
- Riedman M. 1990. The pinnipeds; Seals, Sea Lions, and Walruses. Berkley: Univ California Press, Berkley.
- Rosas FCW, Haimovici M, Pinedo AM. 1993. Age and growth of the South American sea lion, *Otaria flavescens* (Shaw, 1800), in southern Brazil. *J Mamm* **74**(1):141-147.
- 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.
- 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. *Mamm Biol* **69**:1-11.
- Selander RK. 1965. On mating systems and sexual selection. *Am Nat* **99**:129-141.
- Sepúlveda M, Oliva D, Urrea A, Pérez-Álvarez MJ, Moraga R, Schrader D, Inostroza P, Melo Á, Díaz H, Sielfeld W. 2011. Distribution and abundance of the South American sea lion *Otaria flavescens* (Carnivora: Otariidae) along the central coast off Chile. *Rev Chil Hist Nat* **84**:97-106.
- Siler W. 1979. A competing-risk model for animal mortality. *Ecology* **60**:750-757.
- Soto KH, Trites AW, Arias-Schreiber M. 2004. The effects of prey availability on pup mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru. *J Zool Lon* **264**:419-428.
- Soto KH, Trites AW, Arias-Schreiber M. 2006. Changes in diet and maternal attendance of South American sea lions indicate changes in the marine environment and prey abundance. *Mar Ecol Progr Ser* **312**:277-290.
- Svendsen GM. 2005. Estudio de las diferencias en el comportamiento social de lobos marinos de un pelo *Otaria flavescens* entre asentamientos tradicionales de cría y zonas de expansión en el contexto de una población en crecimiento. Grade Dissertation, Universidad de la Patagonia San Juan Bosco, Argentina.
- Svendsen G, Dans SL, Crespo EA, Grandi MF. 2012. WP24: Mortalidad de crías asociada a cambios en la estructura social y al aumento poblacional. In: Crespo E, Oliva D, Dans S, Sepúlveda M (eds) Estado de situación del lobo marino común en su área de distribución. Editorial Universidad de Valparaíso, Valparaíso, Chile.
- 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. *Biol Conserv* **121**:357-367.
- Venegas C, Gibbons J, Aguayo-Lobo A, Sielfeld W, Acevedo J, Amado N, Capella J, Guzmán G, Valenzuela C. 2001. Cuantificación poblacional de lobos marinos en la XII Región, Chile. Informe técnico Fondo de Investigación Pesquera IP-IT/2000-22. Available via DIALOG. http://www.fip.cl/prog_x_year/2000/2000-22.htm. Accessed July 2011.
- Wickens PA. 1993. Life expectancy of fur seals, with special reference to the South African (Cape) fur seal. *S Afr J Wildl Res* **23**:101-106.
- Wickens P, York A. 1997. Comparative population dynamics of fur seals. *Mar Mam Sci* **13**(2):241-292.
- Winship AJ, Trites AW. 2006. Risk of extirpation of Steller sea lions in the gulf of Alaska and Aleutian Islands: A population viability analysis based on alternative hypotheses for why sea lions declined in western Alaska. *Mar Mam Sci* **22**(1):124-155.
- Wolf JBW, Trillmich F. 2007. Beyond habitat requirements: Individual fine-scale site fidelity in a colony of the Galapagos sea lion (*Zalophus wolfebaeki*) creates conditions for social structuring. *Oecologia* **152**:553-567.
- York AE. 1994. The population dynamics of northern sea lions, 1975-1985. *Mar Mam Sci* **10**:38-51.
- Ximénez I. 1975. Dinámica de la población de *Otaria flavescens* (Shaw) en el área de Península Valdés y zonas adyacentes (Provincia del Chubut, RA). Informe Técnico 1.4.1. Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina.