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Vulnerability of South American Pinnipeds Under El Niño Southern Oscillation Events

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1. Introduction

The fur seal and sea lions, as well as other marine vertebrates along the Peruvian coast, were truly the eyewitness of cyclic events of global changes in the Pacific Ocean during *El Niño* Southern Oscillation (ENSO) events. In November 1997, the Punta San Juan Reserve (15°22'S, 75°12'W) concentrated with the National Reserve of *Paracas* (13°54'S) and Punta San Bernardo (15°09'S), over 90% of the Peruvian fur seal and sea lion populations (Majluf & Trillmich, 1981). The ENSO event developed unexpectedly and rapidly early in February of that year and became more intense than anticipated, with sea surface temperatures reaching up to 9°C in some locations along the Peruvian coast (Glantz, 2001). The 1997-98 ENSO was considered the “El Niño of the twentieth century”, challenging the 1982-83 event in terms of intensity, marine mortality and economic loss.

The ENSO is a climatological phenomenon characterized by anomalous conditions in the atmosphere and ocean that are mainly related to warming of the sea surface temperature (SST) from 2°C to 9°C along the coast of Ecuador and Peru (Glantz, 1996). At intervals of two to seven years (Cane, 1983), the Humboldt Current upwelling system, which is the richest in the world (Cushing, 1982; Idyll, 1973), is affected by ENSO, with increased SST and reduced primary productivity which directly influences the depth distribution and abundance of Peruvian anchovy, *Engraulis ringens*, the most important prey of the South American sea lion, *Otaria flavescens*, and South American fur seal, *Arctocephalus australis*, in Peru (Arias-Schreiber, 2003; Idyll, 1973; Majluf, 1992). The South American sea lion and South American fur seal are distributed along the Atlantic and Pacific coasts of South America (from southern Brazil to northern Peru (Capozzo & Perrin, 2008; Rosas et al., 1994; Vaz-Ferreira, 1981, 1982). Nevertheless, the distribution of *O. flavescens* is larger and continuous, while that of *A. australis* has gaps mainly in the central coast of Chile and along the Argentinean coast (Guerra and Torres, 1987; Oliveira et al., 2008; Repenning et al., 1971). In the Peruvian territory these species are distributed among breeding colonies and haul-out areas on both

the continent and islands. *O. flavescens* is the most abundant pinniped species with 118,220 individuals, followed by *A. australis* with 15,317 individuals (Imarpe, 2006). Both have a polygynic breeding system with very few males mating with many females (Capozzo & Perrin, 2008; Majluf 1987). These two species of South American seals were hunted intensively for several centuries, and Uruguay became the last country to prohibit hunting in 1991 (Vaz-Ferreira & Bianco, 1998). Nowadays the most important threat to the conservation of these species are the interactions with fishery activities (mainly in the case of *O. flavescens*), and mortality during ENSO events on the Pacific coast.

Starting in February instead of the usual December, this 1997-98 ENSO hit South American fur seals and sea lions at the time when they normally replenish their reserves for the upcoming breeding season in November-December and January-February, respectively (Majluf, 1998). Most of the female sea lions gave birth prematurely in December 1997 and their pups died within hours of birth, probably as a result of a bacterial infection. At the Punta San Juan colony over 2,000 sea lion pups died in a single week. In the same area all the few fur seal pups that were born died within a few weeks. Their mothers had to spend very long periods at the sea foraging (10-20 days) and the pups died of starvation. Adult fur seals and sea lions did not die significantly until January-February 1998, when sea temperature anomalies peaked at 7-8° above normal (Majluf, 1998). As a final outcome, the Peruvian population of both species, sea lions and fur seals, declined roughly 81% and 72%, respectively (Arias-Schreiber & Rivas, 1998; Arias-Schreiber, 2000), as a result of low food availability due to the replacement of cold and nutrient rich waters of the upwelling system with warm, nutrient-deficient and low productivity waters (Majluf & Trillmich, 1981).

Throughout my field work at Peru I recovered hundreds of skulls and skeletons (Figure 1) of marine mammals in order to prepare a scientific collection for the project. All of the collected animals were a consequence of the remarkable mortality caused by this ENSO, and consisted mainly of adult fur seals of both sexes and adult female sea lions. In fact, the national census conducted by *Instituto del Mar del Perú* (IMARPE) along the Peruvian coast from 1996 to 1997 indicated that the sea lion population declined from 144,087 (Arias-Schreiber & Rivas, 1998) to 27,991 individuals in December 1998 (Imarpe, 2006) and the fur seals from 24,481 in December 1996 (Arias-Schreiber & Rivas, 1998) to 8,223 individuals in December 1999 (Arias-Schreiber, 2000). Due to the drastic population declines, the sea lions were classified as vulnerable (Decreto Supremo No. 034-2004-AG) and the fur seals as in danger of extinction along the Peruvian coast (Decreto Supremo No. 013-99-AG).

Trillmich & Ono (1991) comprehensively documented the consequences of the 1982-1983 ENSO event on many species of pinnipeds along the coasts of North, Central and South America in the book "Pinnipeds and El Niño – responses to Environmental stress." The biology of fur seals, sea lions and also elephant seals were deeply affected by this ENSO event. As a result, authors have reported an increase in pup and adult mortality, an increase in foraging trips, changes in migration movements, establishment of new breeding colonies and diminished reproductive success. Most of these conclusions were based on counting numbers before and after ENSO events.

In fact, the census population size (N) is usually the only information available for most threatened species. However, for evolutionary matters, the effective population size, not the census number, is the prime concern. The effective population size (N_e) is envisioned as the size of an ideal population that has the same rate of increase in homozygosity or gene frequency change as the actual population under consideration (Wright, 1931).



Fig. 1. South American sea lion (*Otaria flavescens*) breeding colony at Punta San Juan, Peru. **A.** during a non-ENSO period (Photo: Larissa Oliveira). **B.** during 1997-98 ENSO (Photo: Patricia Majluf).

An important application of N_e in conservation biology is the estimation of the minimum viable effective population size, particularly in cases like the Peruvian fur seals and sea lions that suffered significant declines after an environmental change due to ENSO. Adequate assessment of viability requires, in part, determining whether the population is large enough to avoid inbreeding or to maintain adaptive genetic variation (Vucetich & Waite, 1998). A population with a high N_e retains high levels of genetic diversity and reduces the probability of effects of inbreeding depression. In contrast, a population with a very low N_e is more susceptible to genetic drift and less able to respond to selection. This is because in small populations there is less genetic variation for natural selection to act upon, and there is a higher probability that beneficial alleles will not be maintained by selection and will instead be lost from the population because of random drift effects (Willi et al., 2007). Furthermore, the estimate of N_e reflects the number of individuals responsible for maintaining the genetic diversity of the species as well as its evolutionary potential. Since the goal is the conservation of species as dynamic entities capable of evolving to cope with environmental change, it is

important that the species' evolutionary potential must be retained in order to respond to the current unpredictable climate change scenario (Frankham et al., 2002). The calculation of N_e numbers for the Peruvian coast fur seals and sea lions provide us with a quick insight into the ENSO effects and the short-term consequences of rapid changes in an ecosystem of large vertebrate species. It is important to mention that besides the ENSO effects, the Peruvian sea lions and fur seals also suffered local extinctions in the region due to indiscriminate commercial sealing for fur, meat and oil until 1946, when the hunting of both species of seals (*O. flavescens* and *A. australis*) was prohibited (Piazza, 1969; Tovar & Fuentes, 1984). The sealing was totally banned only in 1959 (Grimwood, 1969). Nevertheless, despite all the legal protection, seal poaching still occurs in order to supply the Asian aphrodisiac market (Lama, 2010).

Another important conservation problem that affects the Peruvian sea lions is the mortality due to interactions with fishery activities (Arias-Schreiber, 1993; Majluf et al., 2002), which have been documented throughout the species' range (Aguayo & Maturana, 1973; Dans et al., 2003; George-Nascimento et al., 1985; Koen Alonso et al., 1999; Sepúlveda & Oliva, 2005; Szteren & Paez, 2002). The South American sea lion is an opportunistic predator that forages on the most abundant prey (Oliveira et al., 2008), including many benthic and pelagic fish that usually are economically important (Jefferson et al., 2008). As a result, many sea lions were incidentally captured or even intentionally killed by fishery and fish farming operations throughout their range (see Crespo et al., 2009 for a review).

The interactions with the fishery activities could be intensified during ENSO events and increase the mortality of sea lions during this period. In this sense the estimated N_e combined with the current ENSO events and fishery interactions are causes for great concern for the survival of the species. These concerns should be taken into account in future management plans in order to ensure the conservation and protection of this species on the Peruvian coast.

This chapter presents the estimated N_e of the Peruvian population of the South American sea lions and fur seals based on the effects of species polygyny and oscillations in population size in different generations, which includes the fluctuations caused by the most severe ENSO of the century (1997-1998). Also discussed is the importance of this value for the conservation of a population considered to be vulnerable and which faces environmental changes like ENSO events.

2. Effective population size of fur seals and sea lions

Estimated N_e is obtained by genetic (reviewed by Neigel, 1996; Nunney, 2002) and demographic methods (reviewed by Caballero, 1994; Husband & Barrett, 1992; Nunney, 1995; Oliveira et al., 2006; Traill et al., 2007, 2010). Perhaps the most important influence on N_e and a difficult factor to obtain is the temporal oscillation in population size based on long-term census (Vucetich et al., 1997). According to Nunney & Elam (1994), estimates based on data collected during a single season ignore the influence of temporal fluctuation and thus may represent gross overestimates of N_e . Vucetich & Waite (1998) highlight the importance of long-term counts in order to improve the accuracy of the estimates of N_e . Traill et al. (2010) also reinforce that conservationists working within developing nations rarely have the resources available to collect the long-term demographic and other data necessary to model viability for specific species or taxa. Fortunately, due to the systematic efforts of IMARPE for more than 25 years, results from a long-term census size are available for fur seals and sea lions along the Peruvian coast. Therefore I present and discuss data compiled and published by IMARPE staff (Arias-Schreiber, 2000; Oliveira et al., 2006 and Imarpe, 2006), taking into account the

differences in the number of breeding males and females of South American fur seals and sea lions according to N_e calculations proposed by Hedrick (2000) (see below). I also comment on the consequences of this value for the conservation of bottlenecked populations.

For *O. flavescens* I used data from eight census (1984, 1993, 2000, 2002, 2003, 2004, 2005 and 2006 - IMARPE, 2006) (Table 1) and six censuses for *A. australis* (1984, 1992, 1996, 1999, 2005 and 2006 - Arias-Schreiber, 2000; IMARPE, 2006) (Table 2), both activities conducted by IMARPE including the census during 1999 (just after the 1997-1998 ENSO event, Arias-Schreiber, 2000) which covered 71 breeding colonies from South American sea lion and 46 from South American fur seal, from Los Órganos (04°10'S, 81°07'W) to Morro Sama (18°00'S, 70°53'W) and included the most important reproductive colonies of both species on the Peruvian coast (Isla Brava 11°22'S, 77°45'W, Islas Chincha 13°38'S 76°24'W, Punta Arquillo 13°54'S 76°19'W, Morro Quemado 14°20'S, 76°07'W, San Fernando 15°04'S 75°21'W, Tres Hermanas 15°26'S 75°04'W, Punta Atico 16°14'S 73°41'W and Punta Coles 17°42'S 71°23'W, Figure 2).

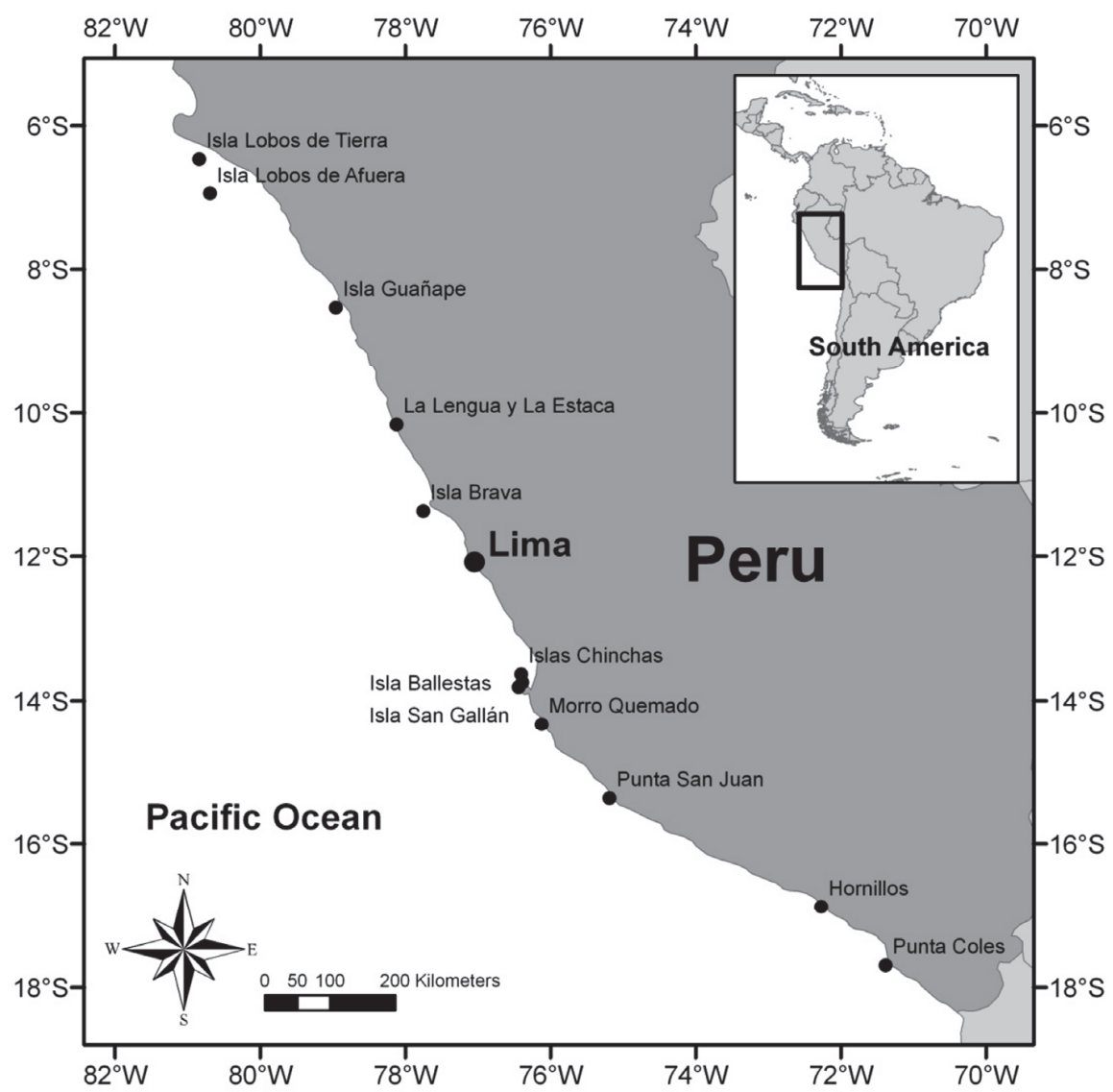


Fig. 2. Most important breeding sites and haul-out areas of South American sea lions (*Otaria flavescens*) and South American fur seals (*Arctocephalus australis*) along the Peruvian coast. These areas were censused between 1984 and 2006 by IMARPE (see text).

In order to estimate N_e we only used censuses that clearly identified adult breeding males and females (Oliveira et al., 2006). Breeding males, also called “territorial males”, are considered all the males that copulate on the beach and assemble harems, while other males that are not in reproductive age and do not mate with females are counted as “subadult” males in the census (Imarpe, 2006).

The South American sea lion presents a polygynic breeding system with very few males being able to mate with many females (Capozzo & Perrin, 2008). The South American fur seal also presents a polygynic breeding system. However, it was modified from lekking to a territorial reproductive system on the Peruvian coast, following changes in population density and availability of space for male territories (Majluf 1987). In both systems, a small number of males are able to mate with many females, so the effective population size should be smaller than the actual population size (Crow and Kimura, 1970). The N_e equation that accounts for the effects of unequal sex-ratio is:

$$N_e = \frac{4N_f N_m}{N_f + N_m}$$

where N_f is the number of breeding females and N_m is the number of breeding males. In order to calculate the effect of changes in population size over time we estimated effective population sizes before and after the ENSO event for both species. To calculate the effective population size prior to the ENSO event for fur seals we used data collected for 1996-1997 by IMARPE (Arias-Schreiber & Rivas, 1998), with a census size of 24,481 individuals, among which 2,903 were reproductive males and 10,720 were reproductive females. For sea lions the census size was 76,349 individuals for the year 1993 (Imarpe, 2006), among which 6,435 were reproductive males and 45,080 were reproductive females.

The estimate of N_e for both species before and after the ENSO of 1997-1998 was then used to estimate an overall effective population size, which accounts for the variation in population size in different generations. The N_e for a population that varies in size over generations is given by the harmonic mean of the N_e in each generation (Hedrick, 2000):

$$N_e = \frac{t}{\sum 1/N_i}$$

where N_i is the effective population size in the i th generation and t is the number of generations considered.

The data obtained here was compared to the minimum viable population size (MVP), calculated by Reed et al. (2003), for 102 vertebrate species, including three pinnipeds. The MVP calculated was on average approximately 5,000 breeding age adults. The MVP can be defined as the smallest size required for a population or species to have a predetermined probability of persistence for a given length of time (Shaffer, 1981). All MVP estimates in the study of Reed et al. (2003) are for a 99% probability of persistence for 40 generations and the models for this estimate are comprehensive and include age-structure, the effect of demographic stochasticity, environmental stochasticity, and inbreeding depression (MacCarthy et al., 2001). The authors estimated MVP using three different criteria: the mean carrying capacity required for a 99% probability of persistence for 40 generations (MVPK), the minimum viable adult population size (MVPA), calculated by the software Vortex (Miller and Lacy, 1999) and the effective population size (MVPN_e). These three measures of

MVP all correlated very strongly with each other ($r > 0.93$ in all comparisons) and the choice of measure does not qualitatively change the conclusions reached in any of the analysis.

3. Results and implications for conservation

The oscillations in census size and its respective effective population size by each year censused for *O. flavescens* and for *A. australis* are presented in tables 1 and 2, respectively. The N_e value that accounts for the effects of unequal sex-ratio for the Peruvian population of South American fur seal, *A. australis*, was 1,220 (year 1999) and the N_e prior to the 1997-98 ENSO was 9,138 for 1996. This yielded an overall effective population size of 2,153 which accounts for both the effects of the mating system and variation in population size. For South American sea lions, *O. flavescens*, the estimate N_e that accounts for the effects of unequal sex-ratio was 22,525 (year 1993) and 2,135 for the year 2000, which means that the N_e prior to the 1997-1998 ENSO was 10 times bigger than the N_e for the year 2000. Nevertheless, the overall effective population size given by the harmonic mean of the N_e in each generation was 7,715, which accounts for both the effects of the mating system and variation in population size. In all, the N_e values for the Peruvian population of *A. australis* and *O. flavescens* are 2,135 and 7,715 specimens respectively.

Year census	N	N_{em}	N_{ef}	N_e year
1984	33,816	5,887	18,872	17,948.94
1993	76,349	6,435	45,080	22,524.69
2000	48,088	558	12,323	2,135.31*
2002	62,840	3,166	29,676	11,443.18
2003	75,158	1,942	27,315	7,252.38
2004	59,399	2,665	19,508	9,378.76
2005	100,256	4,314	38,630	15,522.52
2006	118,220	3,786	40,737	13,856.23

*effective population size declined after 1997-1998 ENSO.

Table 1. Census size and effective population size for *Otaria flavescens* along the Peruvian coast.

Year census	N	N_{em}	N_{ef}	N_e year
1984	15,369	1,827	9,596	6,139.16
1992	27,219	2,557	15,670	8,793.15
1996	24,481	2,903	10,720	9,137.54
1999	8,223	3,215	337	1,220.11*
2005	14,320	716	4,725	2,487.12
2006	15,137	919	4,135	3,007.57

Table 2. Census size and effective population size for *Arctocephalus australis* along the Peruvian coast. *effective population size declined after 1997-1998 ENSO.

These results showed that even under the same conditions of ENSO and suffering similar selective pressures, both species presented highly different results, which is probably due to differences in original census size.

The South American sea lion is the most abundant pinniped species along the Peruvian coast, the last census from 2006 counted 118,220 individuals distributed on breeding colonies and haul-out areas on the continent as well as on islands (Imarpe, 2006). On the other hand, the South American fur seal population was estimated 15,317 individuals for the same year, after a fast recovery from the 6,257 remaining fur seals after 1997-98 ENSO (Imarpe, 2006). It is obvious that the census size population declined significantly for both species. However, are these remaining N_e critical for the conversation of both species along the Peruvian coast?

The calculated N_e for the Peruvian population of *A. australis* ($N_e = 2,135$) seems extremely large when compared with another pinniped species (14 Guadalupe fur seals (*Arctocephalus townsendi*) in 1954 (Hubbs, 1956); 20 Northern elephant seals (*Mirounga angustirostris*) in 1985 (Hedrick, 1985) and another 596 in 2003 (Reed et al., 2003); 3,249 Southern elephant seals (*M. leonina*); 76 Hawaiian monk seals (*Monachus schauinslandi*) and 2,344 grey seals, *Halichoerus grypus*, (Reed et al., 2003)). However, according to Reed et al. (2003), for 102 vertebrate species, including three pinnipeds, the minimum viable population size (MVP) calculated was on average approximately 5,000 breeding age adults. The mean N_e estimated for 102 vertebrate species was 1,752 individuals (SD = 156) (Reed et al., 2003), which is a very close value to the 2,153 individuals estimated for the Peruvian population of *A. australis*. In this sense the estimated N_e for the Peruvian population of fur seal represents a critical value, because it is significantly lower than the average MVP and close to the N_e values estimated for vertebrates.

Moreover, recently Oliveira et al. (2009) found that this population decline affected significantly the N_e , causing a genetic bottleneck. A direct consequence of short periods of

small N_e (bottlenecks) or continued small population sizes is typically the loss of genetic diversity. The loss of genetic diversity in a bottlenecked population is a matter of concern because decreased polymorphism may reduce the evolutionary potential of a population to respond to a changing environment (Fisher, 1930). Furthermore, numerous studies have shown a direct correlation between genetic diversity and measures of fitness (e.g. Leary et al., 1983; Kohen et al., 1988; Soule, 1979), mainly related to inbreeding depression. The bottleneck found in the nuclear genes of South American fur seals could be an indirect result of the synergic effect between the repetitive ENSO events and the human impact in the past (sealing and overfishing) on the Pacific population of South American fur seals.

It is important to mention that a population bottleneck does not necessarily doom a species to immediate extinction (e.g. Northern elephant seal - Frankham et al., 2002; LeBoeuf & Bonnell, 1980). However, the loss of genetic diversity is likely to make it more prone to extinction due to the emergence of new diseases or environmental changes. Further, the population will be partially inbred, and is likely to have reduced reproductive fitness as a consequence. An important feature of such bottleneck events is the large chance element in the outcome. Some situations will be relatively harmless if few deleterious mutations are, by chance, present in the remaining population. In other cases, populations are not so lucky; deleterious mutations are fixed and the species may decline to extinction.

The estimated N_e of 2,153 combined with the apparently current increase in frequency of ENSO events are reasons of great concern for the survival of the species on the Peruvian coast. According to Majluf (1998), the ENSO event from 1997-1998 caused a high juvenile and pup mortality, as well as a high mortality of reproductive females, due to the need to spend very long periods foraging (10-20 days), suffering subsequently from physical stress and even starvation. Although the South American fur seal population on the Pacific side of its distribution most likely is well adapted to recurrent ENSO events, the already depleted current population may not be able to survive more events similar in magnitude to the 1997-1998 ENSO. Indeed, the continued viability of *A. australis* on the Peruvian coast may depend primarily on nongenetic factors, such as local availability of food resources during breeding seasons and its consequent effects on pup growth and survival. Global warming models predict stronger and more frequent ENSOs in the future (NCDC-NOOA, 2004). If a strong one were to hit the surviving adults in the near future, there would be few juveniles to replace them and the future generations may be compromised and in a much greater risk than ever imagined (Majluf, 1998).

On the other hand, I believe that the estimated N_e of 7,715 individuals for the Peruvian population of *O. flavescens* is not a critical value because it is higher than the mean minimum viable population for vertebrates (7000 breeding age adults, Reed et al., 2003). However, the viability of *O. flavescens* as well of *A. australis* on the Peruvian coast may depend primarily on local availability of food resources and its effects on pup growth and survival (Soto et al., 2004). The species faces the productive but unpredictable Peruvian upwelling ecosystem (Ryther, 1969), and is directly exposed to interannual and highly stochastic fluctuations in the distribution and abundance of its principal prey, *E. ringens* (Arias-Schreiber, 2003). According to Soto et al. (2006) there are strong linkages between maternal attendance patterns and the abundance of prey and oceanographic features close to the rookeries. Acute prey shortage during ENSO resulted in females increasing the length of their foraging trips and decreasing the time they spent onshore with their pups, which died due to starvation (Soto et al., 2004). Thus, stochastic fluctuations in the marine environment should directly affect the maternal behavior and possibly the reproductive success of this species.

ENSO year	Intensity of the event (based on SST)	Gap between events (years)
1877 - 1878	Strong	10
1888 - 1889	Moderate	7
1896 - 1897	Strong	2
1899	Strong	3
1902 - 1903	Strong	2
1905 - 1906	Strong	5
1911 - 1912	Strong	1
1913 - 1914	Moderate	4
1918 - 1919	Strong	4
1923	Moderate	2
1925 - 1926	Strong	6
1932	Moderate	7
1939 - 1941	Strong	5
1946 - 1947	Moderate	4
1951	Weak	2
1953	Weak	4
1957 - 1959	Strong	4
1963	Weak	2
1965 - 1966	Moderate	2
1968 - 1970	Moderate	2
1972 - 1973	Strong	3
1976 - 1977	Weak	1
1977 - 1978	Weak	1
1979 - 1980	Weak	2
1982 - 1983	Strong	3
1986 - 1988	Moderate	2
1990 - 1993	Strong	1
1994 - 1995	Moderate	2
1997 - 1998	Strong	4
2002 - 2003	Moderate	1
2004 - 2005	Weak	1
2006 - 2007	Weak	1

Table 3. ENSO events from 1877 - 2006 based on sea surface temperature (SST) reconstructions (Smith & Reynolds, 2004).

In this sense, the estimated N_e of 7,715 for *O. flavescens* should be considered as a value to be maintained in order to keep the population large enough to avoid inbreeding or to retain adaptive genetic variation to survive to future ENSO events. Moreover, this N_e result has an important application related to management decisions for the conservation of sea lions in Peruvian waters. This N_e value must be taken into account mainly during periods of suggestion of culling, based on the increasing competition between fishery activity and sea lions during ENSO events. In 1997 Peruvian fishermen called for a cull of sea lions to protect fisheries and the Peruvian Fisheries Ministry was considering a pilot program to kill up to 60 sea lions. However, as a result of the 1997-1998 ENSO event the numbers of sea lions onshore were drastically reduced and the program was abandoned (Seal Conservation Society, 2010; Lama, 2010).

The most important drawback of the estimate of N_e is the necessity of a data set from long term censuses that include temporal oscillations in population size (~20 years) (Vucetich et al., 1997). Nunney & Elam (1994) suggested that estimates based on data collected during a single season ignores the influence of temporal fluctuation and thus may represent gross overestimates of N_e . This is why the data presented here are so important and unique in comparison to the information available on pinniped populations from other countries throughout South America. The long-term census size available for fur seals and sea lions along the Peruvian coast are results of the systematic efforts of IMARPE for more than 25 years.

Vucetich & Waite (1998) highlight the importance of long-term counts in order to improve the accuracy of the estimates of N_e . Traill et al. (2010) also reinforce that conservationists working within developing nations rarely have the resources available to collect the long term demographic and other data necessary to model viability for specific species or taxa.

Global warming models predict stronger and more frequent ENSOs in the future (see table 3) (NCDC-NOOA, 2004). I recommend that conservation planners consider the estimated N_e for both species in future management strategies to ensure the conservation of the South American sea lions and fur seals on the Peruvian coast.

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