

Recovery of the South American sea lion (*Otaria flavescens*) population in northern Patagonia

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Abstract: The size of and trend in the South American sea lion (*Otaria flavescens*) population located in northern Patagonia were estimated and changes in the distribution, size, and structure of individual sites were analyzed during the period 1983–2002. Total counts were made during the reproductive season. Regression models were used to analyze the trend. Pups represented around 40% of the animals counted. The annual rates of change for pups and nonpups were not significantly different ($p > 0.05$, $n = 7$), although some rookeries showed higher rates of change for pups than for nonpups. Pup numbers have been increasing at the rate of 3.4% per year at the oldest rookeries, but the rate of increase was higher at new rookeries. Using Bayes' methods, the precision of the estimates and the contribution to the abundance of each rookery produced an alternative estimate of the trend in pup numbers in 5.7%. The key in the recovery of this population includes higher survival rates of juveniles combined with increased available habitat for newly reproducing individuals. This process led to the occupancy of new areas for hauling out and breeding. This hypothesis could explain the higher rates of increase in pups in peripheral areas while reproductive rates remain unchanged.

Résumé : Nous avons estimé la taille et la tendance de la population du lion de mer d'Amérique du Sud (*Otaria flavescens*) du nord de la Patagonie et nous avons analysé les changements dans la répartition, la taille et la structure des sites individuels de 1983 à 2002. Nous avons fait des dénombrements complets durant la saison de reproduction. Des modèles de régression ont permis d'analyser la tendance. Les petits représentent environ 40 % des animaux dénombrés. Les taux annuels de changement pour les petits et les autres lions de mer ne diffèrent pas significativement ($p > 0,05$, $n = 7$), bien que dans certaines échouries les taux de changements sont plus élevés pour les petits que pour les autres. Le nombre de petits augmente au taux de 3,4 % par année dans les échouries les plus anciennes et le taux est encore plus élevé dans les nouvelles échouries. Au moyen de méthodes bayésiennes, la précision des estimations et la contribution de chaque échourie à l'abondance ont généré une nouvelle estimation de la tendance dans le nombre de petits de l'ordre de 5,7 %. Le facteur essentiel de la récupération de cette population est un taux de survie plus élevé des jeunes combiné à la disponibilité d'habitats pour les individus qui débutent leur reproduction. Ce processus a eu comme conséquence l'occupation de nouveaux sites pour l'échouage et la reproduction. Cette hypothèse pourrait expliquer les taux plus élevés d'accroissement des petits dans les zones périphériques, alors que les taux de reproduction demeurent inchangés.

[Traduit par la Rédaction]

Introduction

South American sea lions (*Otaria flavescens*) are distributed along the whole Argentine coast on the southwestern Atlantic Ocean. More than 85 colonies located on the mainland and islands are known (Dans et al. 1996; Reyes et al. 1999; Schiavini et al. 1999). These colonies may represent breeding areas or rookeries during the reproductive season as well as haul-out sites where no reproductive activities take place. There is evidence of seasonal movements of animals between colonies at least in northern Patagonia (41–43°S) (Ximénez 1976; Lewis and Ximénez 1983). The popu-

lation was heavily exploited during the first half of the twentieth century and protected during the 1970s. Currently, it is increasing slowly (Crespo and Pedraza 1991). In 1938, the number of sea lions in northern Patagonia was estimated at 137 500 (Godoy 1963), falling to almost 18 000 by 1946 (Carrara 1952). In southern locations (islands off Chubut, 45°S), where exploitation could have been more limited, the current number still represents one half of the number counted in 1952 (Reyes et al. 1999).

Colonies located in northern Patagonia were the most heavily exploited (Crespo and Pedraza 1991). Almost half of the skins exported from Argentina during the period 1930–

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1960 came from four rookeries located in this region (201 259 from a total of 493 438 skins). These colonies were also the best monitored since 1972. They did not show signs of recovery until 1990, when the number of pups born in the four main rookeries showed a positive annual rate of increase of 1.3% (Crespo and Pedraza 1991). The relatively slow increase and the delay in the recovery were interpreted at that moment as a consequence of sea lion demographics such as their naturally low intrinsic rate of increase.

As an alternative, the population's slow recovery has also been attributed to changes in environmental conditions (e.g., carrying capacity). Soon after the commercial exploitation ceased, the Patagonian high-seas fishery began to be developed and became very important in the 1980s. This may represent the major change that took place in this marine ecosystem and could have produced changes in the community and potential competitive effects on sea lions (Crespo et al. 1997; Koen Alonso et al. 2000).

At that moment, small breeding areas appeared within haul-out sites, where the arrival of presumably young adult males in juveniles areas was observed in previous years (Crespo 1988). This observation pointed out the dynamic nature of colonies and the transformation from haul-out to rookery as one of the potential mechanisms related to the recovery of this population. The expansion of areas used and the increase in the number of breeding sites would also be related to changes in vital rates.

Changes like those described above have been observed in other declining otariid populations as a way to investigate possible causes and consequences of the decline. Some studies suggest that resources other than food availability are important factors determining the expansion of colonies (York et al. 1996; Raum-Suryan et al. 2002). Therefore, studies of other otariid populations recovering after an important reduction may be helpful in better understanding patterns and processes involved in the recovery.

The objectives of this paper were to (i) analyze changes in the size, distribution, and structure of individual colonies of the South American sea lion in northern Patagonia, (ii) estimate the size of and trend in the population, and (iii) identify possible changes in the structure of the population.

Materials and methods

Study area

This study included the colonies located along the Argentine coast between Punta Bermeja and Punta León (Fig. 1). Censuses were carried out during the periods 1983–1987, 1989–1990, and 1993–2002, but the same colonies were not included in all surveys. A database for the periods 1972–1975 and 1982–1983 was also analyzed (Ximénez 1976; Castello et al. 1982; Lewis and Ximénez 1983).

Counting methodology

Total counts were made at the end of the reproductive season (mainly between the last week of January and first week of February), when most of the individuals are present at the rookeries for reproduction, and almost all of the pups were already born. In most cases, the counts were made from land and from elevated points when possible. On a few occasions (Barrancas Blancas in 1995 and Isote Lobos in 1994, 1995,

and 1996), photographs were taken from a high-wing airplane (Cessna B182) and then counts were made from the photographs. However, these counts were not used in the population trend estimate. At least two counts were made both in the field and from the aerial photographs, with a maximum error of 10% allowed between them. The final value was estimated by averaging the selected counts, while those counts falling out of the fixed error were discarded.

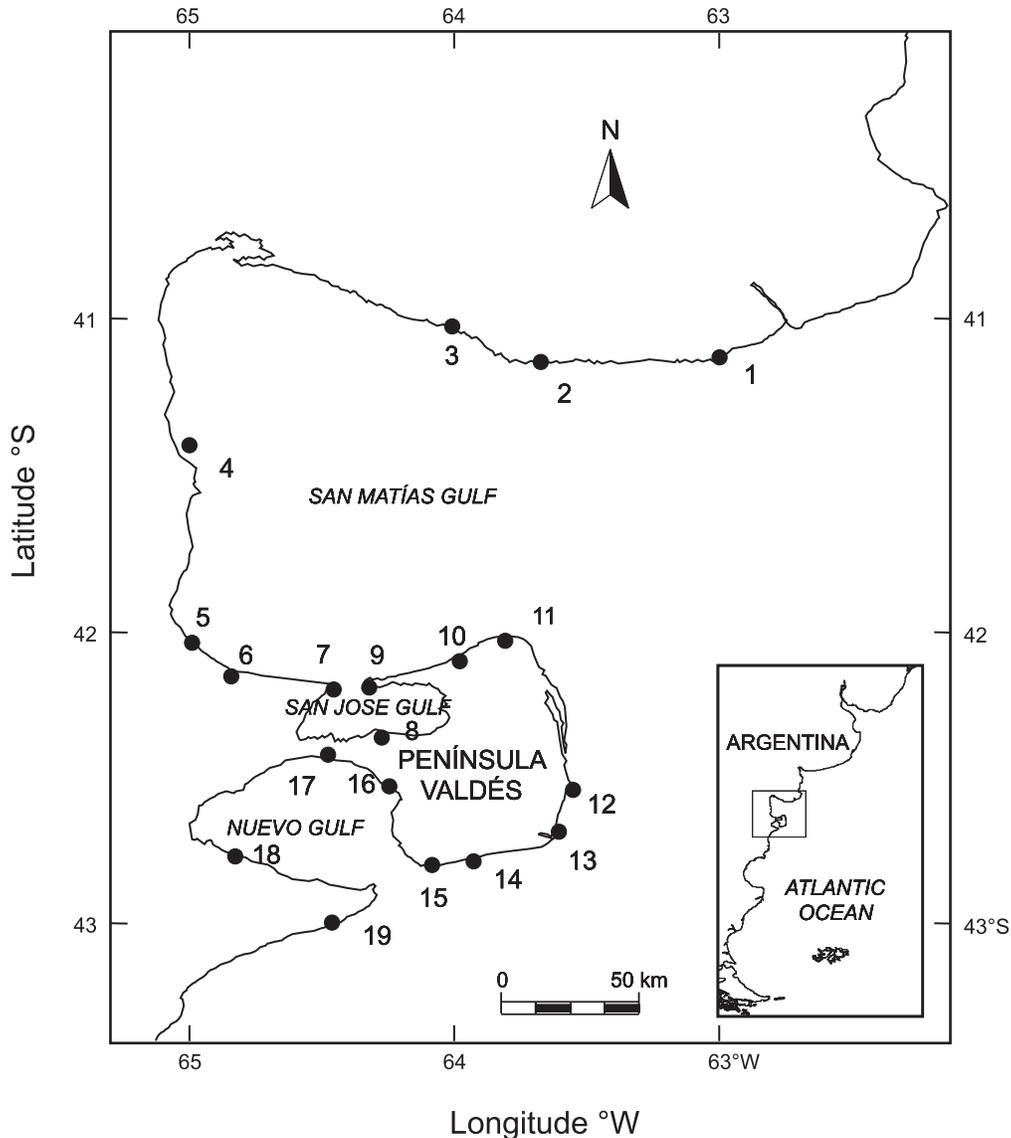
Individuals were counted by age and sex: adult males, subadult males, females in breeding areas (both adult and subadult), juveniles mostly of unknown sex out of breeding areas (including yearlings born during the previous season), and pups (born during the season). These categories were based on body shape and color, location in the rookery, and behavioral cues. The number of animals in each category was counted separately. The total number of animals in each colony was calculated by summing the number counted in each age- and sex-class.

Number and age-class composition of colonies

Numerical models (e.g., regressions, general linear models, and general additive models) can be developed to adjust counts for environmental (tide height, time of day, sea state, and lunar phase) and survey-related effects (Link and Sauer 1997; Calkins et al. 1999; Frost et al. 1999). These models can increase accuracy in estimating and power in detecting population trends by reducing variability in counts (Hastings and Sydeman 2002). However, in this study, surveys were designed to count as many colonies as simultaneously as possible. Thus, it was not possible to survey a colony more than once, and as a result, within-season variability could not be analyzed, precluding the use of such models. However, censuses were carried out during the same fixed time window each year, reducing possible seasonal variations and expecting that during this window, most of animals are ashore. Also, most of the censuses were done in low-tide conditions because beaches are inaccessible otherwise. It is expected that the number of pups will not be affected by availability factors because they are constrained to stay at the rookery. Parturient and postpartum females are constrained to coming back to the same rookery, so the bulk of adult females is available during the surveys. However, other age-classes and particularly juveniles will be highly affected by environmental factors, leading to a higher dispersion of data.

The trend in each colony was analyzed by regressing the logarithm of the number of pups and nonpups on the year of the census. Only two classes were used in this analysis largely because of the variability in the classes that comprise the nonpup group. In several rookeries, it was possible to distinguish females from other classes, although it was not possible in colonies where juveniles were also present. Pups were more constrained to the rookery during the period of time when censuses were made, and as a result, the availability bias in the counts is minimal. Counts of nonpups, on the other hand, are subject both to bias (because of the different availability of age- and sex-classes during the surveys) and to errors resulting from misclassification to class (e.g., adult females and juvenile males appear similar). Because the number of adult males present can also be estimated with minimal error and bias, the relationship between pups and

Fig. 1. South American sea lion rookeries and haul-out sites during the reproductive season (January–February) in northern Patagonia. 1, Punta Bermeja; 2, Faro Belén; 3, Caleta de los Loros; 4, Islote Lobos; 5, Rincon de Elizalde; 6, Barrancas Blancas; 7, Punta Quiroga; 8, Larralde; 9, Punta Buenos Aires; 10, La Armonia; 11, Punta Norte; 12, Punta Hércules; 13, Punta Delgada; 14, La Pastosa; 15, Morro Nuevo; 16, Punta Pirámide; 17, Las Charas; 18, Punta Loma; 19, Punta León.



adult males was also analyzed. The number of adult males present in the rookery is affected by the number of females still in oestrus, so that their numbers peak and then fall along the reproductive season. Crespo (1988) estimated that the number of males in the breeding area peaks on 20 January and then falls to 75% of this around 31 January. Therefore, three periods were considered for analyzing the number of pups per adult male: before 20 January, between 20 and 31 January, and February.

Differences between slopes for pups and nonpups in each individual site were evaluated by *F* tests. Overall differences among trends in the number of pups and nonpups in all rookeries were compared by *F* tests, and all possible pairs of slopes were compared by Tukey–Kramer, *T'*, and GT2 tests (Sokal and Rohlf 1995; Zar 1996). Assumptions of the regression model were verified by visual inspection of residuals.

The historical information collected during the last three decades on each rookery or haul-out was analyzed to further review the changes that had occurred. This information is mostly descriptive and is reported for each specific individual site. Spatial and age-class composition changes in the old or new individual rookeries were reviewed to describe the recolonization pattern.

Population size, trend, and structure

The present population size for northern Patagonia was estimated from counts made in 19 colonies during 2001 and 2002. The very wide area to be surveyed over a short time presented particular problems in providing a population estimate. Then, not all the colonies could be counted each year, sometimes for logistical reasons or because of bad weather conditions. Therefore, counts made in different colonies and

years must be combined. Colonies 8–17 and 19 were surveyed in 2001, while colonies 2–7 and 18 were surveyed in 2002. Although rookery 1 was surveyed in 2002, the census was discarded because of bad weather conditions, and the census carried out in 2000 was considered.

Censuses, even if conducted during the reproductive season, may underestimate the population size because an unknown proportion of animals are at sea; this may include the juvenile component of the population. To estimate total population size, it is necessary to develop and apply a correction factor to account for the animals missed. One approach is that used by Crespo (1988) who developed life tables for this population utilizing the age structure at death assuming a stationary population. Then, from a known number of pups born (f_0 in the life table) and the survivorship schedule, Crespo (1988) estimated the total number of sea lions. The factor was calculated as the ratio between estimated (E) and counted (C) numbers (17 804 and 9834, respectively; Crespo 1988) being $E/C = 1.8$, which means that close to 45% of the animals are not present in the surveys.

Possible changes in the population structure were explored by comparing rates of annual change in different age-classes. These analyses were performed considering eight colonies, which represent around 70% of the total number and 80% of the total of pups counted between 2000 and 2002. These eight colonies included the historical four main rookeries Punta Buenos Aires, Punta Norte, Punta Pirámide, and Punta León (sites 9, 11, 16, and 19 in Fig. 1) as well as colonies at Punta Bermeja, Punta Quiroga, Punta Hércules, and Punta Delgada (sites 1, 7, 12, and 13 in Fig. 1). The following groups were analyzed: pups and nonpups (all age- and sex-classes pooled), juveniles, adult females, adult males, and subadult males. Rates of change were estimated by regressing the logarithm of the number of individuals counted in each class on the year of the census (Caughley 1977) and assumptions of the regression model were verified by visual inspection of residuals.

Population trajectory was estimated in two ways. One way was to regress the logarithm of the total population at key colonies on time (summation of the number of pups and nonpups in all colonies each year). For this analysis, the eight colonies mentioned above were selected because they were surveyed at the same time in the same year. Data for the periods 1972–1975 and 1981–1983 were available, but they only included pup counts at the four main rookeries (Ximénez 1976; Lewis and Ximénez 1983). A second approach was to calculate a weighted average of the trends in individual colonies (Calkins et al. 1999). Each trend was adjusted by the precision of the estimate and the contribution of each colony to the population size. Only colonies with enough information for the period 1983–2001 were considered. This calculation was done following Calkins et al. (1999), who adjusted each trend and its variance by empirical Bayes' methods. For each site, we computed the Bayes weight wt_b as

$$wt_b = vt/(vt + \tau^2)$$

where vt is the variance in the trend estimate, $\tau^2 = Vt - vt_{\text{mean}}$, Vt is the variance among all trends estimates, and vt_{mean} is the mean of all of the variances. Then, the trend estimate as well as its variance were adjusted as

$$t_b = (t_{\text{mean}}wt_b) + [t(1 - wt_b)]$$

$$vt_b = wt_b\tau^2$$

where t_b and vt_b are the trend and its variance adjusted and t_{mean} is the mean of the estimated trends.

For each rookery, we computed the mean contribution to the total number of pups as the average of the abundance weight wt_A along the years. We computed the weight wt_A for each rookery for each year as

$$wt_A = C/\sum C$$

where C is the count of pups in each rookery.

Then, the trend and its variance adjusted by Bayes for the precision were readjusted by the mean abundance weight as

$$t_{b-A} = \sum (\overline{wt_A}t_b)$$

$$vt_{b-A} = \sum (\overline{wt_A}^2vt_b)$$

Results

Trend of major rookeries

During the reproductive seasons of 2001 and 2002, South American sea lions were present at least at 19 colonies. Breeding activities were recorded in almost all of them by the end of the study (Table 1). The four main rookeries were Buenos Aires, Norte, Pirámide, and León and the less important sites at Islote Lobos and La Armonía. Buenos Aires, Norte, and León represented the most important breeding areas in northern Patagonia, accounting for almost 60% of the total number of pups born in 2001.

All of these rookeries showed positive trends in the number of pups as well as in the number of nonpups (Table 2). Some remarkable changes were found at León. This rookery showed a higher rate of increase in the number of pups than in the number of nonpups ($p < 0.05$) (Table 2). At the same time, there was an increase in the extension of the beach occupied each year. Several small groups began to appear southwards each year 1.5–2 km away from the main breeding area. These small groups were mostly juveniles but also included a few females with pups. In 1994, this area of the colony included 96 pups out of a count of 510 individuals (18%). In 2001, the last year of census, there were 240 pups and a total of 651 individuals (36%).

Pirámide was another important breeding area during the first years of the study. However, it only included 8% of the total number born in 2001–2002. The trend in the number of nonpups in this rookery was not significant (Table 2).

In all of these rookeries, the number of pups per adult male seemed to be constant along the study period, being 5.92 (SE = 2.19), 5.21 (SE = 1.18), and 5.71 (SE = 2.61) in Buenos Aires, León, and Pirámide, respectively, while in Norte the ratio was 3.91 (SE = 0.95).

Trend in juvenile aggregations and haul-out sites

Only 3 out of 19 colonies included exclusively juveniles or nonbreeding animals during the whole study period. These colonies were Caleta de los Loros, Hércules, and La Pastosa (Table 1) and included mostly juveniles of both sexes and subadult males. Caleta de los Loros showed a positive trend equal to 11.3% ($p < 0.05$) (Table 2). Although Caleta de los Loros was described as a haul-out during most of the study,

Table 1. Brief history of South American sea lion haul-out sites and rookeries in northern Patagonia between 1970 and 2002.

Location	Description before this study	First census			Last census		
		Year	Pups	Nonpups	Year	Pups	Nonpups
Bermeja	Not available	1982	30	620	2000	480	2356
Belén	Not available	1995	9	403	2002	160	849
Caleta de Los Loros	Not available	1982	0	150 ^a	2002	16	514
Islote Lobos	Rookery ^b	1990	167	464	2002	693	1164
Rincón de Elizalde	Not available	1996	4	451	2002	8	64
Barrancas Blancas	Not available	1995	135	484	2002	509	476
Quiroga	45–70 adult and subadult males ^c	1983	88	233	2002	462	567
Larralde	Not available	Not available			2001	41	190
Buenos Aires	Rookery ^c	1983	957	729	2001	1778	1271
La Armonía	Not available	1990	116	230	2001	510	365
Norte	Rookery ^c	1983	941	910	2001	1975	2243
Hércules	Adult males ^c	1983	0	175	2001	0	122
Delgada	Subadult males and juveniles ^c	1983	0	757	2000	48	1289
La Pastosa	Juveniles ^d	1996	1	1757	2001	2	847
Morro Nuevo	Juveniles ^c	1987	3	477	2001	895	651
Pirámide	Rookery ^c	1983	506	573	2001	824	525
Las Charas	Not available	1998	48	282	2001	45	280
Loma	Juveniles ^c	1986	4	86	2002	52	436
León	Rookery ^c	1983	737	942	2001	1570	1642

Note: Data for between 1983 and 2002 come from this study. Data before this period were available from the literature.

^aThis census was done on 28 March.

^bCastello et al. (1982).

^cMonitored during 1972–1974 (Ximénez 1976).

^dPossibly wintering haul-out referenced as Pico Lobo by Ximénez (1976).

Table 2. Trends in pups and nonpups of South American sea lion haul-out sites and rookeries in northern Patagonia during the period 1983–2002.

Rookery	Pups				Nonpups				<i>F</i> test <i>p</i> ^b
	<i>n</i>	Slope	95% CI ^a	<i>p</i>	<i>n</i>	Slope	95% CI ^a	<i>p</i>	
Bermeja	8	0.131	0.076; 0.186	0.001	8	0.069	0.007; 0.130	0.035	0.341
Caleta de los Loros	No pups				7	0.113	0.031; 0.195	0.001	
Quiroga	13	0.088	0.057; 0.119	<0.001	12	0.054	0.030; 0.078	<0.001	0.040
Buenos Aires	13	0.043	0.025; 0.060	<0.001	13	0.033	0.020; 0.046	<0.001	0.340
La Armonía	7	0.140	0.067; 0.213	0.002	7	0.044	−0.080; 0.168	0.314	
Norte	15	0.040	0.027; 0.053	<0.001	15	0.056	0.036; 0.076	<0.001	0.120
Hércules	No pups				13	0.054	−0.070; 0.178	0.362	
Delgada	9	0.233	0.142; 0.324	<0.001	12	0.014	−0.019; 0.048	0.289	
La Pastosa	No pups				6	−0.107	−0.295; −0.081	0.190	
Morro Nuevo	8	0.376	0.207; 0.546	<0.001	8	0.040	−0.036; 0.116	0.170	
Pirámide	14	0.025	0.012; 0.039	0.002	14	0.017	−0.004; 0.038	0.059	
Loma	10	0.151	0.092; 0.210	<0.001	11	0.117	0.059; 0.174	<0.001	0.290
León	14	0.042	0.029; 0.055	<0.001	14	0.025	0.012; 0.037	0.001	0.042

^aConfidence interval.

^b*F* test for differences among slopes of pups and nonpups.

three adult males and 16 pups were observed there in 2002. Hércules showed large yearly variations with no trend. La Pastosa was first studied in 1996 and there is not enough information to evaluate its trend. Nevertheless, this site represented an important reservoir of nonbreeding individuals, fluctuating between 700 and 1700 animals counted there during 1996–2001.

Trend and changes in newly developed breeding areas

The remaining sites presented a mixed structure of breeding areas with a large number of juveniles or non-

reproductive animals in close proximity. Other sites were small aggregations with few births during the first years of the study but became breeding areas during the study period.

Quiroga and Morro Nuevo represented the most important new rookeries that have evolved from haul-out sites (Table 1). Previous information about Quiroga indicated the presence of subadult males only (Ximenez 1976). By 1983, this colony was mainly composed of juveniles with a small breeding area, with 88 pups. The percentage of pups increased thereafter reaching close to 50% of the total number by 2001. Although both pups and nonpups showed positive

trends, pup numbers increased at a higher rate (Table 2). The pups to adult male ratio was 7.10 (SE = 3.26). Morro Nuevo only contained nonbreeding age-classes and no reproductive events took place during the 1980s (In 1987, only three pups were found at this site). However, by 1995, 50% of the population at this site were pups. The trend in the number of pups was positive, while no trend was observed in nonpup numbers (Table 2).

Bermeja, Delgada, and Loma are important reservoirs of juveniles. They presented small breeding areas in constant growth, although the nonbreeding fraction still represents more than 80% of the total number (Table 1). Both pups and nonpups increased at similar rates (Table 2), while the number of pups per adult male remained at around 3.31 (SE = 0.81). Births were seen only sporadically at Delgada through 1992 (two or three pups in 1972–1975; Ximenez 1976). In 1992, a landslide made the animals move to an adjacent beach and a small group of adult males, females, and pups appeared in the original location. Here, the new breeding area was separated by 1.5 km from the juvenile haul-out.

The remaining sites Belén, Barrancas Blancas, Larralde, Las Charas, and Rincón de Elizalde were monitored after 1995 (Table 1). Even though there are few data for estimating their trends, they seemed to be increasing. Each colony was composed mostly of nonreproductive individuals with a small amount of breeding areas.

Comparison among individual sites

All rookeries showed significant trends in pup production. Different rookeries showed different trends in the number of pups as well as in the number of nonpups (Table 2). Pirámide showed the lowest rate of increase in the number of pups, but it was not statistically different from the other important and traditional breeding rookeries Norte, Buenos Aires, and León ($p > 0.05$). This rookery showed an increase of 2.5% per year in the number of pups. Less traditional breeding sites such as Bermeja, Quiroga, Loma, and La Armonía exhibited higher rates of increase. Although the breeding area is still small, Delgada showed a higher rate of increase and Morro Nuevo the highest among all rookeries, 37.6% per year (Tukey–Kramer and GT2, $p < 0.05$).

With respect to the nonpup fraction, Buenos Aires, León, and Pirámide showed the lowest significant trends, while Loma and Caleta de los Loros showed the highest (Tukey–Kramer and GT2, $p < 0.05$). One interesting result is that Morro Nuevo, Delgada, and La Armonía did not show significant trends in the number of nonpups (Table 2).

Population size, trend, and structure for northern Patagonia

The total number of individuals counted was 16 807 sea lions in colonies 8–17 and 19 in 2001, while 5269 sea lions were counted in colonies 2–7 and 18 in 2002 (Table 3). Although rookery 1 was surveyed in 2002, the census was discarded because of bad weather conditions, and the census carried out in 2000 was considered. Then, in 2001–2002, the total number of sea lions counted was 24 912 (Table 3). Then, applying a correction factor of 1.8, the population size in northern Patagonia was estimated to be 44 842 sea lions. Pups represented around 40% of the total counts, while they would represent 22% of the estimated population size.

Taking into account the data on the eight selected rookeries and haul-outs during the period 1983–2001, the proportion of pups in the population did not change (Fig. 2). Discriminating individuals in the other age-classes whenever possible, the female proportion seemed to remain constant, while the proportion of juveniles would be increasing (Fig. 2). Nonpups seemed to be increasing at a slightly higher rate than pups, but there were no significant differences between them ($p > 0.05$, $n = 7$) (Table 4). Juveniles showed the highest rate of increase, female numbers were increasing at the same rate as pup numbers, while adult and subadult males did not show significant trends (Table 4). The population at these selected colonies increased by 4.3% per year for the period 1983–2000. The ratio of pups per adult male averaged over all of the rookeries during all of the surveyed years did not show a clear pattern of change ($p > 0.05$). Although highly variable among rookeries, the ratio appears to remain constant through time with a mean of 5.52 pups per male during the time window considered here (21–31 January of each year) (Fig. 3).

Assuming that pups and nonpups would be increasing at the same rate, the population trend may be estimated from the trend in the number of pups. The trend observed in the eight selected colonies was estimated to be 3.9% annually for the period 1983–2000. Considering only the four major rookeries, the trend was estimated to be 3.4% for the same period 1983–2000, and including available data for the period 1970–1980, the trend is still positive but lower (2.9%) ($p < 0.001$) (Fig. 4).

The trend estimated by the weighted average is markedly higher than the trend estimated for the eight selected sites and even more considering only the four major rookeries for the same period 1983–2000 (Fig. 4). Considering the precision and contribution to the abundance of each rookery, the weighted average trend in the number of pups was estimated to be 5.7% (Table 5).

Discussion

There is clear evidence that the South American sea lion population in northern Patagonia is steadily increasing. Although a slight increase was detected in the early 1990s, the population increased at a rate close to 5.7% annually during the period 1983–2002. As a result, the population status has almost doubled since the beginning of the study period. This still represents less than a quarter of the original population's estimated size prior to the highest levels of exploitation (Crespo and Pedraza 1991).

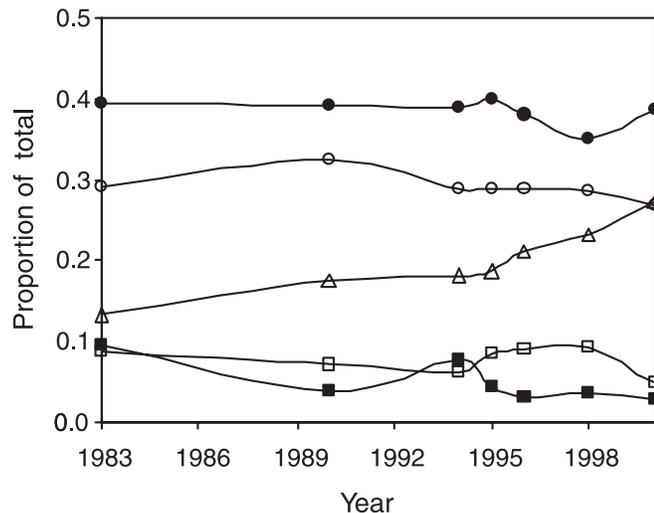
This work also contributes to the knowledge of possible values of annual rates of increase for an otariid population after it was dramatically reduced by exploitation. The abundance levels that this South American sea lion population reached were very low considering that it was reduced to less than 10% of the original size. The observed rate could therefore be interpreted as being very close to its maximum rate. This population is increasing at a relatively high rate and this result agrees with the suggestion that the reduction in population rate of increase at low densities in otariid populations may not be strong (Gerber and Hilborn 2001). However, this population would have low rates of increase when compared with other otariids, such as northern fur seal

Table 3. South American sea lion counts in 19 colonies in northern Patagonia in 2000, 2001, and 2002.

Rookery	Date of census	Year of census	Adult males	Subadult males	Females	Juveniles	Pups	Total
1. Bermeja	5 Feb.	2000	23	35	378	1920	480	2 836
2. Belén	25 Jan.	2002	47	2	39	761	160	1 009
3. Caleta de los loros	24 Jan.	2002	3	12	42	457	16	530
4. Islote Lobos	30 Jan.	2002	32	3	121	315	693	1 164
5. Elizalde	30 Jan.	2002	1	2	1	52	8	64
6. Barrancas Blancas	29 Jan.	2002	39	45	124	268	509	985
7. Quiroga	23 Jan.	2002	65	12	291	226	462	1 029
8. Larralde	7 Feb.	2001	1	4	0	185	41	231
9. Buenos Aires	29 Jan.	2001	175	59	953	84	1 778	3 049
10. La Armonía	29 Jan.	2001	61	2	288	14	510	875
11. Norte	30 Jan.	2001	305	158	1389	391	1 975	4 218
12. Hércules	30 Jan.	2001	0	40	0	82	0	122
13. Delgada	30 Jan.	2001	11	45	0	975	0	1 031
14. La Pastosa	2 Feb.	2001	4	33	0	810	2	849
15. Morro Nuevo	1 Feb.	2001	92	21	611	130	895	1 546
16. Pirámide	31 Jan.	2001	107	11	392	15	824	1 349
17. Las Charas	31 Jan.	2001	6	0	0	274	45	325
18. Loma	28 Jan.	2002	10	1	0	597	52	488
19. León	29 Jan.	2001	342	111	1058	131	1 570	3 212
Total			1324	596	5687	7687	10 020	24 912

Note: Counts for the different age-classes and total number in each colony are given.

Fig. 2. Proportion of South American sea lion individuals in each of the five age-classes considered in this study. The proportions were calculated on the total number of animals present in eight selected sites in seven different years. Open squares, adult males; solid squares, subadult males; triangles, juveniles; open circles, females; solid circles, pups.



(*Callorhinus ursinus*), and even more so when compared with species of the genus *Archtocephalus* (Wade 1998). Antarctic fur seal (*Archtocephalus gazella*) pup counts on South Georgia showed a rate of increase of 16.8% between 1958 and 1972 (Payne 1977).

It is expected that the observed recovery is due to responses in demographic aspects such as survival and reproduction, without immigration from other sites, since all possible sources were also reduced and still recovering

Table 4. Trend in the South American sea lion population in northern Patagonia by age- and sex-class.

Age-class	Change (%)	95% CI	p
Pups	3.9	0.028; 0.05	<0.0001
Nonpups	4.6	0.029; 0.063	0.001
Females	3.8	0.020; 0.055	0.001
Juveniles	8.0	0.051; 0.113	<0.0001
Adult males	3.1	-0.180; 0.080	0.165
Subadult males	-1.9	-0.074; 0.035	0.404

Note: The figures used for this analysis represent the total number of individuals counted in eight selected rookeries and haul-out sites surveyed at the same time between 1983 and 2000 ($n = 7$). Counts were log-transformed. CI, confidence interval.

(Reyes et al. 1999). Possible changes in the structure of this population was also explored as one of the expected consequences of changes in survival and reproduction. The numbers of pups and nonpups are increasing at the same rate. However, among nonpups, juveniles showed the highest rate of annual change, suggesting that their proportion in the population is increasing.

The other noticeable result shown in this paper is that although most colonies presented positive trends, there was a great variability in the rate of change among them, at least in the number of pups in different rookeries. The trend in the number of pups in the major breeding areas during the period 1970–2000 was significantly positive but lower than that estimated for all of the rookeries during 1983–2000 (2.9% and 5.7%, respectively). More important is the fact that the highest rates of increase were seen at those sites that turned into rookeries during the period of the study or the ones that do not represent an important contribution to the total number of sea lions in this population. These higher

Fig. 3. Relationship of the number of South American sea lion pups per adult male and the year of the census. Each datum represents the mean number among all of the rookeries from censuses after 20 January and before 31 January, and the broken line represents the mean number across the years.

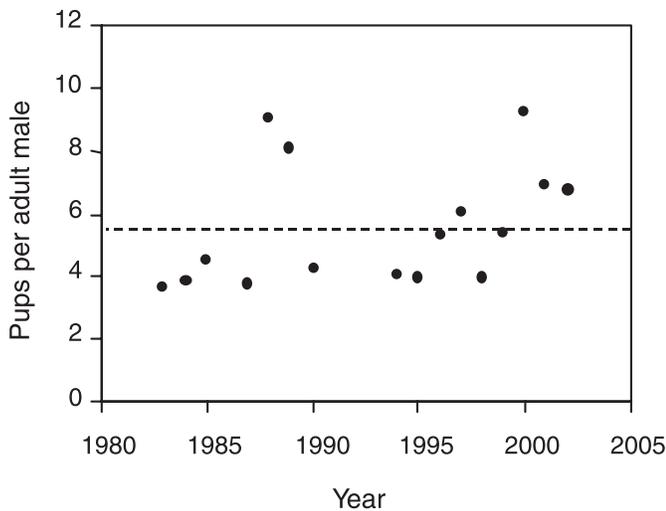
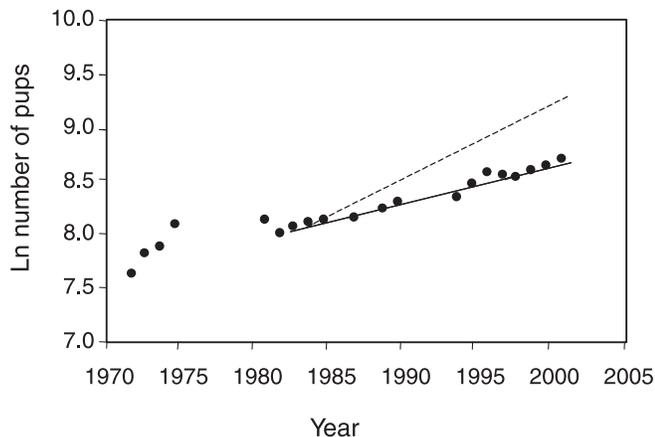


Fig. 4. Counts of South American sea lion pups in the four main rookeries between 1972 and 2000. The trend in these rookeries was estimated to be 3.4% increase per year for 1980–2000 (solid line), while the trend would be estimated to be 5.7% taking into account other rookeries and sites with newly developed breeding areas (broken line).



rates in marginal areas might be partially explained by their small size. However, along with this higher rate of increase, important changes in sea lion distribution were also observed, including the expansion of the original area occupied by a colony, a relocation of the whole colony, and changes in age-class composition. Therefore, aside from any potential bias and comparing with the main rookeries, it is clear that something different is occurring in these marginal areas.

Several factors may lead to recovery of pinniped populations. Demographic aspects with behavioral aspects such as pupping and the utilization of hauling sites for breeding can be interacting and affecting the potential of the population for recovering. The Steller sea lion (*Eumetopias jubatus*) in the north Pacific Ocean is perhaps the species that attracted more attention. York (1994) suggested that the survival of

juveniles was the main factor affecting the population growth. Their stocks, as well as the sites within each one, showed different trends in abundance. While the western stock is still showing the most severe decline, the eastern stock has shown decreasing as well as increasing areas (York et al. 1996; Calkins et al. 1999). The relationship among the location of the breeding site and the foraging area was explored as a possible explanation of these differences. However, York et al. (1996) found that consistent groupings of rookeries with similar trends ranged from couplets of adjacent rookeries (within 37 km of each other) to groupings of five or more sites spread over several hundred kilometres. More recently, studies of dispersal and philopatry suggested that the dispersal of females to new rookeries, while the parent rookery remained stable in size, may have been a density-related response (Raum-Suryam et al. 2002). Aside from the differences in life history between otariids and phocids, a similar density-related pattern was also suggested for the increasing population of grey seals (*Halichoerus grypus*) in the United Kingdom, which showed old stable colonies as well as new colonies becoming established (Pomeroy et al. 2000a). One of the new colonies increased the area occupied instead of increasing the density in the existing breeding area (Pomeroy et al. 2000b). Gerrodette and Gilmartin (1990) suggested a process like this, although at a smaller scale, for Hawaiian monk seals (*Monachus schauinslandi*), remarking the importance of undisturbed beaches by humans.

The results in the present study suggest that the occupancy of new areas for hauling out as well as for breeding may represent the key to the recovery of South American sea lion population. The most important features in this process would be higher survival rates of juveniles combined with available habitat for individuals entering to reproduce and then establishing in new rookeries. This hypothesis could explain the higher rates of increase in the number of pups in the peripheral breeding groups and that the relationships such as pups per adult male remain unchanged. If this hypothesis is supported, the population would not be increasing without available and suitable new sites.

Such spatial and demographic changes when analyzed through time indicate that we are observing a dynamic process driven initially by juvenile animals occupying a new site. The continuing growth of the central breeding areas eventually leads to segregation of adults and pups in one area and juveniles in another. This expansion is promoted by density-dependent factors that limit the number of sea lions reproducing in the well established breeding areas and lead to the fission of the colony. Note that there is a subjective perception that males and females in these new formed breeding areas are smaller in size than those occupying territories in the traditional and old breeding areas. It is not possible to test this hypothesis with the present data but it represents an interesting point to explore in future studies.

As pups and nonpups showed similar trends, the annual rate of change in pups was used as an indirect measure of the population trend. On one side, pup counts may lead to more accurate estimates, since they are more constrained to the breeding site, and then the probability of being counted is high and not affected by environmental factors. However, pups are more susceptible to mortality catastrophic events, leading to years with lower pup production; this will give

Table 5. Trends in the number of South American sea lion pups in each rookery (t) and population trend (t_{b-A}) and its variance (vt_{b-A}) adjusted by the precision of trend estimate and the contribution of each rookery to the total number of pups.

Rookery	t (%)	vt	wt _b	t_b	vt _b	Mean wt _A
1. Bermeja	13.114	5.0697	0.04264	13.0967	4.8536	0.0354
7. Quiroga	8.827	1.4359	0.01245	8.8749	1.4178	0.0436
9. Buenos Aires	4.262	0.6392	0.00558	4.3090	0.6356	0.2282
10. La Armonía	14.046	5.3089	0.04456	13.9858	5.0723	0.0267
11. Norte	3.998	0.3674	0.00322	4.0259	0.3662	0.2343
13. Delgada	23.344	10.2490	0.08260	22.4657	9.4024	0.0022
15. Morro Nuevo	37.621	32.5790	0.02225	32.0774	25.3298	0.0309
16. Pirámide	2.538	0.4090	0.00358	2.5748	0.4075	0.1335
18. Loma	15.108	4.6083	0.03891	15.0144	4.4290	0.0040
19. León	4.210	0.3375	0.00296	4.2346	0.3365	0.2612
t_{b-A}	5.7018					
vt_{b-A}	1.5636					

negative or no significant trend in the number of pups after some suboptimal years but not necessarily a negative trend in the population. Another factor that can bias the population trend estimate based on the rate of change of pups is the fact that density-dependent mechanisms may act before or after the time of the census, giving under- or overestimated rates of change (Berkson and DeMaster 1985). In this particular population, we do not expect that density-dependent mortality of pups may produce strong bias in the trend estimate.

Also, pups are a measure of the productivity of the population, and they provide a better index of population trend than do counts of nonpups (Trites and Larkin 1996). However, pups represent production, and they only add to the population if they survive. Then, if there are more pups being born, either female fecundity has gone up or pup to juvenile survival has been good previously, adding to the total number of females alive.

Most of the breeding sites showed higher rates of change in the number of pups than in the number of nonpups, while most of the haul-outs did not show significant trends. The existence of higher rates of increase in the number of pups in some rookeries, such as León and Morro Nuevo, seem to be associated with the sudden consolidation of new breeding areas in the periphery of the original colony. In addition, the relocation of juveniles to new sites away from the original one was observed. The pups born in the haul-outs that turned into rookeries still represent a low percentage of the total number of animals present in those sites. Also, as most of them are juveniles and nonbreeding individuals, there is a large fluctuation in the number present in the site at the moment of the census. Such variability precludes reliable estimates of the trend in the number of nonpups and the comparison with the trend in pups. In spite of this, it seems that the number of pups is increasing and the number of nonpups in each rookery or haul-out is also increasing.

In addition to possible explanations for the population increase in South American sea lions, this paper also provides implications for management purposes. Península Valdés is a protected area where the land belongs to private owners. The largest and traditional rookeries are protected by gamekeepers. On the other hand, most of the smaller and newly developed breeding sites with a higher rate of increase lack any

protective measures, being subject to perturbations by local people, tourism, or illegal activities.

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References

Berkson, J.M., and DeMaster, D.P. 1985. Use of counts in indexing population changes in pinnipeds. *Can. J. Fish. Aquat. Sci.* **42**: 873–879.

Calkins, D.G., McAllister, D.C., Pitcher, K.W., and Pendleton, G.W. 1999. Steller sea lion status and trend in Southeast Alaska: 1979–1997. *Mar. Mamm. Sci.* **15**: 462–477.

Carrara, I.S. 1952. Lobos Marinos, pingüinos y guaneras de las costas del litoral marítimo e Islas adyacentes de la República Argentina. Tech. Rep. Facultad de Ciencias Veterinarias, Universidad Nacional de La Plata, La Plata, Argentina.

Castello, H., Crespo, E.A., Erize, F., Costa, M.G., Chebez, J.C., and Dunn, M. 1982. Estudio de la preservación y manejo de los recursos faunísticos de la costa Atlántica de la provincia de Río Negro con fines turísticos. Expediente Consejo Federal de Inversiones Nro. 10204. Convenio Consejo Federal de Inversiones Fundación Vida Silvestre, Argentina.

Caughley, G. 1977. Analysis of vertebrates populations. John Wiley & Sons Inc., New York.

Crespo, E.A. 1988. Dinámica poblacional del lobo marino del sur *Otaria flavescens* (Shaw, 1800), en el norte del litoral patagónico.

- Ph.D. thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina.
- Crespo, E.A., and Pedraza, S.N. 1991. Estado actual y tendencia de la población de lobos marinos de un pelo (*Otaria flavescens*) en el litoral norpatagónico. *Ecol. Austral*, **1**: 87–95.
- Crespo, E.A., Pedraza, S.N., Dans, S.L., Koen Alonso, M., Reyes, L.M., García, N.A., Coscarella, M., and Schiavini, A.C.M. 1997. Direct and indirect effects of the highseas fisheries on the marine mammal populations in the northern and central Patagonian coast. *J. Northwest Atl. Fish. Sci.* **22**: 189–207.
- Dans, S.L., Crespo, E.A., Pedraza, S.N., González, R., and García, N. 1996. Estructura y tendencia de los apostaderos de lobos marinos de un pelo (*Otaria flavescens*) en el norte de Patagonia. Informes Técnicos del Plan de Manejo Integrado de la Zona Costera Patagónica (Puerto Madryn, Argentina) No. 13.
- Frost, K.J., Lowry, L.F., and Ver Hoef, J.M. 1999. Monitoring the trend of harbor seal in Prince William Sound, Alaska, after the *Exxon Valdez* oil spill. *Mar. Mamm. Sci.* **15**: 494–506.
- Gerber, L.R., and Hilborn, R. 2001. Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. *Mammal Rev.* **31**: 131–150.
- Gerrodette, T., and Gilmartin, W. 1990. Demographic consequences of changed pupping and hauling sites of the Hawaiian monk seal. *Conserv. Biol.* **4**: 423–430.
- Godoy, J.C. 1963. Fauna Silvestre. Consejo Federal de Inversiones. Serie Evaluación de los Recursos Naturales de la Argentina (Buenos Aires), **8**(1): 1–299.
- Hastings, K.K., and Sydeman, W.J. 2002. Population status, seasonal variation in abundance, and long term population trends of Steller sea lions (*Eumetopias jubatus*) at the South Farallon Islands, California. *Fish. Bull.* **100**: 51–62.
- Koen Alonso, M., Crespo, E.A., Pedraza, S.N., Garcia, N.A., and Coscarella, M. 2000. Feeding habits of the southern sea lion *Otaria flavescens* of Patagonia. *Fish. Bull.* **97**: 250–263.
- Lewis, M.N., and Ximénez, I. 1983. Dinámica de la población de *Otaria flavescens* (Shaw) en el área de Península Valdés y zonas adyacentes (Segunda parte). Contrib. No. 79. Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina.
- Link, W.A., and Sauer, J.R. 1997. Estimation of population trajectories from count data. *Biometrics*, **53**: 488–497.
- Payne, M.R. 1977. Growth of a fur seal population. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **279**: 67–79.
- Pomeroy, P.P., Twiss, S.D., and Redman, P. 2000a. Philopatry, site fidelity and local kin associations within grey seal breeding colonies. *Ethology*, **106**: 899–919.
- Pomeroy, P.P., Twiss, S.D., and Duck, C.D. 2000b. Expansion of a grey seal (*Halichoerus grypus*) breeding colony: changes in pupping site use at the Isle of May, Scotland. *J. Zool. (Lond.)*, **250**: 1–12.
- Raum-Suryan, K., Pitcher, K., Calkins, D., Sease, J., and Loughlin, T. 2002. Dispersal, rookery fidelity, and metapopulation structure of Steller sea lions (*Eumetopias jubatus*) in an increasing and a decreasing population in Alaska. *Mar. Mamm. Sci.* **18**: 746–764.
- Reyes, L., Crespo, E., and Szapkievich, V. 1999. Distribution and population size of the southern sea lion (*Otaria flavescens*) in central and southern Chubut, Patagonia, Argentina. *Mar. Mamm. Sci.* **15**: 478–493.
- Schiavini, A.C.M., Crespo, E.A., and Szapkievich, V.B. 1999. Status de los apostaderos del lobo marino de un pelo (*Otaria flavescens*) en las Provincias de Santa Cruz y Tierra del Fuego. Informes Técnicos del Plan de Manejo Integrado de la Zona Costera Patagónica GEF/PNUD/WCS/FPN (Puerto Madryn, Argentina) No. 40.
- Sokal, R.R., and Rolf, F.J. 1995. *Biometry*. 3rd ed. W.H. Freeman and Co., New York.
- Trites, A.W., and Larkin, P.A. 1996. Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: how many were there? *Aquat. Mamm.* **22**: 153–166.
- Wade, P. 1998. Calculating limits to the allowable human-caused mortality of cetacean and pinnipeds. *Mar. Mamm. Sci.* **14**: 1–37.
- Ximénez, I. 1976. Dinámica de la población de *Otaria flavescens* (Shaw) en el área de Península Valdés y zonas adyacentes (Provincia del Chubut, R.A.). Informe Técnico 1.4.1. Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina.
- York, A. 1994. The population dynamics of northern sea lions, 1975–1985. *Mar. Mamm. Sci.* **10**: 38–51.
- York, A., Merrick, R.L., and Loughlin, T.R. 1996. An analysis of the Steller sea lion metapopulation in Alaska. In *Metapopulation and wildlife conservation*. Edited by D.R. McCullough. Island Press, Washington, D.C. pp. 259–292.
- Zar, J.H. 1996. *Biostatistical analysis*. 3rd ed. Prentice-Hall, Inc., Upper Saddle River, N.J.