A hunted population in recovery: Effective population size for South American sea lions from Patagonia

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Abstract

Effective population size (N_e) is a parameter of central importance in evolutionary biology and conservation. Factors such as unequal sex ratios of breeding individuals, periodic fluctuation in population size and variance in reproductive success can affect the N_e in general. At present, South American sea lions, *Otaria flavescens*, from northern Patagonia, Argentina, belongs to one of the several populations that are recovering from overhunting which occurred in the early 20th century. Here, we present the estimate of N_e for this population that takes into account the effects of their polygynous mating system and variation in population size through time. The resultant overall N_e's were 4171 ± 2450 or 4745 ± 2681 breeding animals depending on the inclusion of peripheral adult males. The estimated N_e's are not critical, because they are close to the average mean minimum viable population for vertebrates (5000 breeding adults). Even though the northern Patagonian population of *O. flavescens* is increasing its abundance is still far below its historical numbers. The N_e estimated should be considered the minimum range to be maintained, especially in light of bycatch related to fishery interactions along the Patagonian coast. We emphasise the importance of estimating N_e for future management plans of the species within different populations.

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Introduction

In practice, wildlife managers and policy-makers typically take rapid decisions with scarce information about the conservation status of a species. The population size or similar estimates are usually the best available information because it is relatively ease to acquire (Reed et al., 2003). For conservation purposes species should be treated as dynamic entities capable of evolving to cope with environmental change, so it is important that the species' evolutionary potential be retained in order to respond to environmental stochasticity (Frankham et al., 2002). The effective population size (N_e) reflects the number of individuals responsible for the maintenance of the genetic diversity of the species as well as its evolutionary potential, so it can be used as a way to determine the conservation status of a species or population.

The effective population size in the genetic sense, is the size of an ideal population that losses genetic diversity at the same rate as the real population under study. An ideal population is a conceptually closed, random-mating population that has a Poisson variation in family size, constant numbers of breeding individuals in successive, non-overlapping generations, and no mutation or selection (Wright, 1931). The effective population size, in a demographic sense, is the size of a population with equal sex ratio, stable age distribution and the same intrinsic rate of increase over the years (Sinclair et al., 2006).

Furthermore, N_e directly influences population viability because the strength of stochastic changes in genetic properties is increased in populations with smaller effective sizes (Hedrick, 2000; Frankham et al., 2002). When there is a variation in population size over time, the lowest population numbers largely determine the overall N_e because after an extreme reduction, all remaining individuals are descendants of the bottleneck survivors (Hedrick, 2000).

The N_e can be calculated from genetic data (genetic diversity in a population and a known mutation rate), or from data of sex composition of breeders (number of breeding animals within a population) (Allendorf and Luikart, 2007). Deviations from the ideal population may result in a reduction in N_e. The most important factors that affect this ideal situation are: unequal sex ratio of breeding individuals related to different mating systems (e.g., polygynous versus polyandrous), periodic fluctuation in population size, variation in family size, and high variance in reproductive success (Frankham, 1995; Hedrick, 2000; Ficetola et al., 2010).

The South American sea lion *Otaria flavescens* is a polygynic pinniped species where males defend territories and females (Vaz-Ferreira, 1981). Due to the differences in the number of breeding males and females, the effective population size is smaller than the actual population size (Crow and Kimura, 1970). At present times, the global population of this species is estimated to be roughly 400 000 animals,

but abundance and trend of populations are extremely dissimilar within their range (Crespo et al., 2010). Populations from Uruguay and austral Chile are decreasing (Venegas, 2001; Páez, 2006), while those from central and southern Chile are stable (Oliva et al., 2008; Sepúlveda et al., 2011). Populations from Malvinas (Falkland) Islands, Peru and northern Chile are slowly recovering (Thompson et al., 2005; Bartheld et al., 2008; Oliveira and Majluf, 2009), and the ones from Patagonia (Argentina) have been recovering since 1990 and recolonizing areas at different growth rates (Crespo and Pedraza, 1991; Reyes et al., 1999; Dans et al., 2004; Schiavini et al., 2004; Grandi et al., 2008). All the published information above represents census size populations and the only effective population size available is for the Peruvian sea lions (Oliveira, 2011).

Although the IUCN Red List status for this species is 'Least concern' (Campagna, 2008), South American sea lion populations not only have different abundances and trends but also face different conservation problems related to the development of marine human activities: fisheries, mining industry, offshore oil and gas development, and tourism. The most studied and well documented conservation problem is the effect of direct and indirect interactions with fishery activities (Aguayo and Maturana, 1973; George-Nascimiento et al., 1985; Arias-Schreiber, 1993, 1996; Crespo et al., 1994, 1997; Ott et al., 1996; Sielfeld et al., 1997; Szteren and Páez, 2002; Dans et al., 2003; Sepúlveda and Oliva, 2005; Sepúlveda et al., 2007; Goetz et al., 2008; Oliveira et al., 2008; Drago et al., 2009, 2010; Machado et al., 2010a, b; Vilata et al., 2010). As a result many sea lions are incidentally captured or sometimes intentionally killed in fisheries and fish farming operations throughout their range (see Crespo et al., 2010 for a review). In the last two decades fishermen from Chile and Peru were calling on the authorities to implement culling as an immediate solution (Sepúlveda et al., 2007; Crespo, 2009). The possibility of culling makes it necessary to have solid scientific information about the status of each population to evaluate the effects of this measure on the persistence of the species.

For the majority of South American sea lion populations the available data are related to censuses carried out to estimate population size and trends over time. The population from northern Patagonia (Argentina) is an exception. It has been monitored almost continuously since 1972 resulting in a data set that comprises 40 years of past census data and changes in social composition (Dans et al., 2004; Grandi et al., 2008). In addition, historical information showed that this population was heavily exploited, resulting in a population decline from 137 500 individuals estimated in 1938 (Godoy, 1963) to 18 396 in 1946 (Carrara, 1952). It was estimated that the population passed through its lowest numbers $\sim$ 5000 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 population is recovering and at present is growing at an annual rate of increase of 5.8% (Dans et al., 2004; Grandi, 2010).

In this context, the availability of long-term detailed demographic information as well as the recovery process of this species in Argentina provides a unique op-

portunity to analyse and interpret the effects of different factors on the N_e estimate. Therefore the aim of this study is to present an estimate of N_e for the northern Patagonia *O. flavescens* population taking into account the effects of a polygynous mating system of the species and the variation in population size through time. Finally, we comment on the consequences of this N_e for the management and conservation of the northern Patagonia population as well as the other South American populations of these sea lions.

Materials and methods

Population data

We used data from detailed population surveys conducted between 1982 and 2009 (Castello et al., 1982; Lewis and Ximénez, 1983; Crespo, 1988; Dans et al., 1996, 2004; Grandi et al., 2008) which covered 33 colonies from Punta Bermeja (41°09′S, 63°09′W) to Punta León (43°04′S, 64°28′W), and included the most important breeding sites in northern Patagonia, Argentina (fig. 1).

Total counts were made separately by age class and sex: adult males (territorial and peripheral), sub-adult males, females, juveniles (both sexes pooled together), and pups (born during the season of the census). These categories were based on body shape and colour, location in the rookery, and behavioural cues (Crespo, 1988; Crespo and Pedraza, 1991). At least two counts were made, and those counts that
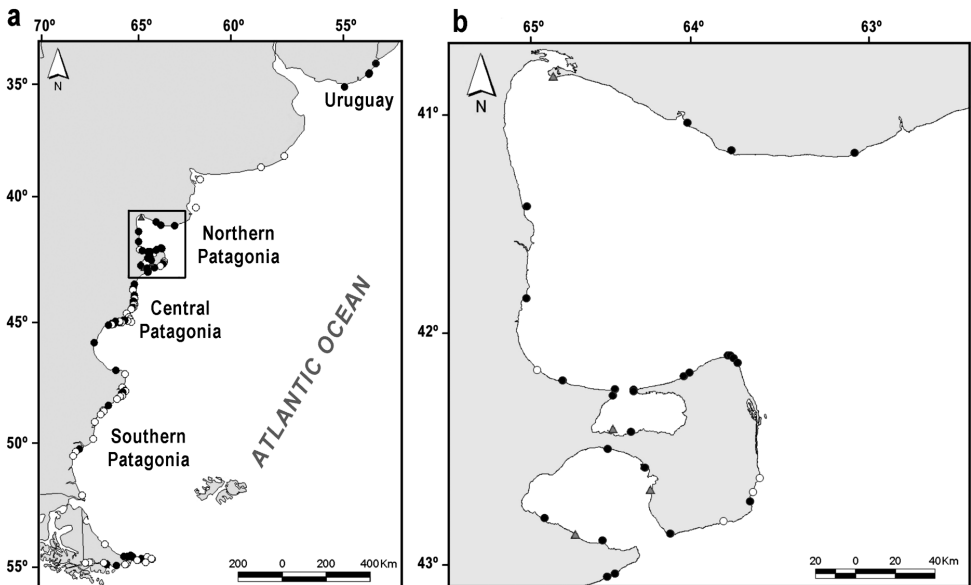

Figure 1. (a) Current distribution of *Otaria flavescens* colonies along the coast of Uruguay and Argentina. The square highlights the studied area from Punta Bermeja to Punta León, northern Patagonia. (b) Detailed studied area at northern Patagonia. ●: breeding colonies, ○: non-breeding colonies, ▲: occasional non-breeding colonies.

differed by less than 10% were averaging to estimate the final value for each category.

Censuses were carried out from an elevated fixed point with binoculars between the last week of January and first week of February, coinciding with the peak of the breeding season when most of the individuals are present at the rookeries for reproduction, and when most all of the pups were already born (Campagna, 1985; Crespo, 1988). Due to presence of individuals from different age-class categories changes along the breeding season (see Campagna, 1985), we had to standardize counts to consider the maximum number of sea lions by categories present each season. So, using data of percentage of presence in land we standardized the census date correcting each census according to the date of the survey: considering 96% before 24 of January and 76% after that date for males (calculated from mark-resighting studies; see Crespo, 1988), and 85% before 24 of January and 99% after this date for pups (Campagna, 1985).

Analysis of the effects of male behaviour on the N_e estimates

The South American sea lion is a sexually dimorphic and polygynous species that forms breeding colonies during the austral summer where adult males compete aggressively with each other to establish and defend territories and females (Campagna, 1985; Campagna and Le Boeuf, 1988a, b). Most of the breeding males and females reside in a densely aggregated central breeding area (CBA) along the water's edge (Campagna, 1985). Adult and sub-adult peripheral males, are excluded from the CBA, but compete with territorial males trying to obtain mates through two strategies: (1) retaining females that arrive from the sea, and (2) initiating group raids into the breeding area to seize females (Campagna et al., 1988). In the context of a polygynous mating system, the effective population size should be smaller than the actual population size (Crow and Kimura, 1970; Storz et al., 2001; Rourke et al., 2009). We estimated the N_e taking into account the skew in the sex ratio for pinniped species based on Oliveira et al. (2006) and Wright (1931):

$$N_{ei} = (4N_{ef}N_{em})/(N_{ef} + N_{em})$$

where N_{ef} is the number of breeding females and N_{em} is the number of breeding males within the population.

Females periodically leave the rookery to feed during the breeding season, while pups stay at the beach. Pups were considered the best indicator of the number of breeding females (Campagna, 1985). Therefore, for the calculation of N_{ei} we considered the amount of pups to represent the actual number of adult breeding females (N_{ef}) in each rookery (as a more conservative number).

In polygynous mating systems, the variance in male mating success can be expected to have a significant influence on effective population size (Nunney, 1993), making it particularly important to estimate the real number of breeding males. In the sea lion mating system the paternity is expected to be frequently assigned to large and dominant males (Bartholomew, 1970; Trillmich and Trillmich, 1984).

Studies of breeding behaviour of South American sea lions show that mating success is different among: a) territorial males holding females inside the CBA, b) adult males holding a female in the periphery (Campagna and Le Boeuf, 1988a), and c) itinerant adult males that raid into the CBA and seize a female (Campagna et al., 1988). Taking into account this type of mating behaviour we considered two scenarios to calculate N_e.

The first and more conservative one was based on the counting of only adult territorial males (N_{em}), which are males that actually copulate frequently, while peripheral males (without holding a female or territory) and sub-adults males do not mate regularly like them. For this scenario we accepted that the mating success of the territorial males is homogenous.

The second scenario incorporates the fact that mating success of territorial males was affected by group raids (an alternative mating behaviour that affects male tenure; see Campagna et al., 1988). Group raiders were adult and sub-adults males (44-66% respectively; Campagna et al., 1988). It was reported that 39% of peripheral adult males that participate of a raid group were able to hold and successfully copulate with a female becoming new territorial males in the CBA. Then, as new residents they could acquire other females and copulate with them (Campagna et al., 1988). In this context, the second scenario estimates the N_{em} including all the territorial males counted plus 39% of the adult peripheral males. For this scenario we added adult males of both categories considering that territorial males already copulate before being displaced by peripheral males, and accepted that all these males have similar chances to copulate, and as a result, equal probability to produce pups for the next generation.

Analysis of the effects of variation in population size through time

Although the northern Patagonia population has been monitored for 40 years, both logistical and economical issues have limited the census activity during this period. In addition, not all the 33 colonies were included in all the surveys because the number of rookeries increased during the study period. New marginal breeding areas were added to the traditional rookeries as a result of population growth and changes in social structure (Grandi et al., 2008). In this sense, in order to increase the accuracy of the calculations of each N_e we only selected seven particular years of census covering the period 1982-2009, those in which the totality of the colonies in the studied area were surveyed in detail (table 1, fig. 1). These estimates of N_{ei} were then used to estimate an overall effective population size, which accounts for the variation in population size in different generations, given by the harmonic mean of the N_e in each generation (Hedrick, 2000; Oliveira et al., 2006):

$$N_e = t / \left(\sum 1/N_{ei} \right)$$

where N_{ei} is the effective population size in the ith generation and t is the number of generations considered. To take into account the uncertainty in the overall effec-

Table 1.

Census surveys of *Otaria flavescens* from northern Patagonia used for the analysis. ATM: adult territorial males; APM: adult peripheral males; N_{ef}: breeding females; N_{ei}: effective population size per year.

Year	Colonies surveyed	ATM	39% APM	N_{ef}	Scenario 1 N_{ei}	Scenario 2 N_{ei}
1982	16	760	155	3130	2446	2832
1990	16	819	112	4615	2782	3099
1995	20	843	161	5766	2942	3420
2005	29	1833	286	9958	6192	6989
2006	33	1969	378	9382	6510	7509
2007	33	2171	308	12 127	7365	8233
2009	33	2534	284	12 097	8381	9142

tive population size, standard deviation of the N_e estimates across time and a 95% confidence interval (CI; Student's $t_{0.05}$, df $= n - 1$) were calculated (Zar, 1984).

Results

The effective population size (N_e) that takes into account only the effects of a polygynous mating system of the species is detailed in table 1, for each year between 1982 and 2009. The N_{ei} results of the skew in sex ratio ranged from 2446 to 8381 in the first scenario (dark stars in fig. 2). In the second scenario the N_{ei} values ranged from 2832 to 9142 (black spots in fig. 2). Both scenarios indicate an increasing trend of N_e through time (fig. 2).
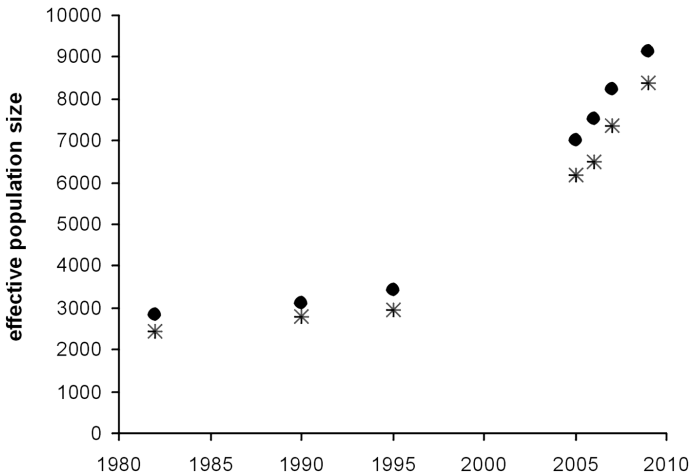

Figure 2. Effective population size (N_e) of South American sea lion, *Otaria flavescens*, of northern Patagonia along the years, taking into account only the effects of a polygynous mating system. ∗: scenario 1; ●: scenario 2 (for the details of scenarios see Materials and methods).

The effective population size (N_e) for the first scenario (which assumes that N_{em} comprises only territorial males, not including raiders) was 4171 ± 2450 breeding individuals ($N_e \pm SD$) that accounts for both effects of unequal sex-ratio and fluctuation in population size along generations. The 95% CI around this estimate fell between 1904 and 6437 individuals.

In the second scenario, which includes 39% of the peripheral males in the N_{em} estimates (besides the regular territorial males) and takes into account the same effects mentioned above, the N_e value was 4745 ± 2681 animals ($N_e \pm SD$). The 95% CI around this estimate fell between 2265 and 7225 individuals.

Discussion

The N_e estimated for the northern Patagonia population of sea lions, which accounts for both effects of mating system and variation in population size through time, ranged from 4171 to 4745 breeding adults, depending on the breeding scenario analysed. Some factors that may influence these estimates of N_e are: variation in reproductive success, the number of population surveys used to incorporate the effect of fluctuation in population size, and the violation of the ideal closed population.

The first factor is the variation in reproductive success among territorial males, and the assumption that peripheral males succeed equally in having descendants. Paternity success by alternative mating systems has been observed for some pinnipeds (e.g., *Mirounga leonina*, Hoelzel et al., 1999; Fabiani et al., 2004; de Bruyn et al., 2011; *Halichoerus grypus*, Worthington Wilmer et al., 1999; Lidgard et al., 2004; *Zalophus wollebaeki*, Pörschmann et al., 2010; *Arctocephalus gazella*, Gemmell et al., 2001; *Callorhinus ursinus*, Kiyota et al., 2008; and *A. forsteri*, Caudron et al., 2009). This suggests that alternative mating strategies play an important role in mating success within polygynous pinniped species including the role assigned to peripheral males in paternity. Unfortunately, there is no information about paternity success for *Otaria flavescens* in any population. Therefore, as it is expected, if individual variance in reproductive success exists, its effect would reduce the estimate of N_e to a smaller value than the one we obtained in this work.

A second factor that may influence these estimates of N_e is the number of population surveys. Estimates based on only a few census counts tend to underestimate the influence of temporal fluctuation in population size (Vucetich and Waite, 1998). In spite of this, wildlife researchers know that it is difficult to find and maintain long term data sets of wild populations, especially in developing countries (Traill et al., 2010). In this sense the long term data set of the northern Patagonia sea lion population remains valuable. Using only seven years of census data could lead to an overestimate N_e, but including more years of data would result in a smaller N_e, because the long-term effective population size decreases as a population is surveyed for longer periods of time (Vucetich et al., 1997; Vucetich and Waite, 1998).

The third factor that can affect the effective population estimates is that the sea lions from northern Patagonia are not part of a closed population. Genetic analysis

suggests that South American sea lions have a strong female philopatry to breeding areas and gene flow is mediated by male dispersion along the Atlantic coast (Feijoo et al., 2011). Breeding colonies analysed in this study had no significant genetic differences from central Patagonia rookeries (Túnez et al., 2010; Feijoo et al., 2011). This fact leads our estimated N_e to be underestimated. Population trends in northern and central Patagonia areas are very similar (Reyes, 2004; Grandi, 2010). The observed trend of N_e in northern Patagonia likely reflects *in situ* recruitment more than southerly immigration. Therefore, the calculation of N_e with genetic data and its comparison with the results presented here represents the next step to explore in future studies.

Taking into account the factors mentioned above, the resultant N_e for the northern Patagonia sea lion population could be biased upwards. Based on these results we considered both values (4171 to 4745 breeding adults), the former as a minimum and conservative estimate and the latter as a maximum value of N_e. We believe the larger value is probably more realistic given that some of the next-generation pups will be offspring from raiders.

The historical records reveal that the sea lions were heavily exploited along the northern Patagonia until the 1960s (Godoy, 1963). The northern Patagonia sea lion population may have been as small as 5000 animals (Koen Alonso and Yodzis, 2005; Grandi, 2010). However, microsatellite analysis showed no genetic bottleneck due to the severe reduction in population size (Feijoo et al., 2011). This result could be related to the rapid re-distribution of genetic variability among colonies due to gene flow possibly mediated by males as well the overlap of generations (Feijoo et al., 2011). Another potential explanation for the high genetic variability after the hunting period is the apparent large size of the original population of sea lions from northern Patagonia. Grandi (2010) estimated that the increasing northern Patagonia population of sea lions is around 46.4% of the original estimated population abundance (prior to the commercial exploitation). The two estimated N_e presented here represent 11.8 and 13.4% of the 35 344 animals counted in 2009 for northern Patagonia population (Grandi, 2010). Our estimates of N_e are substantially lower than the census size population, which is in agreement with the theory for N_e vertebrates that generally represents 10% of the census size population (Frankham, 1995; Vucetich et al., 1997).

The calculated N_e for the northern Patagonia population of sea lions is large when compared with values for other pinniped species (i.e., *Arctocephalus australis* $N_e = 2153$, Oliveira et al., 2006; *Phoca hispida saimensis* $N_e = 250$, Kokko et al., 1998; *Halichoerus grypus* $N_e = 2344$ and *Eumetopias jubatus* $N_e = 450$, Reed et al., 2003). However, if we compare the northern Patagonia sea lion N_e with the estimate for the same species in Peru (7715 breeding individuals; Oliveira, 2011), we observed that even though the population is recovering, the number of individuals responsible for the maintenance of the genetic diversity is small. For conservation biology purposes N_e can be applied as an estimation of the minimum viable population size (MVP). The MVP can be defined as the smallest size required for a

population or species to have a predetermined probability of persistence for a period of time (Shaffer, 1981). According to Traill et al. (2010), the MVP should be at least 5000 adult individuals. A number of studies across taxonomic groups have made similar findings: the median MVP for 102 vertebrate species was 5816 individuals (Reed et al., 2003), 4169 individuals from a meta-analysis of 212 species (Traill et al., 2007), and other theoretical work suggests a minimal between 1000-5000 animals (Lande, 1995; Lynch, 1996).

In this context, the estimated N_e for the northern Patagonia population are not critical values, because they are both close to the 5000 number. Nevertheless, it is also important to mention that taking into account the lower bound of the CIs for both N_e scenarios, the minimum estimated values reduce significantly, ranging from 1904 to 2265 (in the worst case scenario). In this case the N_e estimated appears to be critical, because it is less than half of the recommended MVP (Reed et al., 2003; Traill et al., 2010). However, if we consider the upper bound of the CIs, maximum N_e ranges from 6437 to 7225 breeding animals, which is roughly 1500-2000 individuals higher than the MVP. Taking everything into account, the estimated N_e for the northern Patagonia population should be considered values to be maintained in order to keep the population large enough to avoid losing genetic variability, because they are lower than the average MVP and close to the estimated carrying capacity or number of adults for vertebrates necessary for a robust viability for ten generations into the future (Reed et al., 2003; Traill et al., 2007, 2010).

The estimated N_e close to 5000 breeding animals, in a recovered population are reasons of concern, not only for the maintenance of the northern Patagonia population, but for the persistence of other populations. This population shows one of the highest growth rates for the species, but despite of its recovery the actual abundance is far from the historical numbers at the beginning of the 20th century (Crespo and Pedraza, 1991; Grandi, 2010). This highlight the necessity of regular evaluation on the remaining populations with lower growth rates along the Atlantic and Pacific coasts, especially the ones from Uruguay and austral Chile which are declining (Venegas, 2001; Páez, 2006).

Moreover, the South American sea lion is the only pinniped species in South America with conservation problems related to fishery interactions, including records of incidental captures (Ott et al., 1996; Reyes, 2000; Hückstädt and Antezana, 2003; Oliva et al., 2003; Crespo et al., 2007, 2009; Sepúlveda et al., 2007), indirect effects of fisheries (Crespo et al., 1997) and changes in the marine ecosystem due to overfishing (Koen Alonso and Yodzis, 2005; Drago et al., 2010). The general perception of fishermen is that elimination of sea lions is the solution for the economical damages in nets and catches, that is why they are illegally shot in various locations (Oliva et al., 2003; Sepúlveda et al., 2008; Pavés et al., 2009; Crespo et al., 2010; Machado, 2010). Chilean management policy, in particular, considers sea lions as part of the national fishery resources, and regulates its populations authorizing annual capture quotas (Sepúlveda et al., 2007), but there is

currently a moratorium on killing these sea lions. However, there is an increasing pressure to re-establish quotas, due to economic damages claimed by fish farming industry and other types of fisheries that crashed in the last years (Oliva et al., 2003, 2008; Sepúlveda et al., 2007) due to overexploitation or *El Niño* effects. In addition, multispecies modelling scenarios discussed culling of sea lions as a management strategy to help the recovery of hake (*Merluccius hubbsi*) stocks depleted by the fishery in the Patagonian ecosystem (Koen Alonso and Yodzis, 2005). Hake is the primary prey of South American sea lions males (Koen Alonso et al., 2000). Fortunately, this option has never been seriously considered in Argentina, where sea lions are protected since 1974 by federal law and they also constitute one of the core attractions for tourism, which is a growing industry in Patagonia (Tagliorete and Losano, 1996).

Based on the knowledge gained here we recommend for any future effective monitoring program, to continue systematic surveys for all populations of South American sea lions, mainly concentrating detailed censuses counting all age and sex classes. This will provide new estimates of effective population size for different regions that allow comparisons and updates of population trends. Since culling rarely provide an effective management action (Lavigne, 2003) this could also be an incorrect and risky decision for the conservation of some South American sea lion populations, where low growth rates were reported (Venegas, 2001; Páez, 2006; Oliva et al., 2008; Sepúlveda et al., 2011). This situation could potentially reduce the genetic variability and compromise their persistence in some areas. Indeed, South American sea lion populations are connected by male migration and consequently do not recognize geopolitical boundaries (Rosas et al., 1994; Gehara, 2009; Giardino et al., 2009; Feijoo et al., 2011) and in this sense they can not be managed exclusively with national conservation efforts. Thus, this species depends on international as well as integrated strategies along its historical distribution.

Finally, the estimate of N_e of 4171-4745 breeding adults obtained in this study should be taken into account in any future management plan to ensure the conservation and protection of the species along the coasts of South America. Furthermore, it is important to place this result into the context of an evolutionary paradigm and not a demographic one both proposed by Waples and Gaggiotti (2006). Because even though the northern Patagonia population abundance shows a continuous growth, the resultant numbers of individuals responsible for the maintenance of the genetic diversity as well as the evolutionary potential of the population are less. In the context of conservation and population viability, we emphasise the importance of the N_e for any vulnerable species of mammals or its recovery plan, because positive growth rate of a wildlife population is not enough to guarantee an increase of genetic variability and/or its long-term population persistence especially under fast changing environmental conditions.

Acknowledgements

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