PREY ABUNDANCE AND POPULATION DYNAMICS OF SOUTH AMERICAN FUR SEALS (*ARCTOCEPHALUS AUSTRALIS*) IN PERU

by

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Abstract

South American fur seals (*Arctocephalus australis*) continue to survive in Peru in spite of commercial harvesting, periodic disappearance of prey (*i.e.*, El Niño), and competition with the Peruvian anchoveta fishery. I investigated the ability of the Peruvian population of fur seals to recover from catastrophic declines at two temporal and spatial scales. The first analysis determined intrinsic rate of growth (r) and the potential carrying capacity (K^*—the number of fur seals that could be supported in Peru in the absence of sealing and El Niño) from 1880–2010, and the second used pup counts from 1984–2010 to determine the relationship between prey abundance and the timing of pupping at an important fur seal breeding site in southern Peru. Model results indicated that South American fur seals in Peru have an intrinsic growth rate r of 0.20 and a potential carrying capacity K^* of 115,000 seals. Recent counts (2007) show that current population is at 33% of the estimated mean numbers of fur seals alive from 1880-1925. Analysis of 25 years of counts of pups and adult females at the breeding site showed a correlation between anchoveta biomass and mean birth dates ($r^2 = 0.59$, $P<0.01$) and with the ratio of pups to females ($r^2 = 0.66$, $P<0.01$) in the upcoming breeding seasons. It also revealed a 2-week shift in the mean birth date that may reflect a change in the age structure of the population. Numbers of pups born tended to be lower in years with low anchoveta biomass, as did recruitment of young females. Monitoring daily numbers of pups born and adult females appears to be a useful means to assess the feeding conditions encountered by South American fur seals in Peru. My study also suggests that South American fur seals are adapted to survive in extremely disturbed environments and have the potential to rapidly recover following population declines. Whether or not they ever again achieve their potential carrying capacity will depend upon protection of breeding rookeries, a continued harvest ban, reduced bycatch, incidental captures and illegal poaching, regulation of anchoveta fishing quotas and good environmental conditions.

Preface

I, Susana Cárdenas Alayza am the primary contributor to this thesis in the identification and design of the research as well as in the data analysis and manuscript preparation.

Chapter 2 is based on data compiled from various sources. South American fur seal counts (1996-2007) and hydroacoustic estimates of anchoveta biomass (1985-2010) were made available to me by IMARPE (Instituto del Mar del Perú) and by Mariano Gutiérrez. Historical census data on South American fur seals (1961-1992) was provided by Patricia Majluf of Universidad Peruana Cayetano Heredia. All additional information was extracted from peer-reviewed literature, published reports and online databases. Suggestions on the design and analyses of this chapter were given to me by committee members Daniel Pauly and Carl Walters, by Chiara Piroddi of the Sea Around Us Project and by my supervisor Andrew Trites.

Chapter 3 is based on long-term work conducted by Patricia Majluf and staff and volunteers of the Punta San Juan Project (PSJP) of the Universidad Peruana Cayetano Heredia in Punta San Juan, Peru. All data were collected under government permits and agreements of cooperation between AGRORURAL (ex-PROABONOS) and SERNANP (Servicio Nacional de Areas Protegidas) between 1984 and 2010. I was in charge of collecting part of this data for the PSJP during fur seal breeding seasons of years 2004, 2005 and 2006. South American fur seal counts (1984-2010) were made available to me by PSJP and the estimates of anchoveta biomass and landings used in the analysis were provided by IMARPE and Mariano Gutiérrez. All additional information was extracted from peer-reviewed literature. Suggestions on the design of this chapter were given to me mainly by my supervisor Andrew Trites and by my committee members Daniel Pauly and Carl Walters.

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ENSO	El Niño Southern Oscillation
IMARPE	Instituto del Mar del Perú (Peruvian Marine Research Institute)
PSJ	Punta San Juan

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There are many people I would like to thank for making this endeavor possible. I would first like to thank my supervisor Dr. Andrew Trites for giving me the opportunity to join the Marine Mammal Research Unit, allowing me to develop my own research interests with a study species that differed to that of others the lab was familiar with. When this adventure began, we were both yet to learn how south Pacific—everything—can be so much different from its northern counterpart. Starting with fur seals! Thanks Andrew for your support and patience to make this happen.

I would also like to thank the members of my thesis committee Carl Walters and Daniel Pauly for their support, guidance and always taking the time to wrap their heads around my research. I would like to thank Carl for always being straightforward and honest about my work and steering me in the right direction. I would like to thank Daniel for always encouraging me to do more, for teaching me that anecdotes are data and reminding me to never loose sight of the bigger picture.

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Financial support for my first year was gratefully appreciated from PEO International Trust Fund. For subsequent funding I would also like to thank Villy Christensen, and Daniel Pauly from the Sea Around Us Project to whom I am very grateful for taking me on as a research assistant for a research project with Peru. Besides funding me this project allowed me to strengthen links with the marine science community in my home country.

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Tiphainne Jenniard Du Dot, Ruth Joy, Beth Young and Brian Battaile for all their statistical advice and bits of useful R code—besides the many good times. I would also like to thank all the members of MMRU for innumerable coffee breaks, practice talks and fun times. I would especially like to thank Frankie, Erin, Liesbeth, Chad, Tiph, Rowenna and Brian for all their support and friendship throughout my time at UBC.

Most of my work could not have been possible without information given to me from various sources. First and foremost, I would like to thank the people at IMARPE for sharing the data solicited for the production of this thesis. I could not have been able to explore the bigger picture without this collaboration. I am also very grateful to the crew at CSA-UPCH crew in Lima, Peru for all their help and support throughout this degree. I would specially like to thank Patricia Majluf for opening the doors to the Punta San Juan Project and teaching me a thing or two about South American fur seals, anchovetas and believing that it is possible to change people's minds and more specifically, their *eating* habits. Special thanks to Marco Cardeña of the Punta San Juan Project for always supplying up to date information from the field as I added "one more year" of data into my analyses; and for being the great colleague and friend that he is. A special thanks to Santiago de la Puente for always lending me a hand and putting Peru's legislation and fisheries practice into practical terms. Thanks to Michael Adkesson for being my "partner in crime" in the adventures that now await us at Punta San Juan.

Finally I could not have done this without the support of my family and friends. Many thanks to all the wonderful friends that made my life in Vancouver feel like home. I would specially like to thank Gillian, Danika, Pamela, Katie and Sarah. For only you know how many balls of yarn I have knitted during this degree. Finally, I would like to thank my family. My mom Rosa, dad Jaime and my sister Rosa for all their incredible support, patience and help to make this possible. And last but not least, my deepest thanks to my partner Santiago for all of his support and patience during grad school and because now we know that not even ~8,000km can keep us apart.

Chapter 1: Introduction

Major population declines associated with natural and human caused events are widely understood to be a key factor in the risk of extinction (Gerber & Hilborn 2001). This is particularly true for pinnipeds (seals and sea lions) which were all hunted to critically low numbers and even extinction in a few cases (Riedman 1990, Bonner 1981, Bonner & Laws 1964). Pinnipeds require ice or land for resting and breeding that is in proximity of feeding grounds, and are particularly vulnerable to catastrophic events such as sudden reductions in prey availability (Stirling 1983, Stevens & Boness 2003). Understanding the factors that underlie the population dynamics of pinnipeds is needed to conserve populations of pinnipeds that are in decline or at critically low numbers.

Otariids (fur seals and sea lions) have been part of Peru's marine coastal environment since pre-Inca times. Evidence that humans have exploited South American fur seals (*Arctocephalus australis*) and South American sea lions (*Otaria flavescens*) in Peru exists from ca. 4,000 BC. They were nearly extirpated by indiscriminate commercial hunting from the early 1900s until 1946 (Bonavia 1982, Donnan *et al.* 2009, Reeves *et al.* 1992). By the late 18th century, commercial sealing for blubber and fur was firmly established in the southern hemisphere (Weber *et al.* 2004, Riedman 1990).

In Peru, commercial harvest activities are believed to have reduced fur seal numbers to the point that few, if any, South American fur seals were presumed to be alive by the late 20th Century (Majluf & Trillmich 1981, Muck & Fuentes 1987). It is not well known which of the two sympatric species of pinnipeds in Peru was the main target for the commercial harvest. What is not in doubt, however, is that fur seals were limited to small isolated groups and sea lions were greatly diminished by mid 1940s (Kostrisky 1963, Piazza 1969). This led to the banning of all sealing in 1959, although illegal poaching continues to occur (Majluf 1984). Population numbers increased following protection, but declined by 72% when the abundance of anchoveta was severely reduced by the 1997/98 El Niño event (Arias-Schreiber & Rivas 1998).

The El Niño Southern Oscillation (ENSO) cycle of alternating warm El Niño and cold La Niña events is the most prominent climate signal on earth (McPhaden *et al.* 2006).

ENSO originates in the Tropical Pacific through interactions between the ocean and the atmosphere, but its effects are felt worldwide (McPhaden *et al.* 2006). The Humboldt Current upwelling system, is affected by ENSO, with increased sea surface temperatures and reduced primary productivity directly influencing the depth distribution and abundance of anchoveta, the preferred prey item of South American fur seals in Peru. The 1982/83 and 1997/98 El Niño events were the strongest on record for the past century (Chavez *et al.* 1999) and caused numerous populations of marine mammals and birds to decline due to the drastic shortage in prey (Fiedler 2002).

Punta San Juan (15°22′ Lat. S) is a government-managed guano reserve on the southern coast of Peru (Fig. 1.1) that was home to almost 50% of the fur seal population in Peru before the 1997/98 El Niño (Majluf & Trillmich 1981).

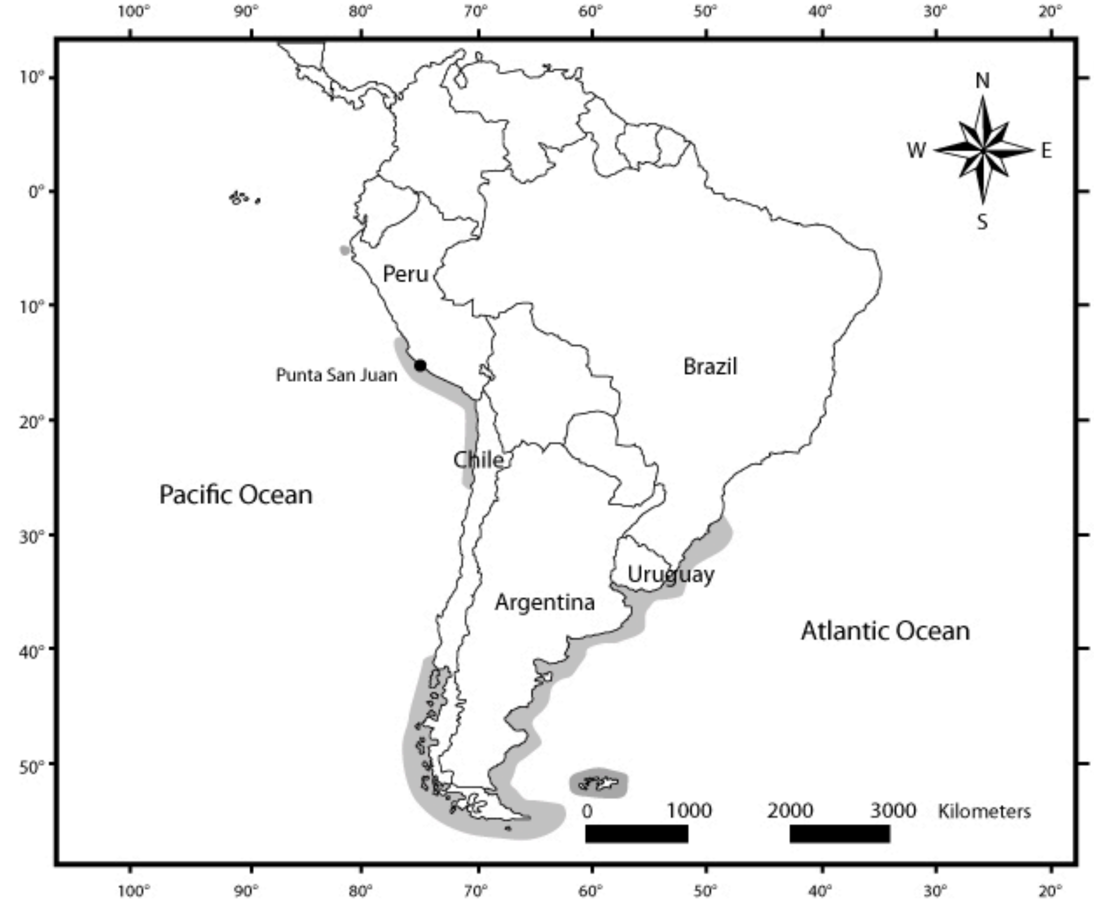

Figure 1.1 Range of South American fur seals in South America (shaded in gray).

Punta San Juan has been recognized as the location of the strongest upwelling core in Peru (Zuta *et al.* 1978, Bakun & Weeks 2008, Cushing 1982). Cold waters close to the coast, combined with the southerly location (15°S), strong local winds and extremely low continental shelf, results in a tendency for upwelling to persist longer at Punta San Juan than elsewhere in Peru even when surrounding areas are affected by El Niño conditions (Majluf 1991a). However, this was not enough to protect the Punta San Juan fur seal populations from the extremely high intensity and duration of the 1997/98 El Niño that dramatically reduced ocean productivity and diminished all populations of marine predators endemic to the Humboldt Current system (Chavez *et al.* 1999, Majluf 1998).

The 1997/98 El Niño started in February instead of the usual December. This change in timing is believed to have impacted South American fur seals while they would have normally replenished their reserves for the upcoming breeding season (October to December), causing the few fur seal pups that were born to die within a few weeks of birth. Adult females had to spend longer periods at sea foraging (10-20 days) causing their pups to die of starvation. The death of the pups was followed by significant mortalities of juvenile and adult fur seals in January and February, when sea temperature anomalies peaked at 7-8°C above normal (Majluf 1998).

Fewer than 5,000 fur seals survived the 1997/98 El Niño throughout Peru. This drastic population decline resulted in the conservation status of South American fur seals being reclassified as in danger of extinction on the Peruvian coast (Decreto Supremo No. 013-99-AG). The South American fur seals were also added to Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). There is little information on the potential consequences of the historical commercial hunt or of the effects of ENSO on the conservation status of the species (Oliveira *et al.* 2009).

1.1 South American fur seals

The South American fur seal is distributed from Uruguay in the east, to Peru in the west, and all around the southern tip of South America including the Falkland Islands (Fig. 1.1). They have a discontinuous distribution along the coast of Chile and have no colonies or haulouts between 23°- 43° (Lat. S.). The presence of the South American fur seal in Peru is linked to the flow of the cold and productive waters that run along the west coast of South America (Majluf 1987a). The Humboldt Current system and specifically the Peruvian upwelling system, is the most productive ecosystem in the world in terms of fish biomass production (Zuta *et al.* 1978, Bakun & Weeks 2008). In turn, this large biomass of pelagic fish generates a high abundance of prey that is readily available in most years to apex predators such as the South American fur seal. As with most other large pelagic vertebrates in Peru, South American fur seals rely largely on the Peruvian anchovy or anchoveta (*Engraulis ringens*), a small clupeid fish which is ecologically and economically the most important pelagic fish species in the Humboldt Current ecosystem (Espinoza & Bertrand 2008, Cushing 1982, Bakun & Weeks 2008).

South American fur seals can be found year round at breeding rookeries on the coast of Peru since adult females return throughout the year to these sites to nurse their offspring (Majluf 1987a). Like all fur seal species, they have polygynous mating systems, where some reproductive males have access to several reproductive females. In Peru, between the months of September and December adult males or bulls compete at the breeding rookeries for territories to hold tenure that adult females will use to give birth (October-December) and nurse their offspring (Majluf 1987a). Females come ashore 1-4 days before the birth of the pup and stay with the newborn for about one week during the perinatal period. During this time, the mother guards and suckles her young and individual recognition between mother and pup becomes established.

One week post-partum, fur seal mothers will enter a brief estrus, copulate and leave for the first time to forage at sea. The mothers then alternate between foraging trips at sea of 1-8 days duration and 1-3 day stays ashore with pups (Majluf 1987a). Copulation leads to a fertilized zygote, which is arrested in its development for about 3-4 months after which implantation takes place and embryonic development sets in. One year after giving birth, females will return to the breeding beaches to pup again. If rearing takes longer than a year, a second pup may be born while the first one is still dependent and competition for the mother's milk between the older and young sibling occurs (Trillmich 1990).

1.2 Thesis goals and structure

The overall goal of my thesis was to better understand the roles that hunting, fishing and El Niño have played in the population dynamics of South American fur seals in Peru. I was particularly interested in understanding the apparent ability of the Peruvian fur seal population to recover from catastrophic declines. I was also interested in establishing whether a relationship exists between fluctuations in prey abundance and reproduction of South American fur seals that could be used to ensure their long term conservation.

My thesis has four sections. Chapter 1 provides a General Introduction to my two data chapters. The first data chapter (Chapter 2) uses a simple logistic growth model to reconstruct historical abundance and estimate the intrinsic rate of growth and potential carrying capacity of South American fur seals in Peru from 1880–2010. It considers the long-term effects that have contributed to mortality and population growth of South American fur seals. The second data chapter (Chapter 3) examines how prey abundance (anchoveta) in the waters off Peru affected the number of pups born and the timing of breeding of South American fur seals at Punta San Juan during a 25 year window (1984 - 2010). By examining changes in population growth and the effects on reproduction at these two scales, I sought to gain insight into the recovery response of fur seals to discrete events (*i.e.,* El Niño) and some of the cumulative threats that have taken place in Peru (*i.e.,* harvest regimes and incidental captures) that have and continue to contribute to fur seal mortality (discussed in Chapter 4—General Conclusions). Chapters 2 and 3 are written as manuscripts and contain some necessary repetition of information.

Chapter 2: Historical abundance and population growth rate of South American fur seals in Peru, 1880-2010

2.1 Summary

South American fur seals (*Arctocephalus australis*) continue to survive in Peru in spite of commercial harvesting (1925–1946), periodic disappearance of prey (due to reoccurring El Niño events), and competition with the Peruvian anchoveta fishery. I investigated the apparent ability of the Peruvian fur seal population to recover from catastrophic declines using a simple logistic growth model that reconstructed historical abundance and estimated the intrinsic rate of growth (*r*) and the potential carrying capacity (*K**) for 1880–2010. I ran my population model with different combinations of parameters, and used minimum sum of squared deviations between observed and predicted counts to determine the best combination of parameters that explained observed numbers of seals. In all, I ran 42,924 models using 21 values of *r* (0.08-0.28) and 73 values of *K** (40,000-400,000 individuals) for 28 scenarios involving different assumptions about historical and non-reported harvest rates for fur seals. I also included two additional variables in the population model to account for seals that died from environmental conditions associated with warm sea surface temperature anomalies and fluctuations in prey biomass. The model indicates that South American fur seal have a high *r* of 0.20 and a potential carrying capacity *K** of 115,000 (the number that could be supported in the absence of sealing and El Niño). Recent counts (2007) indicate that South American fur seals in Peru are at 33% of the average 68,000 seals (range 39,000-98,000) estimated to have occurred before sealing reduced the population. My study suggests that South American fur seals are adapted to survive in extremely disturbed environments and have the potential to rapidly recover following population declines (*i.e.,* due to El Niños). Whether or not they ever again achieve pre-sealing abundance will depend upon (i) protection of breeding rookeries, (ii) a continued harvest ban, (iii) reduced bycatch, incidental captures and illegal poaching, and (iv) regulation of anchoveta fishing quotas, and (v) good environmental conditions.

2.2 Introduction

The presence of South American fur seals (*Arctocephalus australis*) and sea lions (*Otaria flavescens*) and their relationship with humans has been documented in Peru since pre-Inca times (Donnan *et al.* 2009, Bonavia 1982). Drawings on ceramic pots of native people hunting pinnipeds date as far back as 4,000 BC (Donnan *et al.* 2009, Bradshaw *et al.* 2000, Reeves *et al.* 1992), and trading records and ship logs show that commercial sealing for blubber and fur was firmly established in the southern hemisphere by the late 18th century (Riedman 1990, Weber *et al.* 2004). In Peru, commercial harvest activities seem to have reduced fur seal numbers to the point that few, if any, South American fur seals were presumed to be alive by the late 20th Century (Majluf & Trillmich 1981, Muck & Fuentes 1987).

Harvest records leave no doubt that large populations of pinnipeds once existed in Peru (Gamarra 1943, Majluf & Trillmich 1981, Piazza 1969, Kostrisky 1963). Between 1925 and 1946, 806,525 seal skins were exported from Peru (Majluf & Trillmich 1981) with a single company alone reporting a kill of 36,500 individuals (88% of them pups) between December 1941 and March 1942 (Piazza 1969, Muck & Fuentes 1987). Failure of the harvest records to distinguish between fur seals and sea lions makes it unclear which species were actually killed (Majluf 1984, Majluf & Trillmich 1981). What is not in doubt however is that by 1943, fur seals in southern Peru were limited to small isolated groups and sea lion colonies were greatly diminished (Gamarra 1943, Piazza 1969). In 1946, hunting of both species was prohibited from occurring between January and April (Piazza 1969), and sealing was banned year-round beginning in 1959. However, this has not stopped illegal poaching and indiscriminant killing (Majluf 1984, P.Majluf, pers. comm.).

The earliest counts suggest that fur seals in Peru numbered as few as 40 seals in the 1950s (Piazza 1969) to over 20,000 seals in 1979 (Majluf 1984, Majluf & Trillmich 1981). The first “official” fur seal census by the Peruvian government reported fewer than 4,000 individuals in 1961. Counts were also made in 1963, 1968, 1971, 1974, 1976-1979 and 1984, but visits to locations were not systematic among years. The timing of the annual census also varied by time of year and time of day, and the sex and age categories were often misidentified (Majluf & Trillmich 1981). This lack of standardized census methodology reduces confidence in the accuracy of the estimates (E. Goya, pers. comm.). After 1992, IMARPE (Instituto del Mar del Peru, Peruvian Marine Research Institute) took charge of assessing marine resources, and improved the reliability of the estimates by standardizing the census methodology. The maximum number of fur seals counted since the mid-1980s was close to 25,000 animals in 1992, and was under 14,000 individuals in 2007 (IMARPE, unpubl. data).

In addition to hunting, South American fur seals have also been significantly affected by the El Niño Southern Oscillation (ENSO). ENSO events occur every 2-7 years and are characterized by a significant warming of the ocean that lasts from 9 months to 2 years. These events vary in strength and affect the abundance and distribution of Peruvian anchovy or anchoveta (*Engraulis ringens*), which are the principal prey of fur seals in Peru (Paredes & Arias-Schreiber 1999, Zavalaga *et al.* 1998, Vásquez 1995). The two most intense ENSO episodes in more than a century occurred in 1982 and 1997, and affected all trophic levels from marine mammals, birds, and fish, through to zooplankton and phytoplankton (Chavez *et al.* 1999). Fur seal studies during these ENSOs' recorded high reproduction failure among adult females, zero pup survival and high mortality of all other age classes (Majluf 1991a, Apaza *et al.* 1998, Arias-Schreiber & Rivas 1998). The first of these two ENSO events (1982-1983) resulted in the loss of the entire pup cohort (Trillmich *et al.* 1991), while the second major ENSO (1997-1998) caused the Peruvian fur seal population to decline by ~72% (from 24,481 in December 1996 to 8,223 individuals in December 1998, Arias-Schreiber & Rivas 1998, Oliveira *et al.* 2006). The catastrophic decline that followed the 1997-1998 ENSO led to the South American fur seals being categorized as in danger of extinction in Peru (Decreto Supremo No. 013-99-AG).

Assessing the current state of the South American fur seal population in Peru and its prospects for recovery requires identifying the threats. It also requires quantifying the inherent ability of the population to grow, as well as the historic ability of the environment to support fur seals in Peru. To that end, I fit models to existing time series of harvest records and population estimates (1880 to 2010), and linked them to indices for environmental conditions to (i) estimate the historical pre-sealing abundance of South American fur seals in Peru, and (ii) estimate the population parameters r (intrinsic growth rate) and K^* (potential carrying capacity). I also assessed (iii) the relative importance of factors that have driven the decline of South American fur seals in Peru since the mid-20th century.

2.3 Materials and methods

2.3.1 Population estimates

South American fur seal breed at rookeries along the coast of Peru from (5° 20'S) to Ilo (17°42'S), but mostly occur from 13° to 17° (Lat. S.) (Fig. 2.1). Population fluctuations have resulted in rookeries being abandoned and reoccupied over time. Some sites were not surveyed after they were believed to be abandoned, while others that were recently recolonized might have been missed. The first population assessments of pinnipeds in Peru reported a total of 40 fur seals in 1951 (Piazza 1969), which likely reflects the minimal number of locations visited. A specialized commission initiated by the Ministry of Agriculture in the 1960s and 1970s resulted in a nationwide population census of fur seals and sea lions in Peru and attempted to improve census methodology. However, it was not until 1992 that the hit-and-miss census methodologies were replaced with a comprehensive sampling design (E.Goya, pers. comm.).

Since 1992, fur seal censuses have been conducted by the Instituto del Mar del Peru (IMARPE) during the breeding peak (mid-November to early December) on an annual basis (when budgets permitted). IMARPE corroborates the presence of fur seals at rookeries by visiting all known and pre-existing rookeries, and asking local fishermen if they know of other fur seal colonies. During a census, direct counts of fur seals begin at 0600 AM at each beach or rookery from high vantage observation points using binoculars and counters. Fur seals are counted by categories *i.e.,* according to sex and age classes: pup, juvenile, sub-adult male, territorial male, adult female and undetermined. For the purpose of my model, I only used the total reported Peruvian fur seal counts from 1961 to 2007 (n = 22 years) as a measure of observed total abundance.

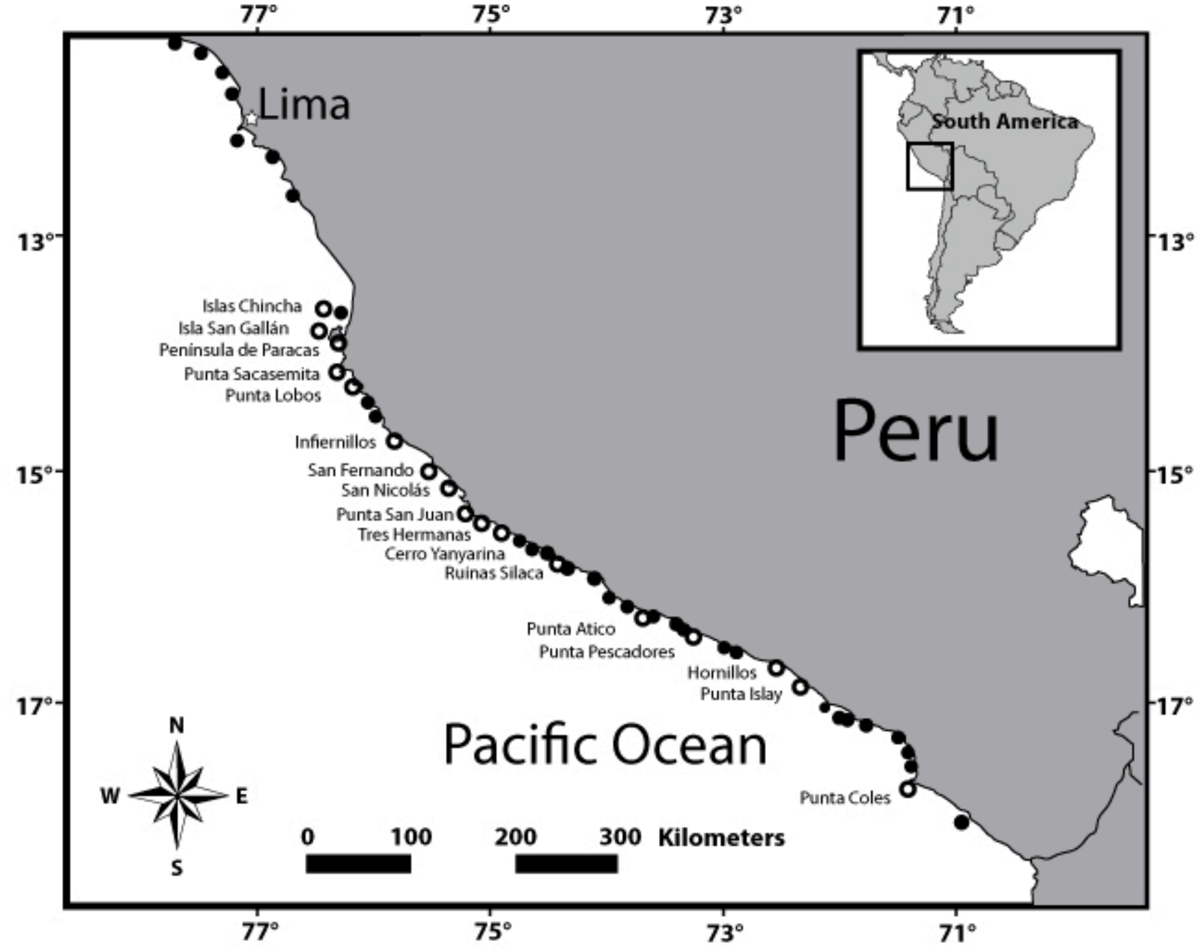

Figure 2.1 Distribution of historical South American fur seal rookeries and haulout sites in southern Peru. Occupied (empty circles with labels) and abandoned (black dots without labels) breeding rookeries are shown. Occupied breeding sites are based on IMARPE (2006), but the recently discovered breeding rookery at Isla Foca (5°20'S) in northern Peru is not shown. Map adapted from Oliveira *et al.* (2006), reprinted with permission of L. Oliveira.

2.3.2 Catch and the abundance model

I estimated annual abundance (N_{t+1}) of South American fur seals from 1880 to 2010 as a function of logistic growth minus the number of animals harvested or caught each year:

$$N_{t+1} = N_t + r_{\max} \cdot N_t \cdot (1 - \frac{N_t}{K}) - C_t \qquad \text{Eq.1}$$

where N is numbers of fur seals, r_{max} is the maximum intrinsic rate of population growth, K is the carrying capacity, C is catch or harvest and t is time in years. This production or logistic growth model is a density dependent model that limits the maximum size of the population to its carrying capacity, *K*. Carrying capacity should be pre-exploitation numbers as far back as the data series permits hind casting (*i.e.,* assuming that $N_1 = K$). However, there is unlikely to have ever been a carrying capacity in the true meaning of the word because fur seals have continuously been removed from the Humboldt Current ecosystem by naturally occurring El Niño events. Thus, carrying capacity for seals in this relatively unstable ecosystem is better thought of as *potential* carrying capacity, K^* — the number of fur seals that could be supported in absence of sealing and El Niño events.

I estimated K^* (by substituting K^* for *K* in Eq. 1) and the maximum intrinsic growth rate (r_{max}) or net production (*i.e.,* growth + new production – mortality for the population) for the period 1880–2010. I also spun the model up to 1880 by transposing a 30 year mirror image of prey abundance estimates and sea surface temperature anomalies (from 1880-1909) to initialize the model with 30 years of pseudo data (for the period 1850-1879).

In terms of catch (*C*), details on harvest activities for South American sea lions and South American fur seals are scarce or unclear (Kostrisky 1963). Harvest records containing the number of *lobo marino* skins exported from Peru during 1925-1946 were compiled and published in 1981 (Majluf & Trillmich 1981). *Lobo marino* or sea wolf (literal Spanish to English translation) is the generic term for both species of pinnipeds that inhabit the coast of Peru. Unfortunately, the species of *lobo marino* is not specified in the export records. I therefore assumed that 1% or more of the reported pelts could have been fur seals, and that the rest were sea lions.

Catch in my model was the annual sum of four categories: commercial harvest, unreported harvest, poaching and bycatch (or incidental capture). I estimated the number of fur seals that were estimated to have died each year due to each of these human related causes as follows:

i. ***Commercial harvest.*** Official harvest records reported total number of *lobo marino* skins exported from 1925-1946. To estimate the number of skins pertaining to fur seals, I used a sliding scale set at 1% intervals to allow the model to consider the possibilities that the total reported harvest of *lobo marinos* consisted of as few as 1% fur seals to as many as 100% fur seals from 1925-1946. Commercial harvest of pinnipeds was legal in Peru until 1959. However, it reopened from 1971-1974 for pups alone, during which annual numbers pups killed were 557, 246, 1680 and 1705 per respective year (Piazza 1969). I kept these numbers constant for all simulations. However, to estimate numbers of pups harvested in other years, I assumed that 30% of mean commercially harvested seals during 1925-1946 represented the pup portion of the population affected. I based this percentage on a life table for northern fur seals (Lander 1982).

ii. ***Unreported harvest.*** Based on sources that mention the existence of a small local pelt trade in Peru (Kostrisky 1963), I assumed that 5% of the fur seals harvested were not officially reported for export. I thus increased the total catch by 5% (an arbitrary but reasonable percentage) to account for unreported harvest that was never officially quantified.

iii. ***Poaching.*** Illegal harvest occurred during the years when commercial harvesting was prohibited by law. Kostrisky (1963) indicates that approximately 6,000 *lobos marinos* were poached *per annum* in Peru in the early 1960s, when harvesting was already banned. I therefore assumed that poaching could account for 1-100% of the total catch (as I did for estimating the commercial harvest) to estimate numbers of fur seals poached illegally from 1959-1970 and from 1977-2007.

iv. ***Bycatch.*** Reported numbers of fur seals accidentally caught and drowned in fishing gear in Peru is scarce or non-existent. However, a single local study conducted in the Bay of Punta San Juan reported that fur seals died at the hands of artisanal fisheries at a rate of 0.04 per trip, or 1 fur seal for every 25 trips that used drift gill nets and hook and line as fishing gear (Arias-Schreiber 1993a, Majluf *et al.* 2002). Using this information, I calculated the number of fur seals that could have died each year from incidental captures or as bycatch along the distribution range of fur seals in Peru for these fishing gears. I used the estimated amounts of landings by gear type in the waters of Peru since the 1950s from the *Sea Around Us* Project database (*www.searoundus.org*) to estimate the proportion of the fur seal population that died in drift gill nets and hook and line gear (1950-2006). These two types of fishing gear contribute most to fur seal mortality as reported by Arias-Schreiber (1993a). I then scaled the reported estimate for fur seal mortality per gear-type for Peru from Punta San Juan (Arias-Schreiber 1993a) to the number of fishing trips at ports proximate to fur seal breeding rookeries as reported by the artisanal fisheries research unit at IMARPE (Estrella 2007). Due to lack of recent information, I used the same values estimated for 2006 for 2007-2010. Thus, I assumed that the number of fur seals killed varied consistently with the trend of gear-types used, rather than a fixed percentage. Unfortunately, there are no other studies available to compare fur seal mortality rate due to bycatch for other years or sites in Peru.

2.3.3 Prey biomass and environmental conditions

In addition to accounting for the direct effect of catch on numbers of fur seals (Eq. 1), I also wanted to estimate the numbers of fur seals alive as a function of the indirect effect that changes in environmental conditions and prey biomass have on fur seal numbers.

I linked the effect of sea temperature anomalies to South American fur seal survival according to:

$$N_{t+1} = N_t + r_{\max} \cdot N_t \cdot (1 - \frac{N_t}{K^*}) - [C_t + (N_t \cdot T^*)] \qquad \text{Eq. 2}$$

where T^* is the temperature effect index (T^*). This index was based on monthly sea surface temperature anomalies (SSTA) from the 3.4 El Niño region (120°W - 170°W and 5°S - 5°N) from 1880-2007 (NCAR-CDG 2010) (Fig. 2.2). I preferentially used the sea surface temperature anomalies from the 3.4 El Niño Region because local temperatures off the coast of Peru were not available for the entire study period. I then estimated the temperature effect index by summing monthly mean sea surface temperature anomaly values for the three trimesters considered crucial to fur seal survival: i) 3 months of the breeding season (October, November and December); ii) 3 months prior to the breeding season (July, August and September); and iii) 3 months after the breeding season (January, February and March) as shown by:

$$T^* = \sum (\overline{SSTA}_{priorbreeding} + \overline{SSTA}_{breeding} + \overline{SSTA}_{postbreeding}) \qquad \text{Eq. 3}$$

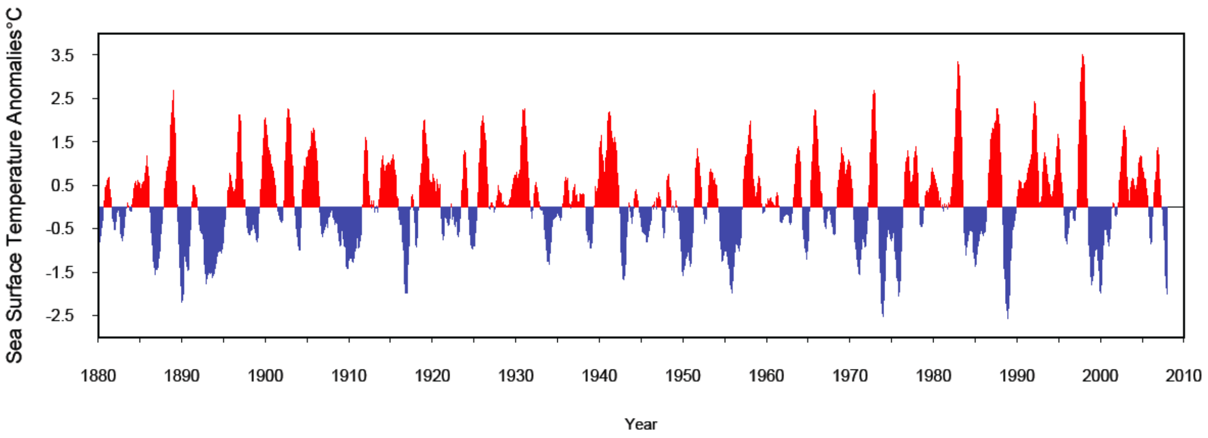

Figure 2.2 Monthly sea surface temperature anomaly time series from the 3.4 El Niño region (120°W - 170°W and 5°S - 5°N) for 1880-2007. Positive (red) anomalies were used to construct the temperature effect index (*T**) to estimate the proportion of South American fur seals that were killed due to El Niño events. Negative (blue) anomalies were not used for the analysis. Data were open access and obtained from http://www.cgd.ucar.edu/cas/catalog/climind/TNI_N34/index.html.

The estimated proportion of fur seals that died when sea surface temperature anomalies were positive was scaled according to the temperature effect index that corresponded with the known number of fur seals that died in 1997 because of the warm anomalies of the 1997-1998 El Niño (which killed at least 50% of the population, Apaza *et al.* 1998, Arias-Schreiber & Rivas 1998). Since no El Niño events occurred after 2008, I assumed that no El Niño associated mortalities occurred from 2008 to 2010. I then applied the temperature effect index to estimate the proportion of animals affected by changes in sea surface temperature from 1880-2010 (Fig. 2.2). Only temperature anomalies >0 were considered to reduce population abundance. Values <0 had no effect on numbers.

To incorporate the possible effect of prey abundance on fur seal numbers, I adjusted the effect of ENSO by the biomass of prey present to:

$$N_{t+1} = N_t + r_{\max} \cdot N_t \cdot (1 - \frac{N_t}{K^*}) - [C_t + (N_t \cdot T^* \cdot \exp(-A))] \qquad \text{Eq.4}$$

where A is an index of prey abundance (range 0-1). In this way, a major ENSO would have less impact on the seals if prey biomass was high, and would have a greater effect if biomass was low. I derived the index of prey abundance from the annual biomass estimates of anchoveta from 1925-2010—the principal prey of South American fur seals in Peru (Vásquez

1995, Arias-Schreiber 2000, Paredes & Arias-Schreiber 1999). I then lagged the index to the previous year under the assumption that fur seals rely on the biomass from the previous year (*t-1*) for survival and reproduction during year (*t*). Time series of anchoveta biomass were constructed from three data sources: 1925-1958 (Jahncke *et al.* 2004), 1953-1985 (Pauly & Palomares 1989), and 1989-2010 (hydro-acoustic surveys conducted by IMARPE).

The biomass of anchoveta in Peru prior to 1925 is believed to have been between 3 and 9 MT (million tons), and may have exceeded 9 MT at the onset of industrial fishing in the 1950s (Pauly & Palomares 1989). However, the fishery collapsed in 1972, and the biomass remained low (<3 MT) until 1985. Since 1985, anchovy biomass has risen from 3 to 9 MT (2010), but interannual fluctuations due to constantly occurring El Niño events are evident throughout the complete time series (*e.g.* 1982-1983, 1997-1998). For modeling purposes, I assumed that anchoveta biomass from 1880-1924 averaged 5 MT based on the frequency of El Niño events that occurred during this period.

I calculated the time series of prey abundance (A) for anchoveta by setting the highest prey biomass in the time series (20 MT in 1970) to a relative value of 1 and used this scaling factor for the entire time series. I then linked the abundance function to the index for environmental conditions that influences a loss term for the population (Eq. 4). This removed fur seals during years of diminished prey biomass.

2.3.4 Model runs and optimization

The best values of r and K^* that predicted viable numbers of South American fur seals (*i.e.,* values >0) from 1880-2010 were chosen by running the abundance model (Eqs. 2 and 4) with a variety of different parameter values and calculating the sum of squared devations (SS) between observed and predicted values. I tested 21 values of r ranging from 0.08 to 0.28 in steps of 0.01, and 73 different values of K^* ranging from 40,000 to 400,000 in steps of 5,000 for as many catch scenarios as each model permitted.

Individual matrices containing the sum of squared deviations for each combination of r and K^* were generated for each estimate of the catch time series (called catch matrices). Modeled catch (*i.e.,* the percent of *lobo marinos* skins from 1925-1945 that were assumed to be fur seals) started at 1% of the total skins exported and was increased by increments of 1% until reaching 28% for the ENSO only model (Eq. 2) and 33% for the ENSO and prey abundance model (Eq. 4), beyond which the model failed to produce viable population trajectories. Thus for the two models tested, I produced 28 and 33 alternative catch matrices respectively. From each catch matrix, I used the lowest value for the sum of squared deviations as an indicator of optimal fit to determine the best score for each scenario.

Each of the matrices or scenarios generated had 1,533 population trajectories (21 values of r ×73 values of K^*). Finally, all the values for the sum of squared deviations were compared to select the lowest value and the combination of parameters (percentage of catch, r and K^*) that best predicted fur seal abundance over time for 42,924 simulations for models run under Eq. 2 and 50,589 simulations using Eq. 4. All models and optimization procedures were run in statistical program R v.2.10.1 and Microsoft Excel 2011.

2.4 Results

The minimum sum of squared deviations from all catch matrices indicated that the best population parameters were $r = 0.20$ and $K^*= 115{,}000$ seals ($SS = 0.54 \times 10^9$). These values were derived from the ENSO modified model (Eq. 2) and corresponded with 8% of the known catch pertaining to fur seals (Fig. 2.3). As expected, combinations of r and K^* values were inversely related such that a decrease in r leads to an increase in K^* (Fig. 2.5). The model that linked temperature anomalies to prey biomass from the previous year (Eq. 4) did not improve the fit of the model to the data (r=0.16, K^*=115,000, SS= 0.55×10^9 under a 9% catch scenario). Thus, I adopted the simplest model (Eq. 2).

The population trajectory I derived yielded a ‘one-way’ declining path that is characteristic of many exploited marine mammal populations (Christensen 2006). It shows that high catches during the first two decades (1925-1945) reduced the Peruvian fur seal population by more than 80%. Recent counts (2007) are about 20% of the average 68,000 (range 39,000-98,000) individuals estimated to have occurred before the onset of sealing (Fig. 2.6).

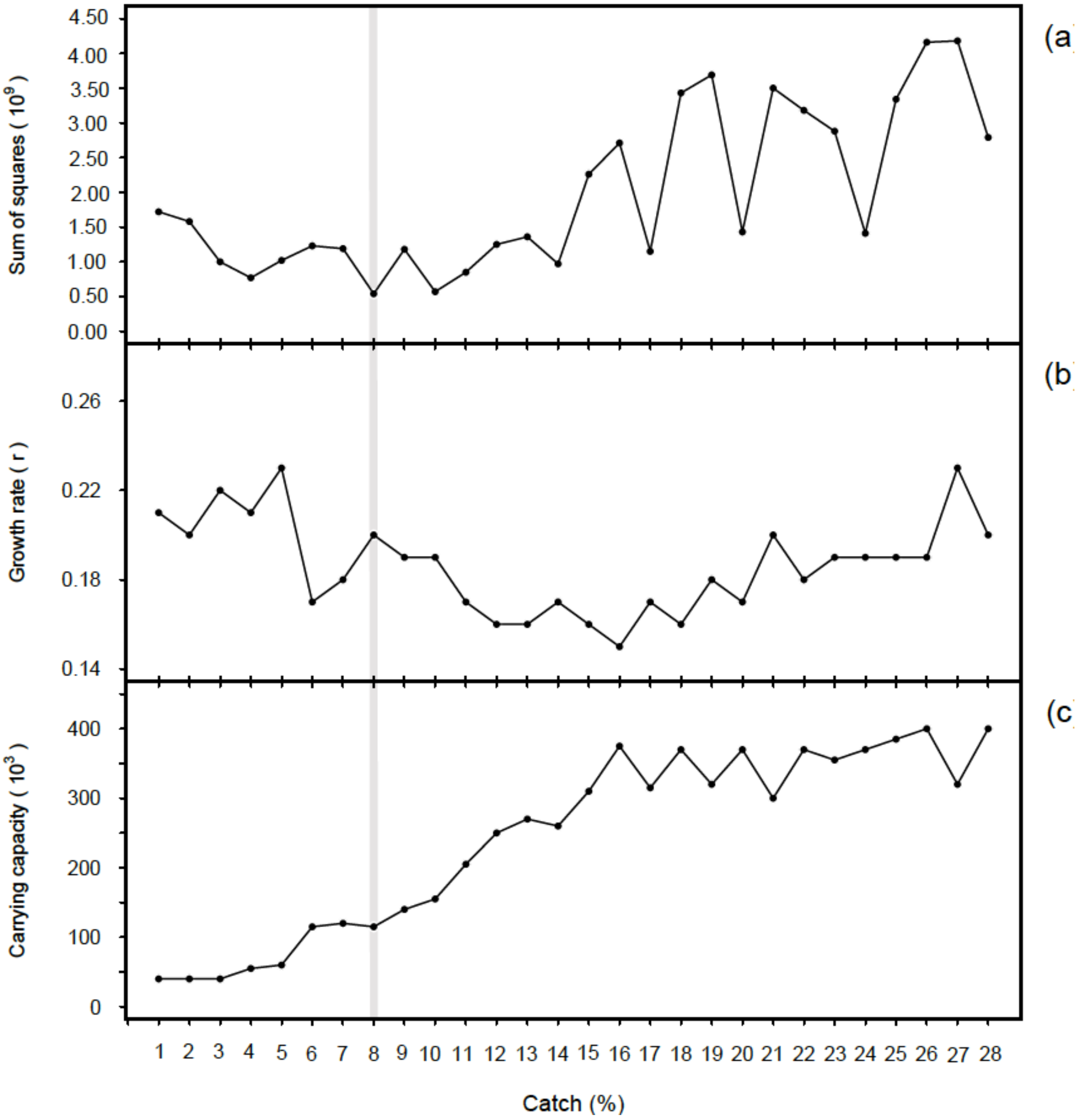

Figure 2.3 Combinations of (a) minimum sum of squared deviations, *SS*; (b) growth rate, *r* and (c) carrying capacity, *K* values for 28 catch matrices for models that reconstructed numbers of South American fur seals in Peru from 1880-2010. Catch is the proportion of reported *lobos marinos* skins exported from 1925-1945 that were assumed to be South American fur seals. Minimum sums of squares correspond with best population model that corresponds to 8% of fur seal skins (*SS* = 0.54 x 10^9, *r* = 0.20, *K** = 115,000) as shown by the shaded region.

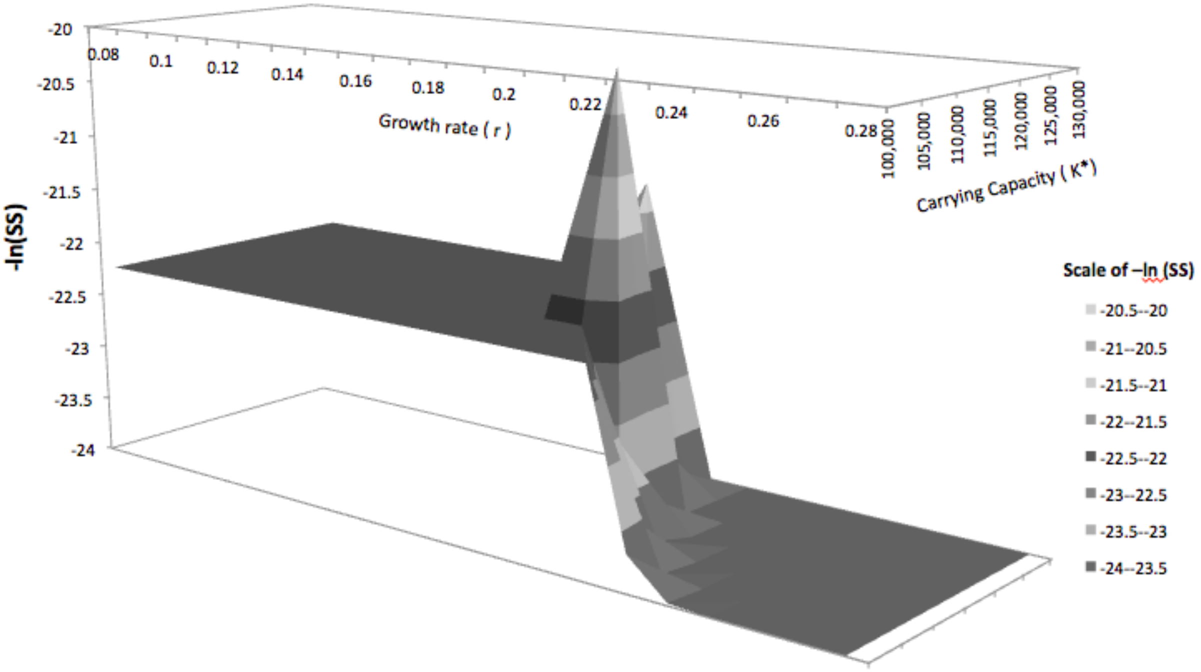

Figure 2.4 Three dimensional surface plot showing low (light gray) to high (dark gray) scores for the negative natural logarithm of sums of square scores (-ln[SS]) that resulted from the final optimization procedure to estimate best population parameters *r* and *K** of all population models. Negative natural logarithm transformation inverts the *SS* scale. Thus, the best score (*SS* = 0.54 x 10^9) is shown as the dark peak that corresponds with parameter values *r* = 0.20 and *K** = 115,000.

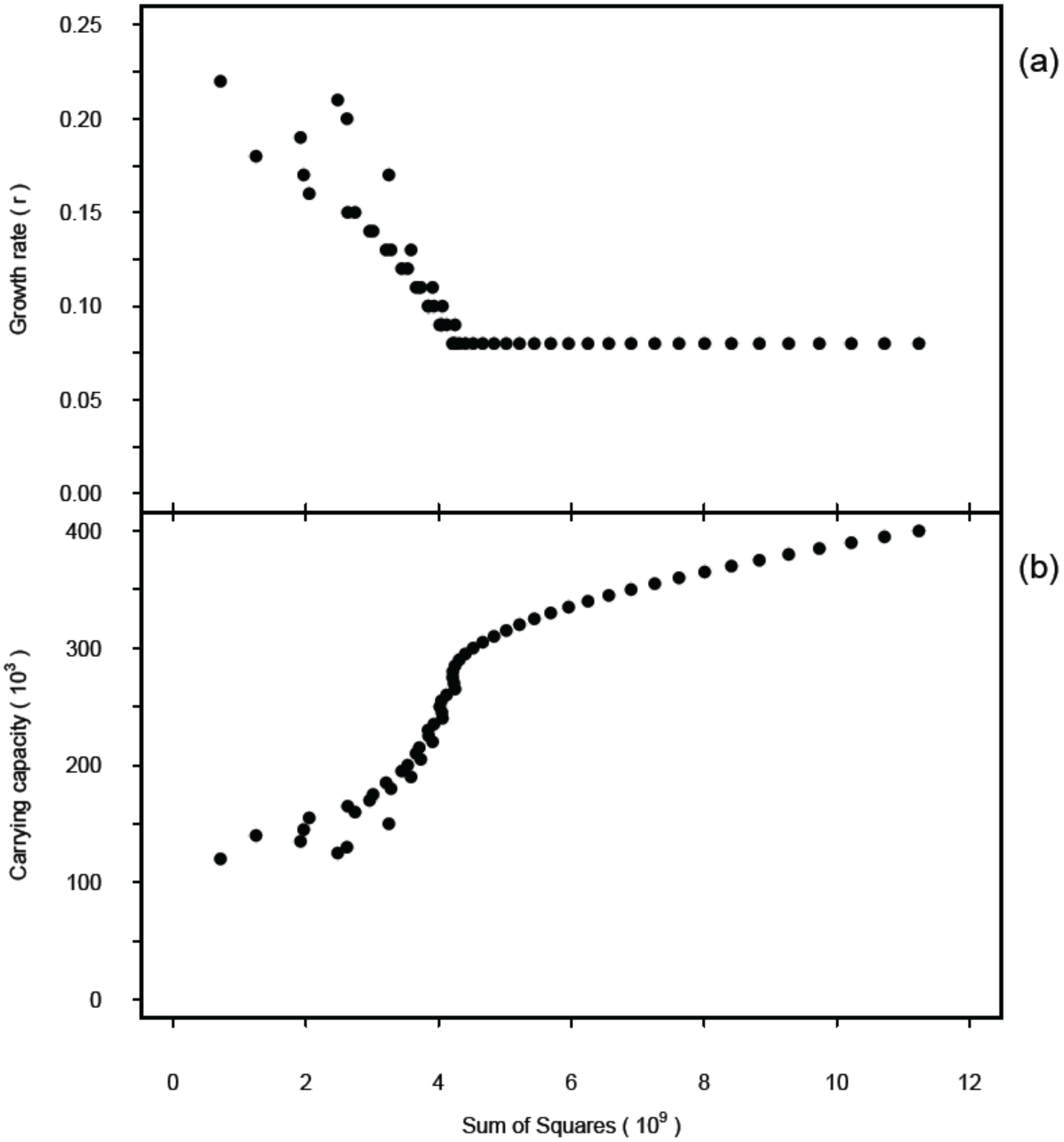

Figure 2.5 Combinations of (a) growth rate, *r* and (b) carrying capacity, *K** according to *SS* scores (on x-axis) that yield viable population trajectories for South American fur seals in Peru. They show the expected inverse relationship between population parameters *r* and *K**.

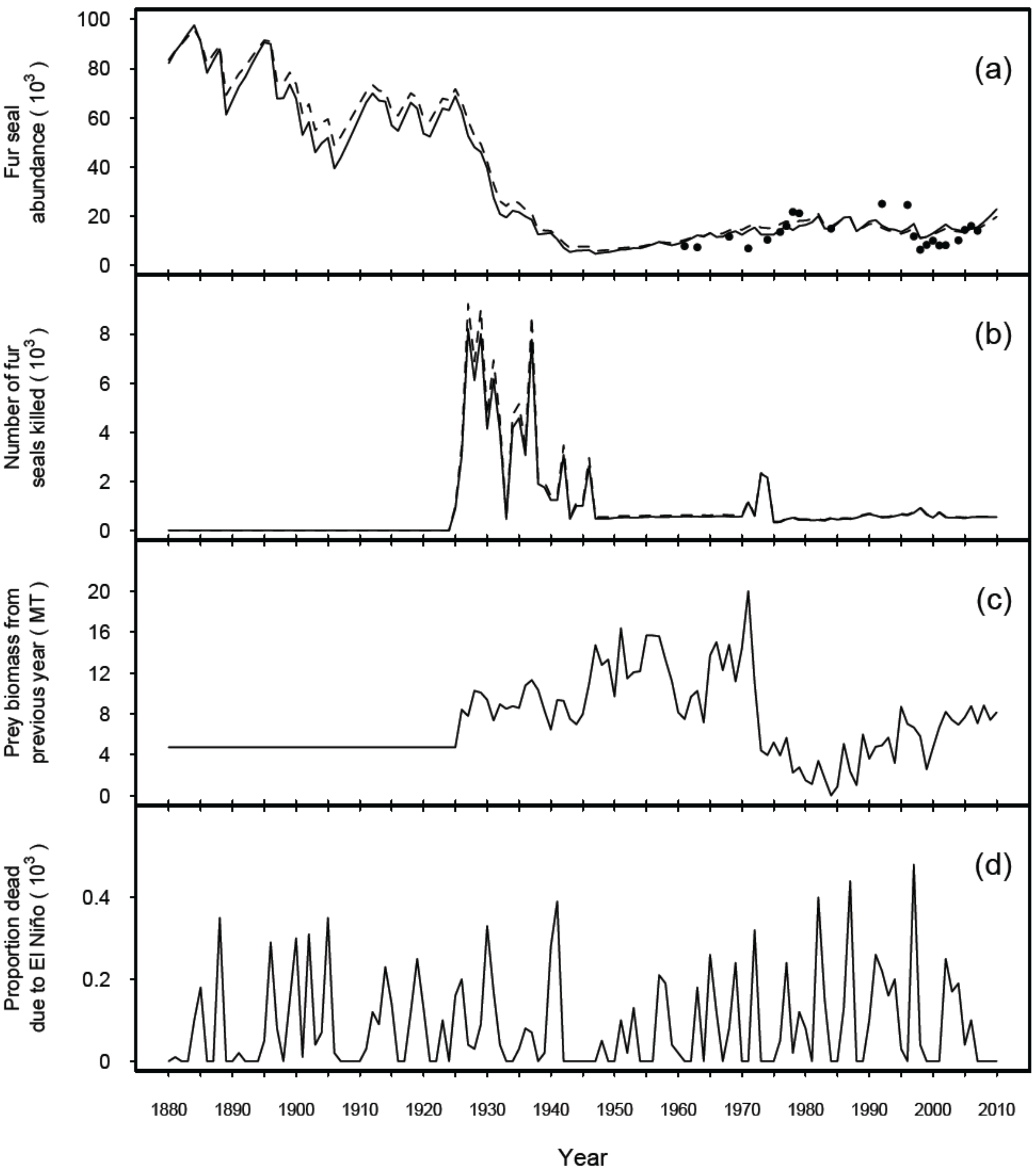

Figure 2.6 South American fur seal population model predictions and components. (a) Population trajectory for South American fur seals in Peru from 1880-2010 as obtained by the abundance model (solid line, Eq. 2; dashed line, Eq. 4) and the observed census counts (circles). Both models included (b) the number of fur seals that were killed due to human activities (solid line, Eq. 2; dashed line, Eq. 4) and (d) the proportion of fur seals estimated that died due to El Niño events. The dashed line (a) incorporated prey biomass (c).

2.5 Discussion

An intrinsic growth rate (r_{max}) of 0.20 and a potential carrying capacity (K^*) of 115,000 individuals were the population parameters that best explain the relative harvests and abundance of South American fur seals in Peru from 1880 to 2010. Based on environmental data available since 1880 and catch information available from 1925, my model suggests that there may have been ~68,000 (range 39,000-98,000) individuals before the onset of reported harvest activities in 1925 and that commercial harvest was responsible for the >80% decrease in fur seal numbers by the mid-20th century (Fig. 2.6). The numbers of fur seals present before harvesting (1880-1925) were ~60% of the potential carrying capacity of 115,000 individuals for South American fur seals in Peru (*i.e.,* the number that could have been supported in the absence of removals due to El Niño and sealing). However, numbers predicted by the model to have been present prior to 1925 could have been higher if sealing had been occurring in Peru during this time period.

Sealing had been a thriving industry in the southern hemisphere since the late 18th century (Lento *et al.* 1997, Riedman 1990), but information about numbers of pelts taken are unavailable in Peru prior to 1925. It would appear however from my model that fur seals constituted a mere 8% of the total *lobo marino* pelts exported (compared to the potential 92% that were sea lions). This small percentage contrasts sharply with the high commercial value of fur seal pelts in the international market (Reeves *et al.* 1992, Weber *et al.* 2004), and suggests that the international sealing industry may have not have been significant in Peru.

The logistic growth model I used was simple but reasonable for estimating potential carrying capacity and the high intrinsic growth rate of South American fur seals. Obtaining a better understanding of the driving forces that affect vital rates and population dynamics of this species will require developing a sex-age structured model. However, the type of information needed for such models (*i.e.,* birth and survival rates by sex and age class) is not currently available for fur seals in Peru. Thus, a more complicated model is not justified, and the logistic model is preferred in the absence of other information because of its simplicity (principle of parsimony).

I structured my population growth model to include the main factors that negatively affected fur seal abundance in Peru from 1880-2010 (catch, prey biomass and environmental conditions) and linked these factors to a wide range of possible growth rates (*r*) and levels of carrying capacity (*K**). However, quantifying each factor without data required making assumptions about how they contributed to fur seal mortality.

2.5.1 Catch

Catch comprised four categories (commercial harvest, unreported harvest, poaching and bycatch) for which I made a number of reasonable assumptions in the absence of information on exact numbers of dead fur seals over an extended time. Model results of mortality by catch categories showed that the commercial harvest accounted for the largest number of fur seals killed. However, only 8% of the seal skins exported from Peru from 1925-1946 appear to have been from fur seals. The remaining 92% of the exported skins that had to have come from South American sea lions may reflect their wider distribution and more predictable presence along the entire coast of Peru. Sea lions seem to have many more colonies than fur seals, and there are more reports of sea lions being culled to use their hides for industrial purposes (Kostrisky 1963).

2.5.2 Prey abundance and environmental conditions

Since anchoveta is economically and ecologically the most important component of the Humboldt Current ecosystem, I linked the potential carrying capacity of Peruvian fur seals in the model (*K**) to anchoveta biomass and the strength of the ENSO events. I derived the time series of anchoveta biomass estimates from multiple sources that used different methods and data of variable quality. Hence, the time series must be considered a rough proxy for anchoveta biomass during my study period.

Another implicit assumption of my model was that South American fur seals did not switch their diets and consume other prey species during years of diminished anchoveta abundance. Anchoveta has been reported to make up to 85% of the South American fur seal diet during non El Niño years (Majluf 1987a, Vásquez 1995, Paredes & Arias-Schreiber 1999, Arias-Schreiber 2000, Arias-Schreiber 2003, Zavalaga *et al.* 1998). I therefore assumed that fur seals ate only anchoveta and modeled fur seal population growth based only on anchoveta consumption as did Muck and Fuentes (1987). Other prey items in fur seal diets have been reported (*e.g.* sardines and mackerel) during El Niño years (Majluf 1985), but the extent of prey switching or diversification of the diet is unknown. There are unfortunately no long-term studies on temporal variation in diet and consumption for South American fur seals to improve this aspect of the model.

El Niño events are widely recognized to reduce the abundance and availability of prey and cause the starvation of South American fur seals (Apaza *et al.* 1998, Barber & Chavez 1983, Chavez *et al.* 1999, Majluf 1991a, Glynn 1988). I quantified this environmental effect on fur seal mortality using the relationship between the sea surface temperature anomalies from the 3.4 El Niño Region and the number of dead animals counted during the 1997/98 El Niño as a measure of the reduction in anchoveta (prey) biomass. Although the distance between the 3.4 El Niño Region and the coast of Peru is considerable, significant relationships with the sea surface temperatures at this location have been reported (Purca 2005). Thus, I used the anomalies from the 3.4 El Niño Region as a proxy for the effect of the environment on fur seal mortality in Peru. The number of animals that die due during an El Niño event has only been quantified once, during the 1997/98 event, which meant I could only scale the number of animals affected by sea surface temperature anomalies to the proportion of animals that died in 1998 (Apaza *et al.* 1998, Arias-Schreiber & Rivas 1998).

I assumed that South American fur seals were sensitive to environmental changes that might be associated with sea surface temperature between July (3 months prior to the breeding season) and March (3 months after breeding), with the breeding season included. This 9-month window is likely a time of high-energy expenditure for female fur seals. It includes the last trimester of gestation (July-September) when reproduction may be terminated (Trillmich & Limberger 1985, Trites & Donnelly 2003). It also includes the pupping period (October-December) and a time of intensive energetic demands on lactating females that are nursing pups and any other offspring they may not have weaned (January-March) (Guinet *et al.* 1998, McKenzie *et al.* 2005, Pitcher *et al.* 1998). Bioenergetic models and energy budgets are unavailable for South American fur seals, but the maternal attendance studies conducted at Punta San Juan, Peru are consistent with this 9-month window being a time of high energy requirements (Majluf 1987a) .

2.5.3 Population growth rate, carrying capacity and dispersal

The 11 recognized species of fur seal share many common life history traits. They have polygynous mating systems, with males beginning to defend territories at breeding rookeries between 6 to 10 years of age. Females become sexually mature at 3 or 4 years of age, give birth to one pup per year, and go on foraging trips that last 1.5 – 2.5 days on average (Majluf 1987a) to maintain the supply of milk necessary to nurse their pups until weaning. Whether or not the 11 fur seal species also share common intrinsic growth rates is unknown.

Maximum reported growth rates (r_{max}) of fur seals range from 0.02 to 0.22 (Boveng *et al.* 1998, Eberhardt & Siniff 1977, Wickens & York 1997, Hucke-Gaete *et al.* 2004, Fedorov & Philander 2000, Boyd *et al.* 1995). Fur seal intrinsic growth rates are not as commonly calculated compared with population rates of increase, which are based on numbers of pups born over shorter periods of time. However, some r_{max} values are available for some species of fur seals. At the low end of this r_{max} scale are Cape fur seals (*A. p. pusillus*, 0.03, Wickens & York 1997) . Species with the potential for moderate rates of growth include Subantarctic fur seals (*A. tropicalis*, 0.14, Wickens & York 1997). Those with the highest intrinsic population growth rates are the Antarctic fur seal (*A. gazella*, 0.20, Hucke-Gaete *et al*. 2004) and South American fur seals in Peru (0.20, my study). Consequently, the rate of increase calculated for the recovering population of South American fur seals at Punta San Juan in southern Peru after a dramatic decline due to the 1997/98 El Niño is 0.26 (Chapter 3). However, the rate calculated for the population of South American fur seals off Uruguay is 0.02 (Lima & Páez 1997), which is low compared to my estimate. This difference may further underline other differences recently shown between the genetic and morphological characteristics of populations of South American fur seals on the Atlantic and Pacific coasts of South America (Oliveira 1999, Oliveira *et al.* 2008, Oliveira *et al.* 1999).

Like all fur seal species, Antarctic fur seals were nearly driven to extinction during the 18th and 19th centuries when they were hunted for their fur (Payne 1977). Protection (Hodgson *et al.* 1998) has enabled Antarctic fur seals to grow steadily since the 1950s at a rate of 10% or more per year, allowing them to recover significantly at certain sites (Hucke-Gaete *et al.* 2004). However, protection under CITES and high intrinsic growth rates have not resulted in a return to pre-exploitation numbers of South American fur seals in Peru (Fig. 2.6). Antarctic fur seals have also not yet reached pre-exploitation levels due perhaps to environmental change and fluctuations that occur when populations approach carrying capacity (Hucke-Gaete *et al.* 2004). This could be another similarity with South American fur seals—whose population recovery appears to be hampered by the combined synergistic effects of poaching, competition with the anchoveta fishery, and catastrophic reductions in prey abundance caused by natural occurring El Niño events in the waters off Peru. Another possible hypothesis to the lack of recovery in South American fur seals may be that carrying capacity has changed to a lower level between the first half of the 20th century and present day. This would imply that fur seals on the coast of Peru would not be able to recover to historic levels of estimated K^* under current environmental conditions.

The anchoveta fishery began in Peru in the 1950s and quickly became one of the world's largest single species fisheries. This fishery may also be the biggest competitor of South American fur seals (Muck & Fuentes 1987). I modeled prey abundance available to fur seals at a given time by lagging biomass estimates from 1925-2010 by one year. This was to account for consumption of biomass by fur seals in the previous year and introduced stochastic effects of fluctuating prey biomass on seal numbers. For years prior to 1925 (1880-1924), I assumed that the anchoveta biomass was constant (*i.e.,* 5 MT), which was >50% of the biomass during the remainder of the anchoveta time series. A more realistic way to account for the effects of changes in prey availability on fur seal numbers would be to model the spatial availability of the prey for foraging fur seals. Unfortunately, this information does not currently exist for fur seals in Peruvian waters.

My population model assessed the population status of South American fur seals within the coastal waters of Peru, and did not contemplate the dispersal of fur seals beyond these limits. However, fur seals are known to disperse widely during El Niño events, often to southerly locations in search of prey. Anchoveta are known to travel south towards Chile and move deeper in the water column as sea surface temperatures increase. These observations are consistent with the colonization of the islands to the north of Chile that occurred with the start of the 1982 –1983 El Niño (Guerra & Torres 1987). Increases in fur seal numbers in northern Chile have continued since that time, as numbers have gradually decreased at the colonies in the extreme north of their range in Peru (Guerra & Portflitt 1991, Sielfeld 1999).

This could be one explanation for the lack of a better fit between the observed and predicted counts in my population model.

North to south movements of fur seals have been documented by sightings in southern Peru (at Punta Atico 16°00'S and Punta Coles 17°42'S) of individuals originally tagged further north (at Punta San Juan 15°12'S). Some of the fur seals from Punta San Juan were also seen as far south as Iquique and Antofagasta in northern Chile in 1998 (W. Sielfeld, pers. comm.). Breeding colonies were also detected close to Taltal, Chile (25°40'S) in 2005 (H. Paves, pers. comm.), and the northern breeding limit in Peru has also recently expanded (Isla Foca, Piura 5°20'S discovered in 2005; D. Olaechea, pers. comm.). These observations show that fur seals have an innate ability to disperse and colonize new areas.

My population model only encompassed the Peru portion of the distribution of the Pacific range of South American fur seals. Ideally, it should have contemplated fur seal counts and rookeries off the coast of northern Chile as well since there is evidence of individual fur seals moving along breeding sites within the extent of the range for the species during and after El Niño events.

I tested different hypotheses using surrogate data to better understand the sensitivity of my population model to uncertainty in the numbers and timing of fur seal harvests. To determine what would happen if commercial harvest had begun prior to 1925, I ran two models with catch values in the earlier years (1880-1924) using surrogate harvest data. The first model assumed that the times series of catches that occurred from 1925-1946 also occurred from 1880-1924 (replicated twice), and resulted in a higher predicted K^* and a lower r value. For the second model, I fixed the catch rate at 2,533 fur seals harvested each year (the average annual catch between 1925-1946) for years 1880-1924 and found a similar change in my model parameters—i.e., K^* also increased and r decreased. Thus, in terms of potential carrying capacity, the abundance of seals in Peru would have had to be higher than 115,000 individuals if there was harvesting of fur seals previous to 1925. However, the r value always remained ≥ 0.18 which is considered high for any mammalian species.

2.5.4 Conservation issues for South American fur seals in Peru

The abundance of South American fur seals in Peru has changed drastically over the past century. My model shows that the severe population reduction that could have led to the extinction of fur seals by the mid-20th century was caused by a combination of hunting (first legal harvest and then illegal poaching), fluctuating prey biomass and reoccurring El Niño events. The last available count of ~14,000 individuals in 2007 for the Peruvian population is still well below the average population of ~68,000 believed to have been present before 1925. However, the high r_{max} and high rate of dispersal suggest it has the ability to recover.

Many pinniped species suffered from the effects of heavy exploitation during the sealing era (*i.e.*, reduced and isolated populations, genetic bottlenecks, etc.). Some, such as the Japanese sea lion and Caribbean monk seal are now extinct. Most species of pinnipeds appear to be no longer at risk of extinction, although a few have been slow to reoccupy their ranges and have questionable futures (Riedman 1990). In Peru, harvesting of South American fur seal has been banned since 1959, but poaching continues to occur at unknown levels. Fishermen constantly complain that fur seals damage their nets and reduce their catches, especially in gillnet fisheries (Arias-Schreiber 2003, Arias-Schreiber 1993b).

Although it is acknowledged that interactions between seals and fisheries mostly affect the sympatric South American sea lion (Arias-Schreiber 1993a, Arias-Schreiber 1993b), fur seals are also held responsible, and therefore also fall victim to the clandestine killings by some fishermen. Some fishermen are known to kill fur seals with shotguns, harpoons, dynamite, and poison (Arias-Schreiber 1993b). Fishing nets also entangle and kill fur seals that are transiting between land and their feeding grounds (Majluf *et al.* 2002). In Peru, Arias-Schreiber (1993b) reported that it is common for some fishermen to kill and use pinnipeds (as bait to catch saltwater snails or winkles *Thais chocolata*). However, the incidence of illegal catches and their impact on populations of fur seals is not known. Petitions by fishermen are periodically made to allow the legal harvesting of fur seals and sea lions in Peru — but, the slow recovery and low numbers relative to pre-sealing abundance in 1880-1924 suggests that South American fur seals may not be able to withstand a sustainable harvest in Peru at current levels of abundance despite their extremely high potential intrinsic growth rate (0.20).

The industrial fishing fleets along the coast of Peru may threaten the pelagic resources on which fur seals depend. These fisheries started in the 1950s and 1960s, and contributed to several collapses of the anchoveta upon which the fur seals depend (Pauly & Palomares 1989, Pauly & Tsukayama 1987). At protected sites during years of good environmental conditions, fur seals have the potential to recover. Fur seals were quick to recover from El Niño events in the past when prey returned and became readily available again. However, they may no longer be able to do so if fisheries remove and reduce the biomass of anchoveta available and needed by fur seals to recover between El Niño events. Populations of fur seals are far smaller today than before fisheries developed, and they appear to be increasing at slower rates compared to fur seal species in areas without fisheries and with abundant food (*i.e.,* Antarctic fur seals around South Georgia, Hucke-Gaete *etal*. 2004, Payne 1977) .

The combined effects of repeated El Niño events and extreme anthropogenic pressures have caused a genetic bottleneck in Peru's population of fur seals (Oliveira *et al.* 2006, Oliveira *et al.* 2009). El Niño is a recurrent and presumably ancient event that may have existed for 5,000 to 2 million years (DeVries 1987, Sandweiss *et al.* 1996). Many species living in marine environments affected by ENSOs have likely adapted to an unpredictable ecosystem by developing flexible life history traits, which allows them to survive changing environmental conditions (Majluf 1987a). However, populations that have been severely depleted, such as those in Peru, may not be able to survive many more events of the magnitude of the 1997/98 El Niño (Oliveira *et al.* 2006, Oliveira *et al.* 2009). The 1997/98 El Niño caused such a drastic decline in effective population size that it could have compromised the evolutionary potential of the species to respond to environmental changes.

The population abundance of South American fur seals has declined over the past century. The available data indicate that the population in Peru was more abundant before harvesting occurred, and that the harvests in combination with mortality associated from reoccurring El Niño events reduced them to critically low numbers. The high intrinsic growth rate predicted by the model suggests that South American fur seals have persistence to thrive in a disturbed environment. Conserving current abundance and promoting population growth will require (i) a continued harvest ban, (ii) collection of information on bycatch, incidental captures and illegal poaching of fur seals, (iii) regulation of anchoveta fishing quotas (that allocate prey for apex marine predators in Peruvian waters) and (iv) strict protection of fur seal breeding rookeries (*i.e.,* guano reserves and other known breeding sites). These four measures are needed to protect the slow recovering population of South American fur seals in Peru before another strong El Niño pushes them once again to the brink of extinction.

Chapter 3: Prey abundance affects the birth rate and timing of pupping of South American fur seals in Peru

3.1 Summary

Reductions in the abundance and availability of prey due to fisheries or natural events are generally believed to cause high mortality and reproductive failure among pinniped populations. However, the relationship between food and the population biology of marine mammals is poorly understood. The goal of my study was to assess whether a relationship could be established between fluctuations in prey biomass and reproduction of South American fur seals (*Arctocephalus australis*) in Peru. Using daily numbers of pups and adult fur seals counted during 20 breeding seasons at Punta San Juan (1984–2010), I calculated the annual mean dates of birth, the durations of the breeding seasons and the relative birth rates—and compared these measures of reproduction to annual estimates of biomass of Peruvian anchoveta (*Engraulis ringens*)—the principal fur seal prey. During this 25-year period, annual changes in anchoveta abundance varied as much as 12-fold, and the rookery experienced periods of increases, declines and abandonment. I found a significant positive relationship between anchoveta biomass and the mean birth date ($r^2 = 0.66$, $P<0.01$) and between biomass and the subsequent ratio of pups to adult females ($r^2 = 0.59$, $P<0.01$) in the following year. I also found a 2-week shift in the mean birth date over 25 years that may reflect a change in the age structure of the population (whereby older females gave birth later than younger females). It also appears that years with low anchoveta biomass decreased pup production and diminished recruitment of younger females. Monitoring daily numbers of fur seal pups born and adult females present thus appears to be a useful means to assess the feeding conditions encountered by South American fur seals in Peru relative to environmental conditions and removals of prey by fisheries.

3.2 Introduction

Animals must be able to anticipate and adjust to variability in climate, prey abundance and predation to maximize survival and reproductive success (Murphy 1968, Gillespie 1977, Price *et al.* 1988, Rutberg 1987, Follet 1985). In general, there is a predictable seasonal component to these environmental factors that dictates the life cycles of most vertebrate species, such as their timings of breeding, the synchronization of births, and the patterns of movements and migrations (ungulates: Langvatn *et al.* 2004, Loe *et al.* 2005, rodents: Scott 1986, Lambin 1993, pinnipeds: Boyd 1991, Trites & Antonelis 1994, Trites 1992, Majluf 1992, Soto *et al.* 2004, Gibbens & Arnould 2009). However, there is also a certain level of variability that surrounds these long term average environmental conditions, to which vertebrate species must adjust. Documenting the plasticity with which species adjust their timing of breeding or other life history behaviours may provide a measure of the environmental conditions within which they live.

Among pinnipeds, reproductive events revolve around a rigid annual schedule that involves mating, delayed implantation, birth, pup rearing, dispersal or migration (Riedmann 1990). The availability of food for mothers and young, the risk of predation, and prevailing climate conditions all have bearing on the general timing and locations of the major life history events (Follet 1985, Riedmann 1990). However, pinnipeds also display considerable plasticity in the precise timing with which they can adjust dates of birth and alter their movement patterns to maximize their survival and reproductive success. Prey shortages, for example, have been known to affect the timing of implantation (Boyd 1996, Berger 1992, Wickens & York 1997); increase the length of foraging trips of lactating females (Boyd 1996, Lunn *et al.* 1994, Soto *et al.* 2004, Trillmich *et al.* 1986); decrease growth rates of pups (Guerra & Portflitt 1991, Lunn *et al.* 1994, Majluf 1987a, Georges & Guinet 2000, Lunn *et al.* 1993); increase pup mortality (Georges & Guinet 2000, Guerra & Portflitt 1991, Trillmich & Limberger 1985); reduce numbers of pups born (Forcada *et al.* 2005, Guerra & Portflitt 1991); delay the timing of births (Gibbens & Arnould 2009, Majluf 1992, Boyd 1996); and extend the length of breeding seasons (Soto *et al.* 2004, Trites 1992, Trites & Donnelly 2003). Thus, the annual timings of life history events of pinnipeds reflect a combination of predictable and unpredictable changes in environmental conditions.

Punta San Juan is home to one of the most important breeding colonies of South American fur seals in Peru (Fig. 3.1). Counts and behavioural observations made at this site for more than 25 years have recorded extreme population fluctuations and changes in their breeding ecology. These data document the abandonment of most beaches due to death or migration in 1997, and follow the subsequent reoccupation and 26% increase in numbers since 2003 (Fig. 3.2). Such counts made before and after the population decline may provide insight into the environmental factors that influence the life cycle and population dynamics of South American fur seals in Peru.

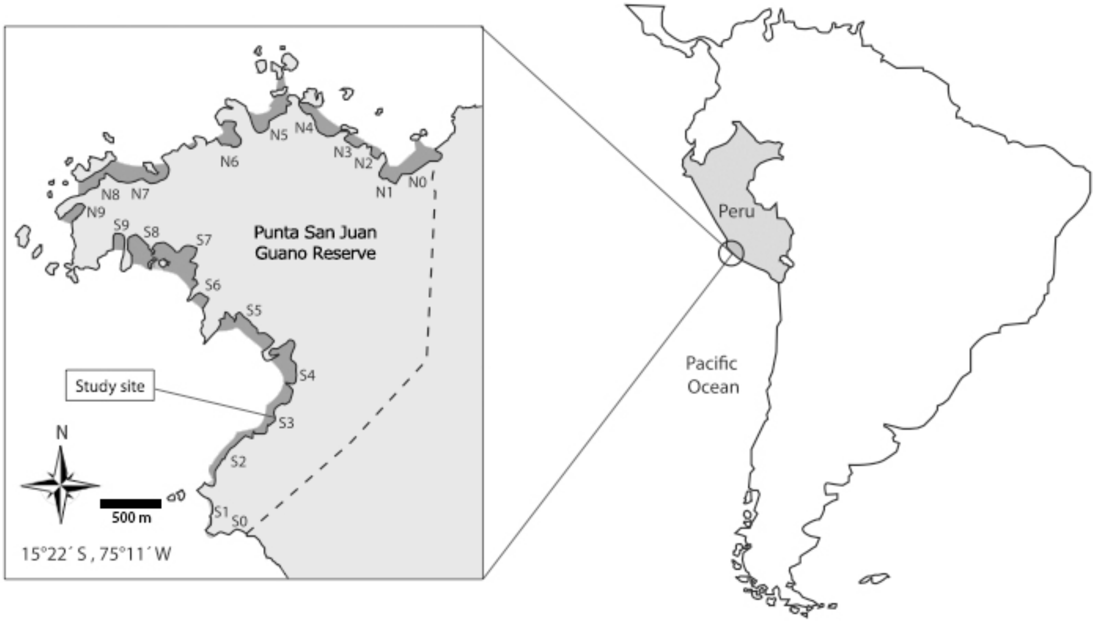

Figure 3.1. Location of the Punta San Juan guano reserve in Peru (shaded in gray), and an insert of Punta San Juan showing all fur seal breeding sites with an arrow pointing to Study Site S3, the main breeding colony of South American fur seals. The dashed line marks the concrete wall surrounding Punta San Juan. Map of Punta San Juan guano reserve adapted from Paredes and Zavalaga (2001) reprinted with permission of R. Paredes.

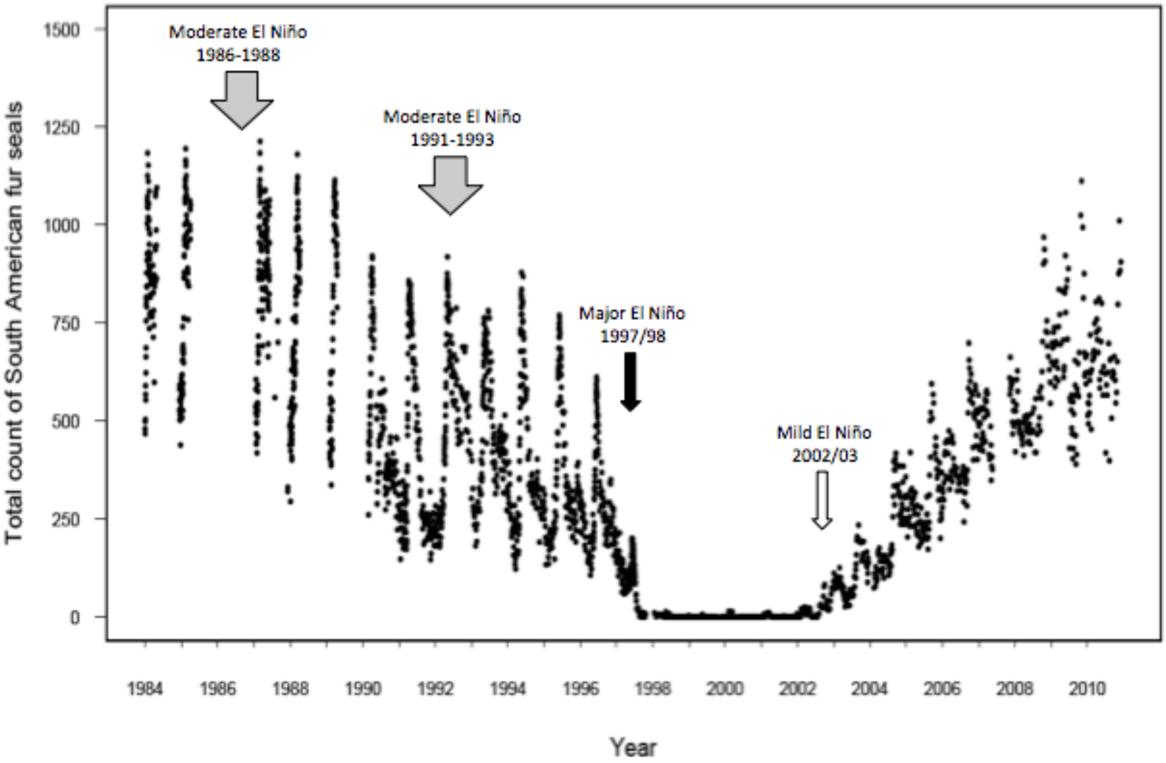

Figure 3.2. Time series showing counts of South American fur seals at Study Site S3, the main fur seal breeding site at Punta San Juan, from 1984 to 2010. Arrows point to main El Niño events of mild (2002/2003), moderate (1986/1988, 1991/1993) and major (1997/1998) intensity that have taken place throughout the study period.

In Peru, South American fur seals (*Arctocephalus australis*) are tied to the strong upwelling Humboldt Current ecosystem (Majluf 1987a, Majluf 1987b) — one of the most productive marine systems in the world (Gutiérrez *et al.* 2007, Bouchón *et al.* 2000, Carr 2002). This marine ecosystem is dominated by Peruvian anchoveta (*Engraulis ringens*), which are the primary prey for large populations of seabirds and marine mammals along the coast of Peru (Bakun & Weeks 2008, Jahncke *et al.* 2004, Majluf & Reyes 1989, Ballance *et al.* 2006). The Humboldt Current ecosystem is also one of the most unpredictable ecosystems in the world due to El Niño events, and the synergistic effects of fishing, poaching, and bycatch (Chapter 2). All of these factors drive the extreme fluctuations of South American fur seal numbers, which were reduced in Peru by 72% following the strong 1997/98 El Niño (Arias-Schreiber & Rivas 1998, Oliveira *et al.* 2006, Oliveira *et al.* 2009).

The goal of my study was to assess whether a relationship exists between fluctuations in prey availability and reproduction of South American fur seals in Peru using 25 years of data collected at Punta San Juan (1984–2010). I therefore calculated reproductive rates, mean dates of birth, and durations of breeding seasons from daily counts of pups born and adults present — and compared these metrics of reproduction with annual estimates of biomass and fishery landings of Peruvian anchoveta. I show that monitoring daily numbers of fur seals on breeding colonies is a useful means to assess the feeding conditions encountered by South American fur seals in Peru relative to environmental conditions and removals of prey by fisheries.

3.3 Materials and methods

3.3.1 Study site

Data were collected between 1984 and 2010 at Study Site S3 at the Punta San Juan guano reserve (PSJ) in the province of Ica in southern Peru (15°22' S, 75°11' W; Fig. 3.1). This major breeding site for South American fur seals is a 54-hectare headland with 20 sites (beaches and rookeries combined) along its coastline. Study Site S3 is approximately 120 × 50 m in area and is surrounded by a 25-30 m high cliff, which allows observations and direct counts without disturbing the seals.

Punta San Juan is part of a recently formed network of guano reserves administered by the Peruvian governmental institution SERNANP (*Servicio Nacional de Areas Naturales Protegidas* — the National Protected Areas Service) in conjunction with AGRORURAL, a department of Peru´s Ministry of Agriculture, whose main goal is to harvest and distribute bird guano as fertilizer to Peruvian farmers. Bird guano builds up from resident nesting 'guano birds' (Red eyed cormorants, Peruvian boobies and Peruvian pelicans) at sites such as Punta San Juan. Measures of protection have been given to the guano birds since the early 1900s (*i.e.,* concrete walls that isolate headlands from predators and human disturbance, and the presence of a permanent guard). This protection has in turn made guano reserves alternative refuges for many other marine vertebrate species such as South American fur seals, South American sea lions, Humboldt penguins and other sea birds which gather to rest and breed in large numbers (Majluf 1991b). Within this network of guano reserves, Punta San Juan is a special case with permanent staff of resident field biologists that have monitored the resident populations of seabirds and marine mammals year-round since the early 1980s.

3.3.2 Fur seal counts

Fur seals were counted 3–7 times each week during the breeding season (October – December) and 1–3 times per week during the non-breeding season (January – September) throughout the study period (1984–2010). Counts began at 0600 from high vantage points using hand-held tally counters and 20×40 or 10×50 binoculars. During counts, fur seals were divided into categories according to sex and age classes: pups, juveniles, sub-adult males, territorial males, adult females and undetermined. Since the early 1980s, Study Site S3 has held >40% of the abundance of South American fur seals at Punta San Juan (Majluf 1987a). Because of this and its lack of visual obstacles and accessibility that permitted full visibility of fur seal colony from cliff tops, this beach was used as a proxy to monitor real-time fluctuations in the resident population. Thus, the time series for beach S3 has the longest and most detailed counts available from Punta San Juan from 1984–2010 (with the exception of years 1986 and 2007, when no observations were made).

3.3.3 Breeding behaviour

Three response variables (number of pups born, mean birth date and pupping synchrony) were estimated from direct pup counts to characterize the breeding season and understand interannual variability and potential relationships with the environment. The direct pup counts from October 1st – December 31st of each year were fit with three types of sigmoid models using the (i) Gompertz function, (ii) three-parameter logistic function and (iii) four-parameter logistic function, following methods in Trites (1992). Model fits with best (lowest) AICc scores (Akaikes Information Criterion for small sample sizes) were used to characterize breeding parameters for all years with counts. Exploratory analysis showed that pup counts (y) as a function of date (x) were best described using the four-parameter logistic function:

$$y = a + \frac{b-a}{1+e^{c(d-x)}} \qquad \text{Eq.1}$$

with asymptotes at the left (*a*) and right-hand (*b*) ends of the *x*-axis and scales (*c*) the response to *x* at about the midpoint (*d*) where the curve has its inflexion (Crawley 2007). Fits of this four-parameter logistic model to pup counts were tested under a significance level of α=0.05.

Mean birth dates were calculated as the date in the *x*-axis that corresponds to the inflection point in *y* (*c* in Eq. 1). The length of the breeding season was estimated as the number of days it took to produce the 90 percentile (between 5- 95%) of the total number of pups born. The total number of pups born was estimated as the mean number of pups from the 99-100% percentile of the predicted model. Additional measures estimated to describe breeding seasons included the maximum pup count, which was the maximum number extracted from direct counts of pups registered; the maximum number of pups born per day, which was determined by calculating the daily difference of the cumulative numbers produced by the logistic function for each year; the date the first pup is born, which was estimated as the date when direct pup counts grow accumulatively on a day to day basis; and the number of days it took to produce 50% of the pups born.

3.3.4 Prey abundance

Annual records of anchoveta biomass were used as metrics of prey abundance that may be available for South American fur seals. Anchoveta biomass was estimated by acoustic surveys conducted off the entire coast of Peru (3-18°S) by IMARPE (Instituto del Mar del Peru/Peruvian Marine Research Institute). During the period of my study, acoustic surveys to estimate anchoveta biomass were conducted from 1–4 times each year. For years with >1 fish survey, I chose the survey based on i) latitude (surveys had to be complete at all latitudes) and ii) dates (surveys had to have occurred before the onset of the fur seal breeding season of that year). Anchoveta biomass from the two closest surveys were averaged only when an incomplete survey was available (and only had to be done for 1986).

3.3.5 Statistical analyses

Normality, outliers, correlation and colinearity to select variables that were not directly influencing each other was achieved following the recommendations of Zuur *et al.* (2010). All data were tested for normality using the Shapiro Wilk test with a significance level of α=0.05 and correlation tests (Pearson for variables following a normal distribution and Spearman rank for non-normal distribution), and were run under a significance level of α = 0.01. Logistic models were fitted with nls() function using SSfpl(); colinearity and correlations were run with Highstatlib (Zuur *et al.* 2010) with the statistical program R v.2.12.1.

3.4 Results

3.4.1 Fur seal counts

Numbers of pups born were well described by the four-parameter logistic functions for all years ($p \leq 0.05$, Fig 3.3), except for year 2003. In 2003, local staff at Punta San Juan realized that births were occurring again at the study site (fur seals had not bred there since 1997) and began daily counts of pups in November of that year. This resulted in a poor fit of count data to logistic functions and generated estimates with a large standard error (see Table 3.1) making this year an outlier. Thus, 2003 was removed from further analyses.

3.4.2 Breeding behaviour

Mean birth dates estimated from four-parameter logistic functions varied within 22 days throughout my study period, between Nov. 7th (1984) and Nov. 29th (2010). My estimates of the total number of pups born from logistic models varied between 92±0.1 pups (1997) and 401±18.0 pups (2009). Estimates of the total number of pups born were generally a bit higher than the ‘maximum pup count’ extracted from the direct counts time series, which was between 64 (1997) and 398 pups (2009) for all years (Table 3.1).

The date the first pup was born was considered to be the date that pup counts began to increase exponentially between counts. Under this definition, the earliest date the first pup was born was October 10th (1989) and the latest was November 8th (2010), suggesting a shift towards a later onset of the pupping season. Consequently, breeding season length varied from 20±0.03 (1988) to 35±0.11 days (2008) throughout the study period (Table 3.1).

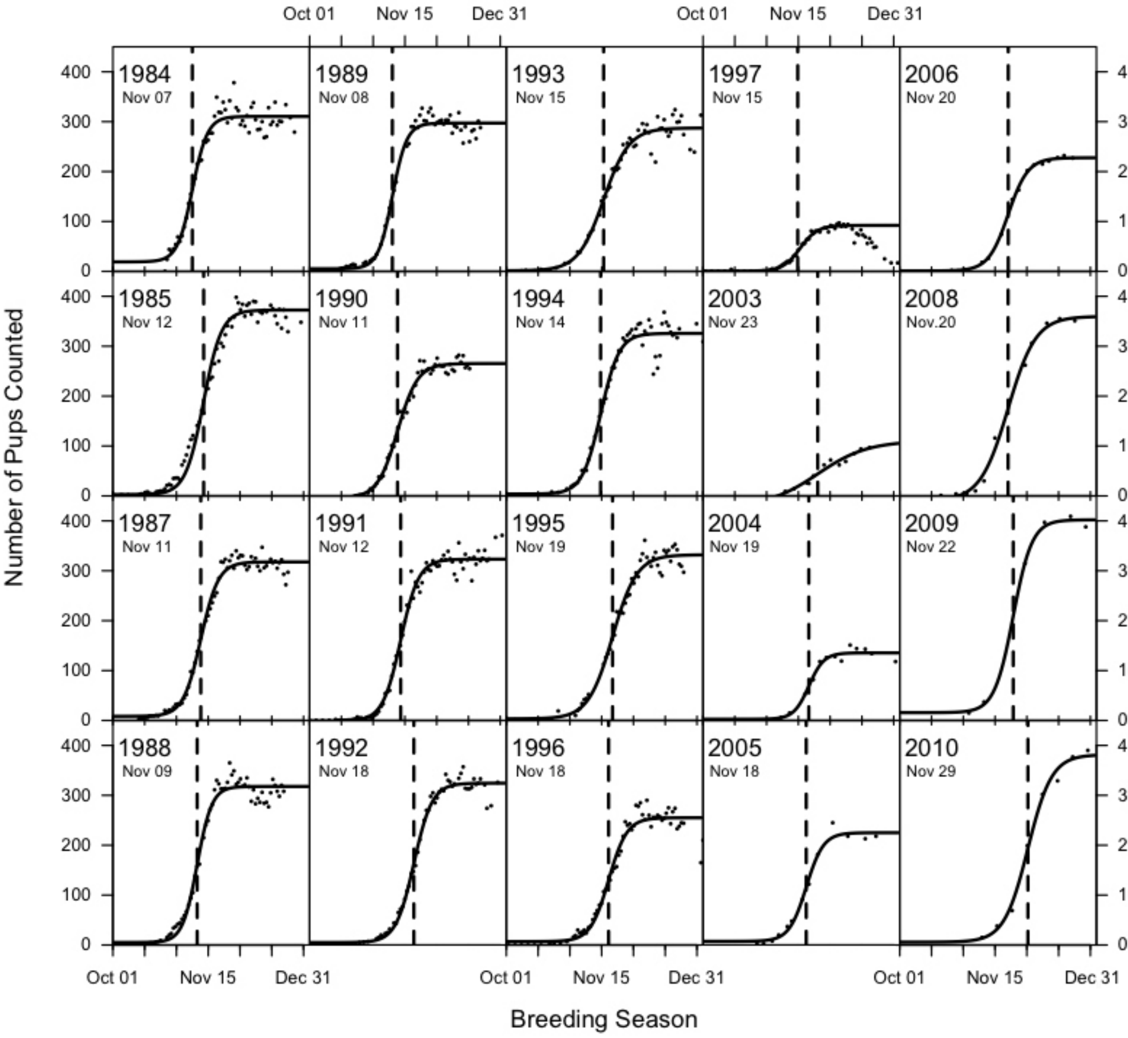

Figure 3.3. Four-parameter logistic model curves (continuous lines) fitted to total number (dots) of South American fur seal pups counted between October 1st and December 31st of 1984-1997 and 2003-2010 (*n*=20). Data were not collected in 1986 and 2007. Dashed lines mark the mean birth date as estimated by the four-parameter logistic models for each year. Corresponding year and mean birth date for each curve are indicated in the upper left corner of each panel.

Table 3.1. Breeding parameters for South American fur seals extracted from direct pup counts at Punta San Juan, Peru for 1984-1997 and 2003-2010. Data were not collected in 1986 and 2007 or in years 1998-2002, when fur seals had abandoned the site.

	Maximum pup count	Date first pup is born	Estimate of Total Pups Born (±SE)	Mean date of birth	Length of Breeding Season (days±SE)	Maximum number of pups born per day
1984	304	-	310±13.75	07-Nov	26± 0.07	21
1985	366	12-Oct	372± 2.94	12-Nov	25± 0.03	22
1986	-	-	-	-	-	-
1987	311	13-Oct	317± 3.76	11-Nov	26± 0.03	19
1988	311	13-Oct	317± 3.15	09-Nov	20± 0.03	23
1989	294	10-Oct	203± 2.83	08-Nov	20± 0.04	15
1990	262	23-Oct	265± 5.62	11-Nov	26± 0.04	14
1991	325	19-Oct	323± 3.52	12-Nov	26± 0.04	19
1992	320	18-Oct	265± 3.24	18-Nov	26± 0.03	14
1993	276	14-Oct	286± 7.09	15-Nov	35± 0.08	12
1994	320	16-Oct	325± 6.20	14-Nov	26± 0.05	19
1995	329	22-Oct	331± 5.34	19-Nov	34± 0.06	14
1996	246	21-Oct	255± 5.35	18-Nov	27± 0.06	14
1997	64	29-Oct	92± 0.09	15-Nov	23± 0.03	6
2003	81	-	81±51.20	23-Nov	46± 1.20	3
2004	135	31-Oct	135± 8.13	19-Nov	21± 0.13	9
2005	216	23-Oct	225± 7.54	18-Nov	26± 0.10	13
2006	227	25-Oct	227± 2.52	20-Nov	27± 0.03	12
2007	-	-	-	-	-	-
2008	353	20-Oct	358±10.52	20-Nov	35± 0.11	14
2009	398	02-Nov	401±18.03	22-Nov	29± 0.20	22
2010	380	08-Nov	379±18.61	29-Nov	34± 0.15	17

Interannual fluctuations in breeding behaviour (1984-2010) were best described by (i) mean birth date, (ii) length of the breeding season and (iii) number of pups born and their standard errors (Fig. 3.4). There appears to be some correspondence between these metrics of reproduction and the four periods of population change ("Stable" from 1984 to 1991, "Declining" from 1992 to 1997, "Abandonment" from 1998 to 2002 and "Recovering" from 2003 to 2010). Mean birth dates showed a strong tendency to occur later in the season as time (periods) progressed. These peak dates occurred between Nov 7th and Nov 12th during the "Stable" period, between Nov 14th and Nov 19th during the "Declining" period and between Nov 18th and Nov 22nd during the "Recovering" period.

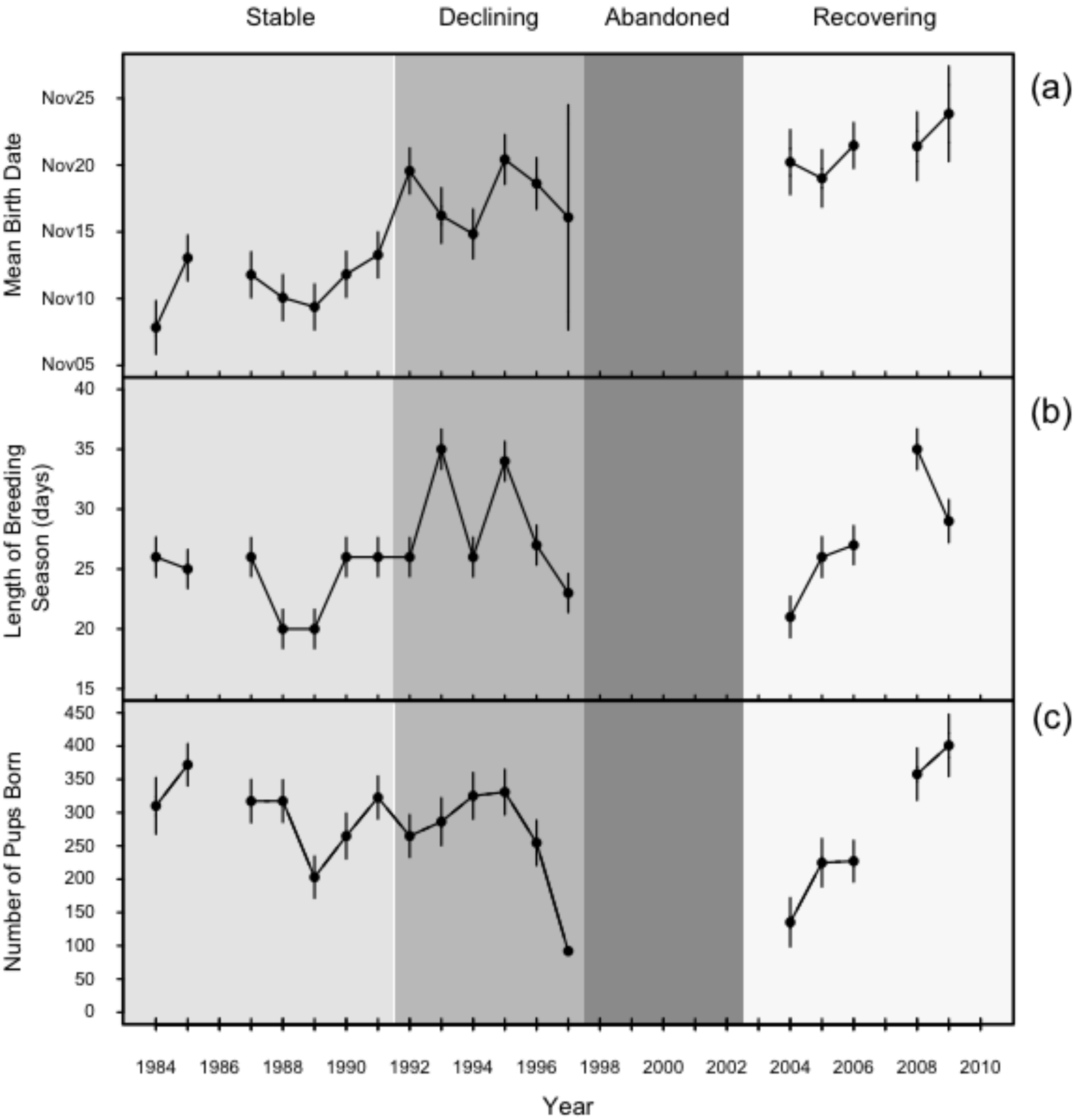

Figure 3.4. Time series for breeding parameters: (a) mean birth date, (b) length of breeding season in days and (c) number of pups born for 1984-1997 and from 2003-2010. Vertical lines represent the standard error for each data point. Standard error for year 1997 is very small and thus is not visible in plot. Different shades correspond to periods according to level of abundance at the beach. Data were not collected in 1986 or 2007. Data for 2003 and 2010 were considered outliers and are not shown.

Variance in the length of the breeding season also increased through time. During the "Stable" period the range of the length of the breeding season varied within 6±0.04 days. However, during the "Declining" period the range of the length of the breeding season increased to 12±0.05 days and had an irregular interannual pattern. More recently, during the "Recovering" period the duration of the breeding season has varied by 14±0.12 days and the number of days needed to produce 90% of pups has been extended.

Variability in the number of pups born also increased through time. The range in numbers born is of 169±10.9 pups during the "Stable" period, and 239±7.0 pups during the "Declining" period before collapsing due to the 1997/98 El Niño. More recently, the increasing population has produced a range of 266±15.5 pups during the "Recovering" period. Trend in variability differs with the trend in average number of pups born during each period. Average values show that the "Stable" period has highest average with 301±20.1 pups, while the "Declining" period shows the lowest average number of pups with a value of 259±87.5. Meanwhile the "Recovering" period reveals an average number of 269±48.5 pups. Considering that the average value for the "Recovering" period is built up from very low numbers, it has a very high average value that continues to increase in time.

Strong trends in breeding behaviour were also detected over the study period. Most notably, there was a significant linear relationship between mean birth dates and years (r^2 =0.77, P<0.01, *n*=19), showing a shift towards giving birth later throughout my study (1984–2008; Fig. 3.5a). A shift towards later mean dates of birth was also detected when the number of pups born per day before (1984 -1997) and after (2003-2010) the 1997/98 El Niño event were compared (Fig. 3.5b). Births before El Niño occurred at earlier dates than after El Niño events. Although comparing extremes of the time series showed a gradual shift through time, distribution of births per day showed a bimodal distribution. There was also a significant positive relationship between the maximum number of females counted on the beach and the number of pups born per day (r^2 = 0.70, P <0.01) as well as with the length of the breeding season (r^2 = 0.69, P <0.01). All this suggests that there was a later onset and peak of the South American fur seal breeding season between 1984 and 2010 at my study site.

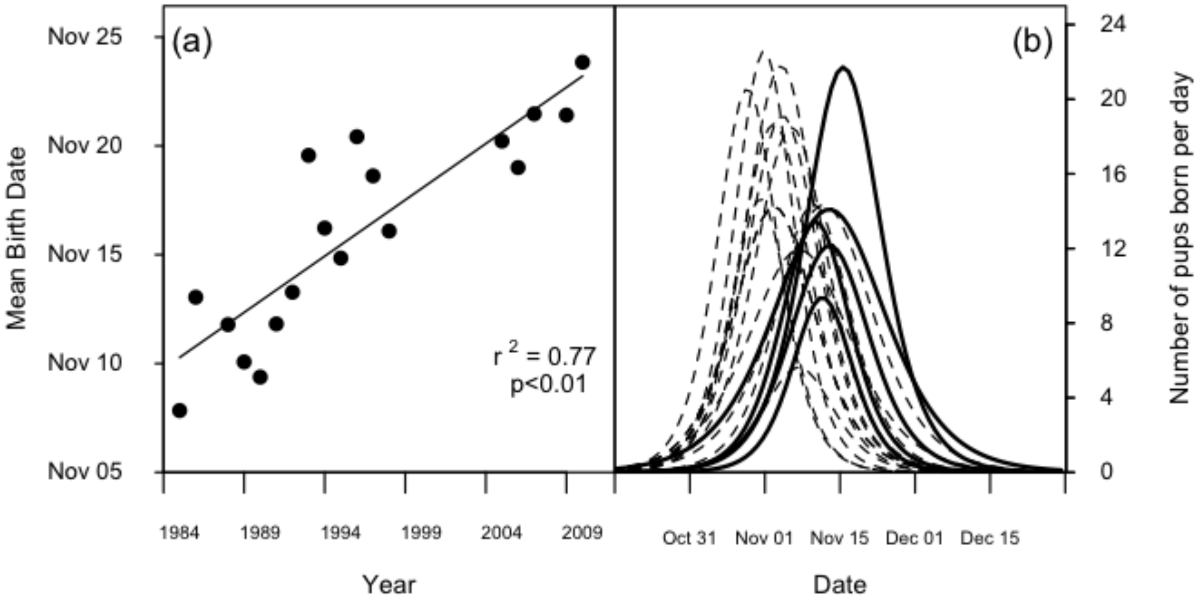

Figure 3.5. Mean birth date by year (a) showing a shift towards later mean birth dates over time (r^2=0.77, P<0.01, *n*=19), and number of pups born per day as predicted from daily pup counts (b) at beach site S3 of Punta San Juan guano reserve, 1984-2010 (*n*=19). Dashed lines represent years before El Niño (1984-1997, *n*=13) and continuous lines are for years after El Niño (2004-2010, *n*=6). No data were collected in years 1986 and 2007; and year 2003 was an outlier and removed from analysis.

3.4.3 Prey abundance

I found a positive relationship between the ratio of females to pups counted on the beach (r^2 = 0.59, P <0.01) and prey biomass from the previous year (Fig. 3.6a) as well as for the mean date of birth and biomass for the previous year (r^2 = 0.66, P <0.01, Fig. 3.6b).

I also tried using annual anchoveta catch as a proxy for prey abundance given that CPUE (catch per unit of effort) data for anchoveta fishing vessels of medium (201-300 MT) and large (301-400 MT) capacity (Espinoza-Morriberón *et al.* 2010) correlated with estimates of anchoveta biomass ($r^2 \geq 0.23$, P <0.01) and catch ($r^2 \geq 0.36$, P <0.01). Consequently, I found a strong positive relationship between biomass and catch (r^2 = 0.31, P <0.01) for my entire study period, but prey biomass from the previous year showed a stronger relationship with measures of reproductive performance (Fig. 3.6).

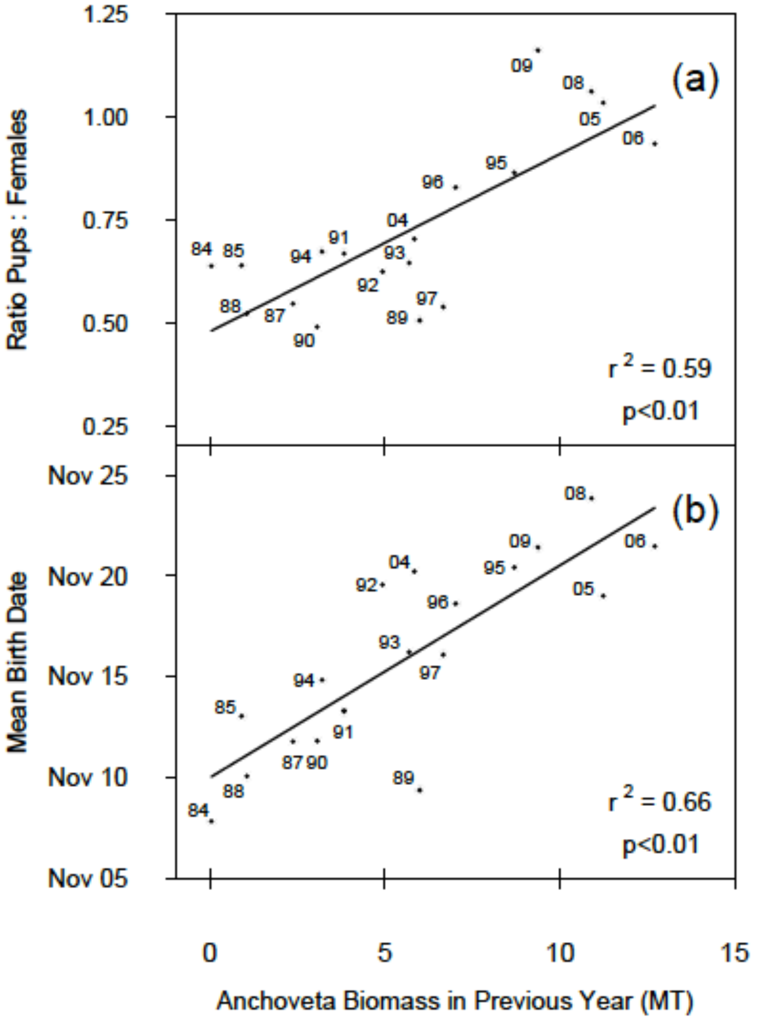

Figure 3.6. Significant linear relationships between (a) the ratio of pups and number of adult females counted ($r^2 = 0.59$, P <0.01, *n*=19) and (b) mean birth dates and anchoveta biomass (MT) from the previous year ($r^2 = 0.66$, P <0.01, *n*=19).

3.5 Discussion

Counts and behavioural observations during 20 breeding seasons at Punta San Juan (from 1984–2010) suggest that reproductive success and breeding behaviour of South American fur seals changed in response to changes in prey abundance. During the most acute shortages of prey (associated with the 1997/98 El Niño), a combination of mass mortality and migration caused the fur seals to abandon the Punta San Juan study site (Apaza *et al.* 1998); as occurred during other El Niño events (Majluf 1985, Majluf 1991a). However, favorable prey conditions in following years resulted in recovery and rapid growth of the fur seal population (Fig. 3.2). This suggests that South American fur seals are capable of recovering from prey depletion events if prey abundance remains above a certain threshold level.

3.5.1 Effects of prey abundance on reproduction

Increases in the ratios of pups born to the number of females present each year (an index of birth rates) were associated with higher abundances of available prey being present in the preceding year (before and during gestation; Fig. 3.7a). These prey biomasses were the anchoveta estimated to be available to the fisheries at a certain time and may not necessarily be available to the fur seals. However, it seems to be a reasonable proxy of feeding conditions for a top predator that mainly feeds on anchoveta in the Humboldt Current Ecosystem.

Good feeding conditions available the year before parturition presumably result in adult females being in good body condition to be fertile and maintain healthy pregnancies. Similar increases in pup production have been reported in other otariids following a year of high food availability (Lunn & Boyd 1993). However, acute prey shortage such as during the 1997/98 El Niño resulted in the majority of females aborting their fetuses with the few pups (*n*=92) that were born that year all dying from starvation (P. Majluf, pers. comm.).

The decreases I documented in the number of pups born during the early 1990s (within the end of “Stable” and during the “Declining” periods) coincided with unfavorable prey conditions associated with two long-duration El Niño events (1986/88 and 1991/93) of moderate intensities. Each of these events lasted more than twelve months and may have caused some level of nutritional stress on adult females. These moderate El Niños did not cause mass mortality of adults, but did appear to explain a decline in numbers of pups born, as well as an increase in total fur seal abundance at other sites further south in Peru, such as at Punta Coles in the 1990s (17°S; IMARPE, unpbl. data) as fur seals presumably searched for better feeding areas. These periods of moderate El Niños also coincided with consecutive years of increased anchoveta removals by fisheries, especially in the area between 4-14°S where the principal stock of anchoveta was exploited, possibly compounding suboptimal feeding conditions for the fur seals.

During the ¨Recovering¨ period, the numbers of pups and total abundance grew exponentially as expected for a population experiencing favourable conditions (enough resources, such as food and space) to allow rapid recovery (Payne 1977). A lack of El Niño events and overall cooler conditions (Punta San Juan Project, unpubl. data) and changes in fisheries management towards lower catches (in relation to biomass levels) may have combined to promote better feeding conditions for fur seal population growth.

3.5.2 Timing of breeding

Changes in the timing of breeding of pinniped populations may be related to the age structure of populations, changes in when food is available and changes in the quantity or quality of available food (Jemison & Kelly 2001). A consequence of the annual breeding cycle in pinnipeds is that resource availability during the most energetically expensive phase of reproduction, the third trimester of gestation (Trites 1991), is impossible to predict at fertilization 10-12 months prior. As my study population declined and recovered, I observed an overall shift of the peak breeding season towards a later mean date of birth. Explaining this shift requires disaggregating the time series according to the contextual environmental conditions of each period (Stable, Declining, Recovering) associated with prey availability and the age structure of the breeding population.

I observed little variability in the timing of breeding during the “Stable” period, which is consistent with behavioural studies during years 1984-1989 (Majluf 1992) that showed no significant change in the mean date of birth. However, inconsistent patterns were observed during the “Declining” period in the length of the breeding season. Mean date of birth also appeared to have been delayed and may have been a behavioural response of nutritionally stressed females that were taking longer to return to the breeding beaches due to the combined effects of the 1991/93 El Niño and increased catch to biomass ratios of anchoveta compared to previous years.

Body lengths of fur seals increase throughout life (Trites & Bigg 1996) as individuals age and become more experienced at finding food (Lunn *et al.* 1994). High-latitude species, such as Antarctic (*A. gazella*) and northern fur seals (*Callorhinus ursinus*) suckle their offspring for the duration of embryonic diapause (Boyd 1991) and wean their pups as the active gestation begins. Older females also tend to give birth first to heavier pups while young, inexperienced females give birth to lighter pups later in the season (Trites 1991, Lunn *et al.* 1993). However, in temperate regions, long-lactating fur seals, such as subantarctic (*A. tropicalis*), Cape (*A. pusillus pusillus*) and Australian fur seals (*A. pusillus doriferus*), suckle offspring for most of the year, and weaning occurs <2 months before the birth of the next offspring. Among these species, the bigger and older females give birth later in the season (Rand 1955, Georges & Guinet 2000).

South American fur seals are similar to Galapagos fur seals (*A. galapagoensis*) in that they can concurrently suckle up to 3 offspring (a pup, yearling and a two year old) in low latitude locations (Trillmich 1990, Majluf 1987a). Thus, they incur the energetic demands of lactation and gestation concurrently (Gibbens *et al.* 2010). Additionally, female South American fur seals must continually return to a central place (breeding colony) to suckle their offspring throughout the year, limiting their foraging range (Majluf 1987a). Thus, a female that was already nursing one or more offspring during a "Declining" phase when prey conditions are unfavorable may delay the time of implantation or be unable to maintain their gestation to full term. This in turn would result in lower birth rates and a later mean date of birth. Also, poor recruitment of young can increase the mean age of a breeding population (York 1994) and could have accentuated the later arrival of the older more experienced females. This is a possible explanation for the later mean birth date and delay in the onset of the breeding season at my study site (see Table 1).

Studies of subantarctic fur seals have reported that old mothers that give birth later in the breeding season were more efficient at transferring energy to their pups compared to younger mothers. They also showed that pups born later in the season had higher birth mass, which allowed them to have a higher birth mass gain during the perinatal period (Georges & Guinet 2000). Higher birth masses of pups born later in the breeding season were observed at Punta San Juan before the 1997/98 El Niño (Punta San Juan Project, unpubl. data), suggesting that the same could have occurred in South American fur seals in Peru when the population's age structure was presumably in equilibrium.

My study site was abandoned for 5 years following the 1997/98 El Niño (Fig. 3.2). However, small numbers of females continued to rear their young on small islands, islets and rocky cliff edges from 1998-2003. From these few individuals, a small group of reproductive females returned to Punta San Juan as conditions improved to reoccupy historical breeding grounds. The group that reoccupied the breeding beach during the "Recovery" period appeared to have had a strong cohort of older experienced females that survived the 1997/98 El Niño (personal observations of tagged females pupping at study site). Arrival of adult age classes to the breeding site (rather than recruitment of newborns) is the only way that the high (>26%) exponential rate of increase could have been maintained in the early recovery period. Thus, it is possible that the bulk of the colony consisted of older females (ages 7 – 11 years old) that gave birth later in the season. However, the timing of breeding should shift back towards an earlier date as females recruit into the recovering fur seal colony. Such a phenomenon has been observed at Steller sea lion (*Eumetopias jubatus*) breeding sites on Sugarloaf Island in Alaska and Año Nuevo Island in California, where the date of birth apparently became later and then after a number of years was early again, possibly due to reductions in the quantity or quality of prey available during the population decline in sea lions (Pitcher *et al.* 2001).

3.5.3 Prey abundance

The marine ecosystem off Peru comprises the northern segment of the Humboldt Current system and produces the world's highest tonnage of fishery landings (Bakun & Weeks 2008). The most important pelagic fish species in the Humboldt Current system in terms of ecology and economics is the Peruvian anchovy or anchoveta. Anchoveta is the major prey of principal top predators including marine mammals, seabirds, fish and fishers (Espinoza & Bertrand 2008). However, every 2-7 years, El Niño reduces fish stocks and restricts fisheries of the Humboldt Current off the coast of Peru.

El Niño is an irregular fluctuation involving the entire tropical Pacific Ocean and global atmosphere (Fedorov & Philander 2000). It consists of an unstable interaction between sea surface temperature and atmospheric pressure — and results in variations in winds, rainfall, thermocline depth, circulation, biological productivity, and feeding and reproduction of fish, birds and marine mammals. El Niño events are characterized by weak trade winds, a deep thermocline and warm sea surface temperatures in the eastern equatorial Pacific—and has an opposite phase called La Niña that is characterized by strong trade winds, a shallow thermocline and cool sea surface temperatures.

Four El Niño events of varying intensities (moderate: 1986-87, 1991-93, strong: 1997-98 and mild: 2002-03) altered the distribution and abundance of anchoveta during my study period. These El Niños shifted the peak of anchoveta spawning from winter-spring to summer and diminished the biomass available for other species to consume in the system (Checkley *et al.* 2009). Spatial distribution of anchoveta also changed, with anchoveta relocating to southerly locations and deeper in the water column to maintain optimal living conditions during the warm conditions of the El Niño events.

El Niño typically causes short-term perturbations in the dynamics of anchoveta from which anchoveta can recover within one or two years during the following La Niña (cold) phases (Alheit & Ñiquen 2004). Warm El Niño and cold La Niña events have had a variety of effects on marine populations and ecosystems, but these effects are generally followed by recovery within a few years as well (*i.e.*, South American sea lions, Soto *et al.* 2004). El Niño effects such as mortality or reproductive failure are most severe on populations dependent on local feeding or breeding grounds in coastal waters or around islands (Fiedler 2002).

Anchoveta constitutes 30-85% of the diet of South American fur seals in Peru (Paredes & Arias-Schreiber 1999, Vásquez 1995, Arias-Schreiber 2000, Arias-Schreiber 2003, Zavalaga *et al.* 1998). Preference for this prey induces fur seals to disperse widely during El Niño events, often to southerly locations in Peru (*e.g.* Punta Atico 16°00'S and Punta Coles 17°42'S) where individuals originally tagged at Punta San Juan (15°12'S) have been re-sighted (Punta San Juan Project, unpubl. data). Increases in fur seal numbers have also been reported in northern Chile since the 1982/83 El Niño (Guerra & Torres 1987) as fur seals gradually declined at northern Peruvian colonies during the 1990s (Guerra & Portflitt 1991, Sielfeld 1999). More recently, some tagged fur seals from Punta San Juan have been seen as far south as Iquique (20°13'S) and Antofagasta (23°39'S) in northern Chile in 1998 (W. Sielfeld, pers. comm.) and recent breeding colonies have been established close to Taltal, Chile (25°40'S) since 2005 (H. Paves, pers. comm.).

The effects of an El Niño event on South American fur seals will vary according to its intensity, duration and the time of year it occurs. Females suckling pups at Punta San Juan during the 1982/83 El Niño made significantly more and longer trips compared with females of similar reproductive status during a non-El Niño year (Majluf 1987a). Low foraging success led to extended trips to sea, acute malnutrition and eventual starvation of pups and yearlings (Trillmich *et al.* 1986). Particularly strong and long El Niño events as in 1997/98 can even lead to the starvation of adults (Apaza *et al.* 1998, Majluf 1998).

In addition to El Niño, the abundance of anchovy and availability of prey can be affected by fisheries. Commercial landings have tended to oscillate with environmental conditions and the biomass of anchoveta. However, the high catch rates in the 1990s occurred during a time of especially low anchoveta biomass. Adaptive fisheries management decisions were adopted following the strong 1997/98 El Niño declines in anchoveta biomass—banning anchoveta captures during the El Niño and allowing anchoveta biomass to recover 2-3 years after the event (Alheit & Ñiquen 2004). Fisheries management has taken an ecosystem approach since 2009 and has established an individual quota system that has diminished catch levels, making the catch to biomass ratio the lowest than in the past 25 years. Thus, improved fisheries management and better environmental conditions have coincided with increases in the growth of South American fur seals at protected sites such as Punta San Juan, and provide some measure of hope that undisturbed rookeries and beaches can promote continued recovery of fur seals in Peru.

3.5.4 Adaptive mechanisms to highly variable systems

The South American fur seal in Peru inhabits a marine ecosystem that experiences huge fluctuations in the availability of forage fishes to fur seals and other top predators. The daily counts and observations of fur seals at Punta San Juan show that mean dates and rates of birth (as measured by the ratio of pups to adult females) are linked to the abundance of prey, as detected by hydroacoustic surveys conducted for the entire coast of Peru. The data also show fur seals are able to survive catastrophic breeding failures and can rapidly recolonize abandoned breeding beaches. Fur seals at my study site recovered at an average rate of 26% per year, which is on par with the maximum estimated growth potential of 20% per year (Chapter 2). An $r_{\max}$ of 20% is among the highest growth rates recorded for marine mammals (the Antarctic fur seal has a rate of 20%, Hucke-Gaete *et al.* 2004). Changes in mean dates of birth and duration of the breeding season suggest that recovery is in part linked to plasticity in the timing of birth, survival of older animals, and the ability to raise more than one offspring at a time.

Female South American fur seals can nurse up to three offspring simultaneously and wean them at 6 to 36 months of age (Majluf 1987a). When food is scarce during El Niño, females make longer foraging trips at sea to replenish the energy transferred to their offspring (Gentry & Kooyman 1986, Trites & Donnelly 2003). However, extremely long foraging trips reduce female body mass and can lead to starvation of offspring on land (Trillmich 1990). Fur seals that inhabit low latitudes under unpredictable environmental conditions, tend to have flexible and adaptive pup rearing strategies (Trillmich 1990). Some of these strategies include flexible duration of pup rearing (lactation) and changes in the duration of female foraging trips. Extended maternal care of multiple offspring presumably enhances survival of South American fur seals during mild El Niños, and likely explains much of their extraordinary growth rates when food is abundant during the recovery phases.

The strategies invoked by the fur seals in low latitudes are opposite to those of the northern and Antarctic fur seals inhabiting subpolar regions where pups are weaned at about 4 months of age (Gentry & Kooyman 1986). Environmental conditions of subpolar regions obligate females to wean pups about the time when winter sets in when they are obligated to migrate in search of food. However, pups in the subpolar regions are weaned in ecosystems that are presumably more predictable in terms of prey availability. Thus, selective forces related to the predictability of the forage base has likely fixed the timing of weaning time in the subpolar and subtropical fur seal species (Trillmich 1990).

3.5.5 Counts and ratios — a useful management tool?

Monitoring daily numbers of fur seal pups born relative to the number of breeding females appears to be a useful means to assess the feeding conditions encountered by South American fur seals in Peru relative to environmental conditions and removals of prey by fisheries. Direct counts during the breeding season such as these have been commonly used to assess changes in other pinniped populations (Hofmeyr *et al.* 1997, Siniff *et al.* 1977, Payne 1977), and have been used to estimate population size and mean dates of births (Trites 1991, Gibbens & Arnould 2009, Pitcher *et al.* 2001, Jemison & Kelly 2001, Dabin *et al.* 2004, Bradshaw *et al.* 1999, Bradshaw *et al.* 2000, Hofmeyr *et al.* 1997, Kirkwood *et al.* 2005, Berkson & DeMaster 1985). Fur seal pups are an easily recognizable age class and are restricted to remain on land during the first months of life, which allows counters to obtain a relative estimate of abundance with low observer error during a short time window (breeding season).

The frequency with which pups and adults are counted dictates the types of questions that can be answered. An index of abundance can be obtained from one pup count per week during the breeding season, but documenting changes in breeding behaviour will require more frequent counts. Having more than one person count simultaneously will allow variance to be estimated between different observers. It is also important that counters be familiar with the sites and the best vantage points to observe the entire area.

Top predators can serve as good indicators of ecosystem health, but a long-term investment must be made to collect meaningful data. Our data show that changes in birth dates, lengths of breeding season, and ratios of pups to adult females reflect changes in the availability of prey and the ability of the ecosystem to support healthy fur seal populations. In a natural changing system such as the Humboldt Current in Peru, fisheries regulation needs to protect the survival and reproduction of top predators such as fur seals, under the premise that unpredictable prey availability may occur at any given time due to El Niño events. Our data suggest that low numbers of fur seals are particularly vulnerable during and after prey depletion events. This puts a responsibility on fisheries management to ensure that prey conditions are sufficient to support the recovery and survival of all components of the Peruvian marine ecosystem.

Chapter 4: Conclusions

4.1 Summary of findings

The overall conclusion from my study is that South American fur seals have the reproductive potential to survive in highly variable environments and are able to recover locally at protected sites from short-term natural prey depletions such as occurred during the 1997/98 El Niño at Punta San Juan. However, a series of overlapping cumulative threats associated with commercial harvest, poaching, bycatch, removal of prey by fisheries and lack of protected areas have occurred—at least—since 1925. These cumulative threats combined with the effects of El Niño diminished the South American fur seal population to low levels in Peru, and have hampered its recovery to historical levels of abundance (Fig. 4.1).

Population recovery can be defined as the re-growth of a population after a decline to exceptional densities (for example of one order magnitude less than pre-decline population size) or local extinction (Gardmark *et al.* 2003). Life history characteristics (such as age at primiparity, pup growth rates, and time of weaning) influence recovery dynamics of populations, but the reverse is also true—population dynamics can determine important life-history traits, since many traits are density-dependent as in the case of fur seals.

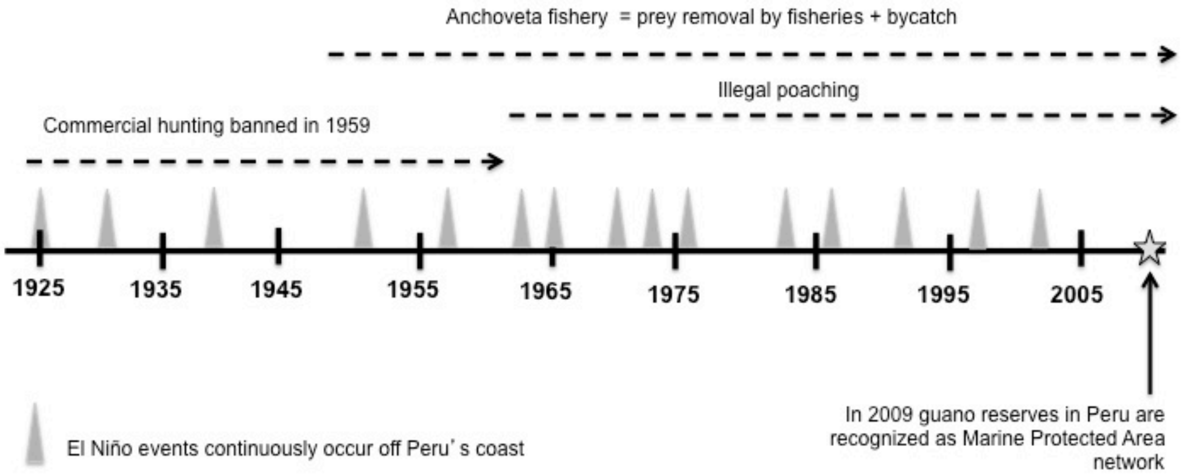

Figure 4.1 Timeline of cumulative overlapping threats that affect the recovery of South American fur seals in Peru showing major El Nino events and the periods of fishing, poaching and commercial hunting since 1925.

In the productive system of Humboldt Current, the entire system—prey and predators—have the potential to recover incredibly fast from the most abrupt environmental changes (*i.e.,* El Niño 1997/98). Thus, in the local Punta San Juan scenario, South American fur seals have recovered from the dramatic decline after the most intense 1997/98 El Niño event on record severely depleted prey abundance.

The rapid decline of South American fur seals in Peru due to the 1997/98 El Niño may have had severe consequences on the population by causing a loss of genetic diversity (*i.e.,* effective population size <7,000 breeding adults after the event) and a subsequent population bottleneck (Oliveira *et al.* 2009). Population bottlenecks are a direct consequence of small or continued small population sizes, which has probably been the case since the 1950s, according to my population model (Chapter 2, Fig. 2.6). The loss of genetic diversity in a bottlenecked population is a matter of concern because polymorphism may reduce the evolutionary potential of the population to respond to a changing environment (Oliveira *et al.* 2009).

The continued viability of South American fur seals on the coast of Peru may depend primarily on non-genetic factors, such as local availability of food resources and its consequent effects on pup growth and survival (Oliveira 2011) which is reflected in the possibility of local population recoveries (Chapter 3, Fig. 3.2). Unfortunately, a series of cumulative overlapping threats (Fig. 4.1) have consistently limited the size of the Peruvian population of fur seals, and may prevent the species from realizing its full potential for recovery.

4.2 Future research and implications of findings

My population model (Chapter 2) indicates that the South American fur seal population off the coast of Peru has an extremely high intrinsic growth rate of 20% compared to intrinsic growth rates reported for most other fur seal species. This high rate of population increase compares favorably with the 26% growth rate that has occurred at the main breeding beach at Punta San Juan since 2003 (Fig. 4.2).

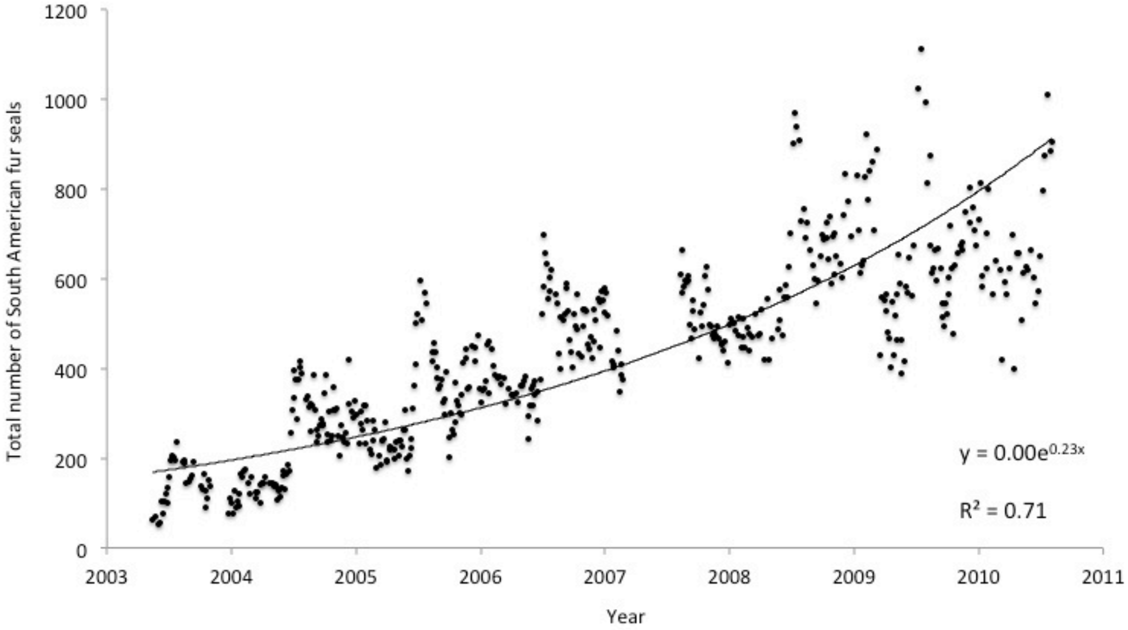

Figure 4.2 Exponential regression of the number of fur seals during the years of recovery (2003-2010) at the main breeding site at Punta San Juan. The annual rate of increase (*r*) is 0.26, which is calculated from the exponent of the slope (0.23) – 1.

These local findings support the population model and corroborates that South American fur seals have the potential to recover at sites while environmental conditions are favorable through immigration, reproduction and subsequent recruitment of older age classes

My population model was simple due to the lack of information available on South American fur seals in Peru, and could be improved by collecting additional data to construct stochastic age structured models and assess possible variance of vital rates, such as birth and survival rates (Jenouvrier *et al.* 2009). Although alternative modeling exercises may suggest intrinsic growth rates <0.20 for South American fur seals, it is interesting to find high recovery responses and growth rates in other species of the Humboldt Current system.

The unique conditions off Peru enable a vast development of rich concentrations of large multi-celled chains of large diatoms. Conveniently, Peruvian anchoveta may directly filter and consume phytoplankton as well as large zooplankton (van der Lingen *et al.* 2006, Bakun & Weeks 2008). Some species of large zooplankton include species of Calanoid copepods such as *Calanus chilensis,* one of the prey items of Peruvian anchoveta (Alamo 1989). These copepods feed on large volumes of phytoplankton provided by the intense upwelling ecosystem of the Humboldt Current and show no evidence of food limitation (Escribano *et al.* 1997). Copepod losses from upwelling and offshore transport are compensated by rapid turnover rates of cohorts permitting rapid population recovery (Escribano *et al.* 1997, Escribano & Hidalgo 2000). Going up the food chain, the Humboldt squid, *Dosidicus gigas*, a voracious cephalopod that has economically and ecologically become very important to Peru´s marine ecosystem and fisheries, shows short generation times coupled with fast maturation which has proven to be advantageous in the expansion of their abundance and distribution (Arguelles *et al.* 2008). Finally, like many other clupeid fishes, Peruvian anchoveta can increase their population size rapidly and recover from population collapse when environmental conditions are favorable, even if this occurs immediately after an El Niño event (Alheit & Bernal 1993, Hutchings 2001, Hutchings 2000). Thus it seems as though high population growth rates are not an uncommon phenomenon amongst prey and predator species of the Humboldt Current system.

Some authors suggest that El Niño, rather than being an unmitigated disaster for Peruvian fisheries, may in the long run be a prime reason for the remarkable fishery productivity of the Peru–Humboldt large marine ecosystem (Bakun & Broad 2003). The El Niño/La Niña period can be considered as a figurative “reset” button for the Peru marine ecosystem of a sort that is not available to the same degree in any of the other similar systems in the world such as the Benguela and California Current systems (Bakun & Broad 2003, Bakun & Weeks 2008). These resets allow rapidly reproducing species to move into environmental “loopholes,” (*i.e.,* niches formerly occupied by other species) and for example can supply predators with high levels of prey biomass immediately after anchoveta depletion is caused by El Niño (Bakun & Broad 2003, Bakun & Weeks 2008, Arguelles *et al.* 2008). Predatory organisms also benefit from resets, as they will also begin to respond to the rapid recovery of prey, but with a lag in their response due to their own natural history traits (*e.g.* fur seals and sea lions).

In terms of South American fur seals in Peru, we may be observing a shifting baseline syndrome (Fig. 2.6). Modern fisheries science has had difficulties accommodating historical data and the risks associated with a shifting perception of the status of stocks or the health of marine ecosystems because each generation of fisheries scientists has evaluated changes under the assumption that the baseline for stocks and species composition were those that were present at the beginning of their careers (Pauly 1995). Hence it is possible that if I did not go as far back in time as possible and did the best effort possible to include all of the variables that contribute to mortality when hindcasting the historical abundance of South American fur seals, I could have developed a very different point of reference as the historical abundance for this species in Peru. This holds true for the predicted values of K^* for 1850 (K^*=115,000) and average abundance estimated for before the onset of harvest of about 68,000 individuals (range: 39,000-98,000). This decrease in abundance was due to mortality associated with varying environmental conditions (*i.e.* El Niño), and later by the commercial harvest in the mid 20th century. Some of the historical information found for years prior to the 1980s lacked rigorous scientific methodology and could be considered "anecdotal" information. It nevertheless served as data and the basis for understanding relative abundance and estimating a historical carrying capacity.

One-way downward trajectories have been the case for many marine mammal populations that have been reconstructed with the best available information. Interestingly, the decrease in abundance of South American fur seals between 1880 and 2010 indicate that there was in fact a literal "shifting baseline" in the population abundance of fur seals in Peru before and after the mid-20th century. A possible explanation for this is that the potential carrying capacity changed to some lower value. However, information may be too sparse to investigate finer details of the historical changes in abundance associated with natural and anthropogenic effects, especially since—for the most part—the sealing story for most pinnipeds remains a big mystery (Christensen 2006).

Steps needed to promote population growth and conserve South American fur seals in Peru include (i) maintaining the ban on commercial harvest, (ii) protecting important breeding sites (and even more so if they are historical), (iii) improving fisheries management aiming to leave a considerable prey biomass in the waters off Peru, and (iv) regulating bycatch and direct killing of South American fur seals.

Ideally future work in this area of study should include: (i) estimating local prey biomass available to fur seals coupled with (ii) conducting diet studies to help better understand the true relationships between marine predators and local prey available to them. These studies can be complemented by (iii) constructing bioenergetics models of adult females to understand the energetic budget behind lactation of offspring, (iv) documenting maternal attendance patterns, and (v) recording pup growth rates to understand the direct linkages between prey availability, foraging trips and rearing of offspring. Another important source of mortality that should be incorporated into population models is the population health status of South American fur seals, for which baseline information is currently being collected (Punta San Juan Project, unpubl. data). Finally, researchers should continue conducting direct counts of fur seal rookeries and emphasize the collection of daily pup and adult counts during the three month breeding season (October-December) to understand recovery dynamics and life history traits of fur seals at other important breeding sites along the coast of Peru in long term time series like the ones used in this study.

Bibliography

Alamo, A. 1989. Stomach contents of anchoveta *(Engraulis ringens)*, 1974-1982. Pages 105-108 *in* D. PAULY, P. MUCK, J. MENDO and I. TSUKAYAMA eds. *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*. IMARPE-GTZ-ICLARM.

Alheit, J. and P. Bernal. 1993. Effects of physical and biological changes on the biomass yield of the Humboldt Current Ecosystem. Pages 53-68 *in* K. SHERMAN, A. LEWIS M and B. D. GOLD eds. *Large Marine Ecosystems: Stress, mitigation and sustainability*. AAAS Publication, Wasington DC, USA.

Alheit, J. and M. Ñiquen. 2004. Regime shifts in the Humboldt Current ecosystem. *Progress In Oceanography* **60:** 201-222.

Apaza, M., A. Figari and P. Majluf. 1998. Mortalidad de los mamíferos marinos durante El Niño 1997-98 en el litoral Sur de San Juan de Marcona, Ica – Perú. [Marine mamal mortality during El Niño 1997-98 at San Juan of Marcona, Ica, Peru]. *8a. Reunión de Especialistas en Mamíferos Acuáticos de América del Sur*. Recife, Brasil.

Arguelles, J., R. Tafur, A. Taipe, P. Villegas, K. Friedman, N. Dominguez and M. Salazar. 2008. Size increment of jumbo flying squid *Dosidicus gigas* mature females in Peruvian waters, 1989-2004. *Progress In Oceanography* **79:** 308-312.

Arias-Schreiber, M. 1993a. Estudio de la pesquería artesanal del puerto San Juan de Marcona, Perú. [Artisanal fishery at the bay of San Juan of Marcona, Peru]. *Report for Wildlife Conservation Society, Peru*.

Arias-Schreiber, M. 1993b. Interacciones entre lobos marinos (Fam.Otariidae) y la pesquería artesanal en el puerto de San Juan de Marcona, Perú. [Artisanal fisheries and pinniped interactions at the bay of San Juan of Marcona, Peru]. BSc. Thesis, Universidad Agraria La Molina, Lima.

Arias-Schreiber, M. 2000. Los lobos marinos y su relación con la abundancia de la anchoveta peruana durante 1979-2000. [Pinnipeds and their relationship with Peruvian anchoveta abundance during 1979-2000]. *Boletín del Instituto del Mar del Perú*. **19:** 133-138.

Arias-Schreiber, M. 2003. Prey spectrum and feeding behaviour of two sympatric pinnipeds (*Arctocephalus australis* and *Otaria flavescens*) in relation to the 1997/98 ENSO in southern Peru. MSc Thesis, University of Bremen.

Arias-Schreiber, M. and C. Rivas. 1998. Distribución, tamaño y estructuras de poblaciones de lobos marinos *Arctocephalus australis* y *Otaria byronia* en el litoral peruano en noviembre 1996 y marzo 1997. [Distrbution, size and structure of pinniped populations (*Arctocephalus australis* y *Otaria byronia*) in the coasts of Peru from november 1996 to march 1997]. *Informe Progresivo del Instituto del Mar del Perú* **73:** 17-32.

Bakun, A. and K. Broad. 2003. Environmental 'loopholes' and fish population dynamics: comparative pattern recognition with focus on El Niño effects in the Pacific. *Fisheries Oceanography* **12:** 458-473.

Bakun, A. and S. J. Weeks. 2008. The marine ecosystem off Peru: What are the secrets of its fishery productivity and what might its future hold? *Progress In Oceanography* **79:** 290-299.

Ballance, L. T., R. L. Pitman and P. C. Fiedler. 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. *Progress In Oceanography* **69:** 360-390.

Barber, R. and F. Chavez. 1983. Biological consequences of El Niño. *Science* **222:** 1203-1210.

Berger, J. 1992. Facilitation of reproductive synchrony by gestation adjustment in gregarious mammals: a new hypothesis. *Ecology* **73:** 323-329.

Berkson, J. M. and D. P. Demaster. 1985. Use of Pup Counts in Indexing Population Changes in Pinnipeds. *Canadian Journal of Fisheries and Aquatic Sciences* **42:** 873-879.

Bonavia, D. 1982. *Los gavilanes (precerámico), mar, desierto y oasis en la historia del hombre. [Sparrowhawks (pre-ceramic period), ocean, desert and oasis in the life of man]*. Ed. Ausonia, Lima.

Bonner, W. N. 1981. Southern fur seals Arctocephalus (Geoffroy Saint-Hilaire and Cuvier, 1826). Pages 161-208 *Handbook of Marine Mammals*.

Bonner, W. N. and R. M. Laws. 1964. Seals and sealing. Pages 163-190 *in* R. PRIESTLEY, R. ADIE and G. ROBIN eds. *Antarctic Research*. Buttersworths, London.

Bouchón, M., S. Cahuín, E. Díaz and M. Ñiquen. 2000. Captura y esfuerzo pesquero de la pesquería de anchoveta peruana (*Engraulis ringens*). *Boletín del Instituto del Mar del Perú* **19:** 109–115.

Boveng, P. L., L. M. Hiruki, M. K. Schwartz and J. L. Bengtson. 1998. Population growth of Antarctic fur seals: Limitation by a top predator, the leopard seal? *Ecology* **79:** 2863-2877.

Boyd, I. 1991. Environmental and physiological factors controlling the reproductive cycles of pinnipeds. *Canadian Journal of Zoology* **69:** 1135-1148.

Boyd, I. 1996. Individual variation in the duration of pregnancy and birth date in Antarctic fur seals: the role of environment, age, and sex of fetus. *Journal of Mammalogy* **77:** 124-133.

Boyd, I., J. Croxall, N. Lunn and K. Reid. 1995. Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. *Journal of Animal Ecology* **64:** 505-518.

Bradshaw, C. J., C. M. Thompson, L. S. Davis and C. Lalas. 1999. Pup density related to terrestrial habitat use by New Zealand fur seals. *Canadian Journal of Zoology* **77:** 1579-1586.

Bradshaw, C. J. A., C. Lalas and C. M. Thompson. 2000. Clustering of colonies in an expanding population of New Zealand fur seals (*Arctocephalus forsteri*). *Journal of Zoology* **250:** 105-112.

Carr, M. E. 2002. Estimation of potential productivity in Eastern Boundary Currents using remote sensing. *Deep-Sea Research Part II-Topical Studies in Oceanography* **49:** 59-80.

Crawley, M. J. 2007. *The R book*. John Wiley & Sons Inc.

Cushing, D. 1982. *Climate and Fisheries*. Academic Press New York.

Chavez, F., P. Strutton, G. Friederich, R. Feely, G. Feldman, D. Foley and M. Mcphaden. 1999. Biological and chemical response of the Equatorial Pacific Ocean to the 1997-98 El Niño. *Science* **286:** 2126-2131.

Checkley, D., J. Alheit, Y. Oozeki and C. Roy. 2009. *Climate Change and Small Pelagic Fish*. Cambridge University Press.

Christensen, L. 2006. Marine mammal populations: reconstructing historical abundances at the global scale. Pages 161 *Fisheries Center Research Reports*. University of British Columbia. Fisheries Centre, Vancouver.

Dabin, W., G. Beauplet, E. A. Crespo and C. Guinet. 2004. Age structure, growth, and demographic parameters in breeding-age female subantarctic fur seals, *Arctocephalus tropicalis*. *Canadian Journal of Zoology* **82:** 1043-1050.

Devries, T. J. 1987. A review of geological evidence for ancient El Niño activity in Peru. *Journal of Geophysical Research* **92:** 14471-14479.

Donnan, C., J. Quilter and P. Fernandini. 2009. *De Cupisnique a los Incas: el arte del valle de Jequetepeque: la donación Petrus Fernandini al MALI. [From Cupisnique to the Incas: the art of Jequetepeque Valley: a donation of Petrus Fernandini to MALI]*. Asociación Museo de Arte de Lima, Lima.

Eberhardt, L. L. and D. B. Siniff. 1977. Population dynamics and marine mammal management policies. *Journal of the Fisheries Research Board of Canada* **34:** 183-190.

Escribano, R. and P. Hidalgo. 2000. Influence of El Niño and La Niña on the population dynamics of *Calanus chilensis* in the Humboldt Current ecosystem of northern Chile. *ICES Journal of Marine Science: Journal du Conseil* **57:** 1867-1874.

Escribano, R., C. Irribarren and L. Rodriguez. 1997. Influence of food quantity and temperature on development and growth of the marine copepod *Calanus chilensis* from northern Chile. *Marine Biology* **128:** 281-288.

Espinoza, P. and A. Bertrand. 2008. Revisiting Peruvian anchovy (*Engraulis ringens)* trophodynamics provides a new vision of the Humboldt Current system. *Progress In Oceanography* **79:** 215-227.

Espinoza-Morriberón, D., R. Oliveros-Ramos and E. Díaz. 2010. Estandarización de la captura por unidad de esfuerzo (CPUE) de la flota industrial de cerco del stock norte-centro de la anchoveta peruana (*Engraulis ringens* Jenyns) [Standardization of the catch per unit effort (CPUE) of the industrial purse seine fleet extracting the north-center stock of the Peruvian anchovy (*Engraulis ringens* Jenyns)]. *Boletín del Instituto del Mar del Perú* **25:** 81-84.

Estrella, C. 2007. Resultados generales de la segunda encuesta estructural de la pesquería artesanal en el litoral Peruano ENEPA 2004-2005. [Main results of the second structural survey of Peruvian artisanal fisheries. ENEPA 2004-2005]. *Informe del Instituto del Mar del Perú*.

Fedorov, A. V. and S. G. Philander. 2000. Is El Niño Changing? *Science* **288:** 1997-2002.

Fiedler, P. 2002. Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability. *Marine Ecology Progress Series* **244:** 265-283.

Follet, B. 1985. The environment and reproduction. Pages 103-132 *in* C. AUSTIN and F. SHORT eds. *Reproductive Fitness*. Cambridge University Press, Cambridge.

Forcada, J., P. Trathan, K. Reid and E. Murphy. 2005. The effects of global climate variability in pup production of Antarctic fur seals. *Ecology* **86:** 2408-2417.

Gamarra, L. 1943. Los lobos marinos. [Pinnipeds]. *Boletín de la Compañía Administradora del Guano* **XIX:** 121-131.

Gardmark, A., K. Enberg, J. Ripa, J. Laakso and V. Kaitala. 2003. The ecology of recovery. *Annales Zoologici Fennici* **40:** 131-144.

Gentry, R. L. and G. L. Kooyman. 1986. *Fur seals: Maternal strategies on land and at sea*. Princeton University Press, Princeton.

Georges, J. Y. and C. Guinet. 2000. Early mortality and perinatal growth in the subantarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island. *Journal of Zoology* **251:** 277-287.

Gerber, L. and R. Hilborn. 2001. Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. *Mammal Review* **31:** 131-150.

Gibbens, J. and J. P. Y. Arnould. 2009. Interannual variation in pup production and the timing of breeding in benthic foraging Australian fur seals. *Marine Mammal Science* **25:** 573-587.

Gibbens, J., L. J. Parry and J. P. Y. Arnould. 2010. Influences on fecundity in Australian fur seals (*Arctocephalus pusillus doriferus*). *Journal of Mammalogy* **91:** 510-518.

Gillespie, J. H. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. *The American Naturalist* **111:** 1010-1014.

Glynn, P. 1988. El Niño-Southern Oscillation 1982-1983: nearshore population, community, and ecosystem responses. *Annual Review of Ecology and Systematics***:** 309-345.

Guerra, C. and K. Portflitt. 1991. El Niño effects on pinnipeds in northern Chile. Pages 47-54 *in* F. TRILLMICH and K. A. ONO eds. *Pinnipeds and El Niño: Responses to Environmental Stress*. Springer-Verlag, Berlin.

Guerra, C. and D. Torres. 1987. Presence of the South American fur seal *Arctocephalus australis* in northern Chile. Pages 33-35 *in* J. CROXALL and R. GENTRY eds. *NOAA Technical Report: Status, Biology and Ecology of Fur Seals*. NOAA-NMFS, Cambridge.

Guinet, C., J. P. Roux, M. Bonnet and V. Mison. 1998. Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. *Canadian Journal of Zoology* **76:** 1418-1424.

Gutiérrez, M., G. Swartzman, A. Bertrand and S. Bertrand. 2007. Anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) spatial dynamics and aggregation patterns in the Humboldt Current ecosystem, Peru, from 1983–2003. *Fisheries Oceanography* **16:** 155-168.

Hodgson, D., N. Johnston, A. Caulkett and V. Jones. 1998. Paleolimnology of Antarctic fur seal *Arctocephalus gazella* populations and implications for Antarctic management. *Biological Conservation* **83:** 145-154.

Hofmeyr, G. J. G., M. N. Bester and F. C. Jonker. 1997. Changes in population sizes and distribution of fur seals at Marion Island. *Polar Biology* **17:** 150-158.

Hucke-Gaete, R., L. Osman, C. Moreno and D. Torres. 2004. Examining natural popualtion growth from near extinction: the case of the Antartic fur seal at South Shetlands, Antartica. *Polar Biology* **27:** 304-311.

Hutchings, J. A. 2000. Collapse and recovery of marine fishes. *Nature* **406:** 882-885.

Hutchings, J. A. 2001. Influence of population decline, fishing, and spawner variability on the recovery of marine fishes. *Journal of Fish Biology* **59:** 306-322.

Imarpe. 2006. Censo Nacional de Lobo Fino (*Arctocephalus australis)* 2006.[National Census of South American fur seal (*Arctocephalus australis*) 2006]. *Informe Interno-Unidad de Investigaciones de Depredadores Superiores*.

Jahncke, J., D. Checkley Jr and G. Hunt Jr. 2004. Trends in carbon flux to seabirds in the Peruvian upwelling system: effects of wind and fisheries on population regulation. *Fisheries Oceanography* **13:** 208-223.

Jemison, L. A. and B. P. Kelly. 2001. Pupping phenology and demography of Harbor seals (*Phoca vitulina* Richardson) on Tugidak Island, Alaska. *Marine Mammal Science* **17:** 585-600.

Jenouvrier, S., C. Barbraud, H. Weimerskirch and H. Caswell. 2009. Limitation of population recovery: a stochastic approach to the case of the emperor penguin. *Oikos* **118:** 1292-1298.

Kirkwood, R., R. Gales, A. Terauds, J. P. Y. Arnould, D. Pemberton, P. D. Shaughnessy, A. T. Mitchell and J. Gibbens. 2005. Pup production and population trends of the Australian fur seal (*Arctocephalus pusillus doriferus) Marine Mammal Science* **21:** 260-282.

Kostrisky, L. 1963. Los mamíferos marinos de importancia económica. [Marine mammals of economic value]. Pages 120 *in* S. D. P. D. M. D. AGRICULTURA ed. *Ciclo de Conferencias sobre Recursos del Mar*. Universidad de San Marcos. Lima, Peru.

Lambin, X. 1993. Determinants of the synchrony of reproduction in Townsend's voles, *Microtus townsendii*. *Oikos* **67:** 107-113.

Lander, R. 1982. A life table and biomass estimate for Alaskan fur seals. *Fisheries Research* **1:** 55-70.

Langvatn, R., A. Mysterud, N. C. Stenseth and N. G. Yoccoz. 2004. Timing and synchrony of ovulation in red deer constrained by short northern summers. *American Naturalist* **163:** 763-772.

Lento, G., M. Haddon, G. Chambers and C. Baker. 1997. Genetic variation of southern hemisphere fur seals (*Arctocephalus* spp.): investigation of population structure and species identity. *Journal of Heredity* **88:** 202.

Lima, M. and E. Páez. 1997. Demography and Population Dynamics of South American Fur Seals. *Journal of Mammalogy* **78:** 914-920.

Loe, L., C. Bonenfant, A. Mysterud, J. M. Gaillard, R. Langvatn, F. Klein, C. Calenge, T. Ergon, N. Pettorelli and N. Stenseth. 2005. Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. *Journal of Animal Ecology* **74:** 579-588.

Lunn, N. J. and I. L. Boyd. 1993. Effects of maternal age and condition on partruition and the perinatal period of Antarctic fur seals. *Journal of Zoology of London* **229:** 55-67.

Lunn, N. J., I. L. Boyd, T. Barton and J. P. Croxall. 1993. Factors Affecting the Growth Rate and Mass at Weaning of Antarctic Fur Seals at Bird Island, South Georgia. *Journal of Mammalogy* **74:** 908-919.

Lunn, N. J., I. L. Boyd and J. P. Croxall. 1994. Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *Journal of Animal Ecology* **63:** 827-840.

Majluf, P. 1984. South American fur seal *Arctocaphalus australis*, in Peru. *in* J. CROXALL and R. GENTRY eds. *Status, biology and ecology of fur seals: Proceedings of an international symposium and workshop*. NOAA Technical Report, Cambridge, England.

Majluf, P. 1985. Comportamiento del Lobo Fino de Sudamérica (*Arctocephalus australis*) en Punta San Juan, Perú, durante "El Niño" 1982-83. [Behaviour of the South American fur seal (*Arctocephalus australis*) in Punta San Juan, Peru during "El Niño" 1982-83]. *in* W. ARNTZ, A. LANDA and J. TARAZONA eds. *Boletín del Instituto del Mar del Perú. "El Niño" Su Impacto en la Fauna marina*. IMARPE, Callao.

Majluf, P. 1987a. Reproductive ecology of female South American fur seals at Punta San Juan, Peru. PhD Thesis, University of Cambridge, Cambridge.

Majluf, P. 1987b. South American fur seal (*Arctocephalus australis*) in Peru. *in* J. CROXALL and R. GENTRY eds. *The status, biology and ecology of fur seals*. NOAA- National Marine Fisheries Service, Seattle.

Majluf, P. 1991a. El Niño Effects on Pinnipeds in Peru. Pages 293 *in* F. TRILLMICH and K. A. ONO eds. *Pinnipeds and El Niño: Responses to Environmental Stress*. Springer-Verlag, Berlin.

Majluf, P. 1991b. Side effects of guano exploitation: unexpected refuges for seals in Peru. *9th Biennial Conference on the Biology of Marine Mammals*. Chicago.

Majluf, P. 1992. Timing of births and juvenile mortality in the South American fur seal in Peru. *Journal of Zoology* **227:** 367-383.

Majluf, P. 1998. Effects of the 1997/1998 El Niño on pinnipeds in Peru. Pages 120 *8a. Reunião de Trabalho de Especialistas em Mamíferos Aquáticos da América do Sul e 2º. Congresso da Sociedade Latinoamericana de Especialistas em Mamíferos Aquáticos (SOLAMAC)*. Olinda, Brazil.

Majluf, P., E. Babcock, J. Riveros, M. Schreiber and W. Alderete. 2002. Catch and bycatch of sea birds and marine mammals in the small-scale fishery of Punta San Juan, Peru. *Conservation Biology* **16:** 1333-1343.

Majluf, P. and J. C. Reyes. 1989. The marine mammals of Peru: a review. *in* D. PAULY, P. MUCK, J. MENDO and I. TSUKAYAMA eds. *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*. IMARPE-GTZ-ICLARM.

Majluf, P. and F. Trillmich. 1981. Distribution and abundance of sea lions (*Otaria byronia*) and fur seals (*Arctocephalus australis*) in Peru. *Zeitschrift Fur Saugetierkunde-International Journal of Mammalian Biology* **46:** 384-393.

Mckenzie, J., L. J. Parry, B. Page and S. D. Goldsworthy. 2005. Estimation of pregnancy rates and reproductive failure in New Zealand fur seals (*Arctocephalus forsteri*). *Journal of Mammalogy* **86:** 1237-1246.

Mcphaden, M., S. Zebiak and M. Glantz. 2006. ENSO as an integrating concept in Earth Sciences. *Science* **314:** 1740-1745.

Muck, P. and H. Fuentes. 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953-1982. Pages 234-247 *in* D. PAULY and I. TSUKAYAMA eds. *The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change*. IMARPE-GTZ-ICLARM, Lima.

Murphy, G. I. 1968. Pattern in life history and the environment. *The American Naturalist* **102:** 391-403.

Ncar-Cdg. 2010. N3.4 (Niño 3.4 Index). http://www.cgd.ucar.edu/cas/catalog/climind/TNI_N34/index.html.

Oliveira, L. 1999. Variaçao geográfica do lobo-marinho sul-americano, *Arctocephalus australis* (Zimmermann, 1783) com base em dados morfológicos e moleculares. [Morphological and molecular evidence for geographic variation in South American fur seals, *Arctocephalus australis* (Zimmermann, 1783)]. PhD Thesis, Universidade de São Paulo, São Paulo.

Oliveira, L. 2011. Vulnerability of South American Pinnipeds Under El Niño Southern Oscillation Events. Pages 237-252 *in* S. CASALEGNO ed. *Global Warming Impacts-Case Studies on the Economy, Human Health, and on Urban and Natural Environments*. InTech, Croatia.

Oliveira, L., M. Arias-Schreiber, D. Meyer and J. Morgante. 2006. Effective population size in a bottlenecked fur seal population. *Biological Conservation* **131:** 505-509.

Oliveira, L., D. Meyer, J. Hoffman, P. Majluf and J. Morgante. 2009. Evidence of a genetic bottleneck in an El Niño affected population of South American fur seals, *Arctocephalus australis*. *Journal of the Marine Biological Association of the United Kingdom* **89:** 1717-1725.

Oliveira, L. R., J. I. Hoffman, E. Hingst-Zaher, P. Majluf, M. M. C. Muelbert, J. S. Morgante and W. Amos. 2008. Morphological and genetic evidence for two evolutionarily significant units (ESUs) in the South American fur seal, *Arctocephalus australis*. *Conservation Genetics* **9:** 1451-1466.

Oliveira, L. R., L. Malaraba and P. Majluf. 1999. Variação geográfica em crânios do lobo-marinho sul-americano *Arctocephalus australis* (ZIMMERMANN, 1783) das populações do Brasil e Peru. [Geographic variation of skull dimensions in popoulations of South American fur seals, *Arctocephalus australis* (ZIMMERMANN, 1783) of Brazil and Peru]. *Comunicações do Museu de Ciências e Tecnologia da PUCRS, Série Zoologia* **12:** 179-192.

Paredes, R. and M. Arias-Schreiber. 1999. Dieta del lobo fino (*Arctocephalus australis*) y lobo chusco (*Otaria byronia*) en la costa peruana durante mayo y junio de 1999. [Diet of South American fur seal (*Arctocephalus australis*) and South American sea lion (*Otaria byronia*) on the Peruvian coast during may and june of 1999]. *Report for: Subdirección de Investigaciones en Mamíferos Marinos*.

Paredes, R. and C. Zavalaga. 2001. Nesting sites and nest types as important factors for the conservation of Humboldt penguins (*Spheniscus humboldt*). *Biological Conservation* **100:** 199-205.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution* **10:** 430.

Pauly, D. and M. Palomares. 1989. New estimates of monthly biomass recruitment and related statistics of anchoveta (*Engraulis ringens*) off Peru (4-14S), 1953-1985. Pages 189-206 *in* D. PAULY, P. MUCK, J. MENDO and I. TSUKAYAMA eds. *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*. IMARPE-GTZ-ICLARM.

Pauly, D. and I. Tsukayama. 1987. *The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change*. IMARPE-GTZ-ICLARM.

Payne, M. 1977. Growth of a fur seal population. *Philosophical Transactions of the Royal Society of London. Biological Sciences* **279:** 647-679.

Piazza, A. 1969. Los lobos marinos en el Peru. [Pinnipeds of Peru]. *Caza y Pesca* **9:** 1-29.

Pitcher, K., V. Burkanov, D. Calkins, B. Leboeuf, E. Mamaev, R. Merrick and G. Pendelton. 2001. Spatial and temporal variation in the timing of births of Steller sea lions. *Journal of Mammalogy* **82:** 1047-1053.

Pitcher, K. W., D. G. Calkins and G. W. Pendleton. 1998. Reproductive performance of female Steller sea lions: an energetics-based reproductive strategy? *Canadian Journal of Zoology* **76:** 2075-2083.

Price, T., M. Kirkpatrick and S. J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. *Science* **240:** 798.

Purca, S. 2005. Variabilidad temporal de baja frecuencia en el Ecosistema de la Corriente de Humboldt frente a Perú. [Low frequency temporal variability in the Humboldt Current Ecosystem in the waters of Peru]. Phd thesis, Universidad de Concepción, Concepción, Chile.

Rand, R. W. 1955. Reproduction in the female Cape Fur Seal, *Arctocephalus pusillus* (Schreber). *Proceedings of the Zoological Society of London* **124:** 717-740.

Reeves, R., B. Steward, S. Leatherwood and P. Folkens. 1992. South American fur seal. *in* R. REEVES, B. STEWARD, S. LEATHERWOOD and P. FOLKENS eds. *The Sierra Club Handbook of Seals and Sirenians*. Sierra Club Books San Francisco.

Riedman, M. 1990. Predation on pinnipeds. *The Pinnipeds: Seals, sea lions, and walruses*. Univ of California Press.

Riedmann, M. 1990. Reproduction and life history. *The Pinnipeds: Seals, sea lions, and walruses*. University of California Press, Berkeley, Los Angeles, Oxford

Rutberg, A. T. 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. *The American Naturalist* **130:** 692-710.

Sandweiss, D., J. Richardson, E. Reitz, H. Rollins and K. Maasch. 1996. Geoarchaeological evidence from Peru for a 5000 years BP onset of El Niño. *Science* **273:** 1531.

Scott, M. P. 1986. The timing and synchrony of seasonal breeding in the marsupial, *Antechinus stuartii*: interaction of environmental and social cues. *Journal of Mammalogy* **67:** 551-560.

Sielfeld, W. 1999. The knowledge and conservation status of *Otaria flavescens* (Shaw,1800) and *Arctocepahlus australis* (Zimmermann, 1783) at the Chilean coasts. *Estudios Oceanológicos* **18:** 81-96.

Siniff, D. B., D. P. Demaster, R. J. Hofman and L. L. Eberhardt. 1977. An Analysis of the Dynamics of a Weddell Seal Population. *Ecological Monographs* **47:** 319-335.

Soto, K. H., A. W. Trites and M. Arias Schreiber. 2004. The effects of prey availability on pup mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru. *Journal of Zoology* **264:** 419-428.

Stevens, M. and D. Boness. 2003. Influences of habitat features and human disturbance on use of breeding sites by a declining population of southern fur seals (*Arctocephalus australis*). *Journal of Zoology* **260:** 145-152.

Stirling, I. 1983. The evolution of mating systems in pinnipeds. Pages 489-527 *in* J. F. EINSBERG and D. G. KLEINMAN eds. *Advances in the study of mammalian behavior*. Special Publication of the American Society of Mammalogy.

Trillmich, F. 1990. The behavioral ecology of maternal effort in fur seals and sea lions. *Behaviour* **114:** 3-20.

Trillmich, F., G. Kooyman and P. Majluf. 1986. Attendance and diving behavior of South American fur seals during El Niño in 1983. Pages 152-167 *in* R. GENTRY and G. KOOYMAN eds. *Fur Seals: Maternal Straegies on Land and at Sea*. Princetown University Press.

Trillmich, F. and D. Limberger. 1985. Drastic effects of El Niño on Galápagos pinnipeds. *Oecologia* **67:** 19-22.

Trillmich, F., K. Ono, D. Costa, R. Delong, S. Feldkamp, J. Francis, R. Gentry, C. Heath, B. Leboeuf and P. Majluf. 1991. *Pinnipeds and El Niño: Responses to Environmental Stress*. Springer-Verlag, Berlin.

Trites, A. W. 1991. Fetal growth of northern fur seals: life-history strategy and sources of variation. *Canadian Journal of Zoology* **69:** 2608-2617.

Trites, A. W. 1992. Reproductive synchrony and the estimation of mean date from daily counts of Northern fur seal pups *Marine Mammal Science* **8:** 44-56.

Trites, A. W. and G. A. Antonelis. 1994. The influence of climatic seasonality on the life cycle of the Pribilof northern fur seal. *Marine Mammal Science* **10:** 311-324.

Trites, A. W. and M. A. Bigg. 1996. Physical growth of northern fur seals (*Callorhinus ursinus*): seasonal fluctuations and migratory influences. *Journal of Zoology* **238:** 459-482.

Trites, A. W. and C. P. Donnelly. 2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. *Mammal Review* **33:** 3-28.

Van Der Lingen, C. D., L. Hutchings and J. G. Field. 2006. Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: are species alternations between small pelagic fish trophodynamically mediated? *African Journal of Marine Science* **28:** 465-477.

Vásquez, P. 1995. Determinación de los hábitos alimentarios de *Arctocephalus australis* y *Otaria byronia* en Punta San Juan de Marcona, Ica, Perú. [Determining feeding habits of *Arctocephalus australis* and *Otaria byronia* in Punta San Juan of Marcona, Ica, Peru]. MSc. thesis, Universidad Nacional Agraria La Molina, Lima.

Weber, D., B. Stewart and N. Lehman. 2004. Genetic consequences of severe population bottleneck in the Guadalupe fur seal (*Arctocephalus townsendii*) *Journal of Heredity* **95:** 144-153.

Wickens, P. and A. E. York. 1997. Comparative population dynamics of fur seals. *Marine Mammal Science* **13:** 241-292.

York, A. E. 1994. The population dynamics of northern sea lions, 1975-1985. *Marine Mammal Science* **10:** 38-51.

Zavalaga, C., R. Paredes and M. Arias-Schreiber. 1998. Dieta del lobo fino (*Arctocephalus australis*) y del lobo chusco (*Otaria byronia*) en la costa sur del Perú, en febrero de 1998; [Diet of South American fur seal (*Arctocephalus australis*) and South American sea lion (*Otaria byronia*) in the southern coast of Peru, Feburary 1998]. *Informe Progresivo del Instituto del Mar del Perú* **79:** 3-16.

Zuta, S., T. Rivera and A. Bustamante. 1978. Hydrologic aspects of the main upwelling areas off Peru. *in* R. BOJE and M. TOMCZAK eds. *Upwelling Ecosystems*. Springer-Verlag, Berlin.

Zuur, A. F., E. N. Ieno and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1:** 3-14.