

**THE EFFECTS OF PREY ABUNDANCE ON THE DIET, MATERNAL
ATTENDANCE AND PUP MORTALITY OF THE SOUTH AMERICAN
SEA LION (OTARIA FLAVESCENS) IN PERU**

by

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A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR
THE DEGREE OF
MASTER OF SCIENCE
in
THE FACULTY OF GRADUATE STUDIES
ZOOLOGY

NOVEMBER 2004

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

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Abstract

The Peruvian upwelling system is one of the most unpredictable but productive marine ecosystems in the world that is regularly affected by El Niño and La Niña events. As a consequence, South American sea lions (*Otaria flavescens*) inhabiting the Peruvian coast face stochastic fluctuations in the abundance and distribution of their prey.

The goal of my study was to determine the effects of marine environmental changes on the reproductive success of South American sea lions in Peru on the Ballestas Islands during the 1997-2002 breeding seasons. I also wanted to assess whether changes in diet and maternal behaviour during this time were proxies of major changes in the abundance of marine resources.

South American sea lions consumed primarily anchovy and squat lobster during the 1999-2001 La Niña, but consumed a greater diversity of prey when abundance was low during the 1997-1998 El Niño. Lactating females also modified the length of time they spent at sea and onshore in response to changes in the abundance of prey. Low abundances and quality of prey during El Niño caused females to continue foraging for longer periods. This resulted in greater times between nursing episodes, and ultimately led to the starvation of pups. In contrast, during the 1999-2001 La Niña, females spent shorter times at sea and longer times onshore as prey became more abundant.

Pup production and mortality were also directly related to the abundance of prey. Pup mortality reached 100% during El Niño and remained high during the favourable conditions of La Niña due to the short-term effects that El Niño had on population dynamics and subsequent maternal behaviour. Abortions were also higher during El Niño compared to other years, while numbers of pups born were significantly reduced during and after El Niño due to the death of a high proportion of the adult population.

My study suggests that South American sea lions in Peru are highly vulnerable to extreme changes in prey abundance. It also demonstrates that sea lion reproductive parameters, maternal attendance, and diet are strongly related to marine environmental conditions and annual variations in prey abundance. As a result, South American sea lions appear to be good

indicators of stochastic changes in the distribution and abundance of marine resources in the Peruvian upwelling ecosystem.

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Acknowledgements

I am grateful to the Peruvian Marine Research Institute (IMARPE) who provided the financial and logistical support for my entire project. Also thanks to Idea Wild for providing logistical support. I am very grateful to my friend Milena Arias-Schreiber from IMARPE, who trusted me and gave me the opportunity to lead this project. Special thanks to Miguel Ñiquen, Erick Diaz, Martin Trujillo and Mariano Gutiérrez for providing me with unpublished data on the abundance and distribution of anchovy as well as data from anchovy catches from commercial fisheries from IMARPE. Also thanks to Milena and Jose Carlos Márquez for the data on diet that I included in my thesis and did not always collect. Thanks also to Renato Guevara for helping me through financial support from IMARPE for the last breeding season at the islands.

Thanks a lot to my field assistants during this long journey. Thanks Roberto, Ximena, Cynthia, Fernando, Angel, Francesca, Judith, Marcelo, Akemi, Gaby, Martín, Karina, Giss, Christian, Susana, Milagros, Jean, Angie and Doris. Without you guys, it would not have been possible to collect all the data. Thanks for your patience and friendship! We had a great time!

I would like to specially thank my friends Roberto Manrique “Peto” and Julian Uribe “Pele”, for being there when I needed you the most. Thanks Roberto for give me the strength to continue at the islands, and thanks Pele for your friendship, help and interest for ensuring our well being at the islands.

Thanks to my supervisor Andrew Trites for introducing me to the world of SPLUS. Now I see the light you were talking about! Thanks Andrew for your guidance and for helping me to improve my writing. Thanks also to the members of my Committee, David Rosen and Anthony Sinclair for the helpful comments on my thesis.

Thanks to my friends at the Marine Mammal Research Unit. Thanks to those nice people who made me feel not far away from home. Thanks especially to my friend Ruth Joy, for helping me so much in the fight with SPLUS to analyze data and get the graphics done.

Thanks also to the amazing people of Room 10, Laura, Michelle and Saeko. Girls you made my time fun at UBC! Thanks a lot Laurita for your time correcting my English, especially my "grammar", and also for correcting my second chapter over and over again. Thanks to Arliss, Dom and Mary-Anne for the genial suggestions you gave me that improved my manuscript. Thanks Pamela for the times you made my life easy at the office.

I would like to specially thank my family, my parents María, Antonio, and my brother Bell, for giving me the encouragement to leave home for something different and better. Thanks a lot for the incredible effort in helping me to cover my studies here. Thanks also for your love and for being always by my side. Thanks for caring for my Josefina!!! Finally, I would like to thank my Martin, for all his help and support. Just for being the way you are. Thank you!!

Chapter 1: General Introduction

The South American sea lion (*Otaria flavescens*) is distributed along the coasts of South America, from northern Peru along the Pacific coast to southern Brazil in the Atlantic coast (Vaz-Ferreira 1982). They breed during the austral summer and have a breeding season that appears to change in length with latitude (Campagna 1985, Soto 1999). Female sea lions give birth to a single pup onshore, and will nurse for approximately one week before initiating regular attendance cycles (foraging trips and subsequent visits onshore to nurse their pups; Campagna & Le Boeuf 1988). Little is known about the timing of weaning in South American sea lions or when dependent young may supplement their milk diet with fish. However, known individuals of up to three years of age have been observed nursing on a regular basis in Peru (Soto 1999).

The Peruvian upwelling ecosystem is one of the richest ecosystems of the world. However, it is subject to drastic and stochastic fluctuations of productivity, which in turn affect the abundance of principal prey resources sought by pelagic predators. These fluctuations in productivity are caused by one of the strongest natural disturbances of marine and terrestrial ecosystems, the El Niño Southern Oscillation. An El Niño event results in warm sea surface temperatures, decreased primary production, and a deepening of the thermocline. This reduces the upwelling and concentration of nutrients, and thereby alters the abundance, distribution and availability of prey to pelagic predators (Barber & Chavez 1986, Fiedler 2002, Trillmich 1993). The other major oceanographic event in Peru is La Niña (known as the El Niño cold phase), and is characterized by an increase in primary marine productivity, a shallow thermocline and cool sea surface temperatures (Fiedler 2002) resulting in favourable conditions for predators feeding on pelagic resources. Such diametrically opposed oceanic events as El Niño and La Niña presumably mean that apex predators that inhabit the Peruvian coast have incurred strong selective pressures to thrive in the face of contrasting episodes of prey abundance.

Provisioning of young is energetically the most expensive component of reproduction and parental care in mammals (Clutton-Brock 1991). Female sea lions provide all of the nutritional resources required by their young. Thus, parental care is dependant on the

foraging success of the female, which ultimately determines offspring survival and future reproductive success (Bonner 1984). Lactating females need to acquire enough energy to recover from the perinatal fast and also require energy to travel, forage and produce milk to nourish their pups (Costa *et al.* 1989). Since lactating females have limited body reserves, they rely on the abundance of prey close to the breeding rookery to produce enough milk to care for their pups and ensure their survival. Therefore, reduced prey abundance may result in females being unable to acquire enough energy to meet their metabolic needs, and may prevent them from adequately provisioning their young, thereby affecting pup survival.

Reproductive and behavioural parameters of sea lions are probably a proxy for the state of the physical environment and a measure of the overall health of the ecosystem. In several otariid species, changes in maternal attendance behaviours have been associated with fluctuations in the abundance of prey resources (e.g., Costa *et al.* 1989, DeLong & Antonelis 1991, Heath *et al.* 1991, Majluf 1991, Ono *et al.* 1987, Trillmich & Dellinger 1991). The numbers of pups born and rates of pup survival have also been linked to fluctuations in prey abundance (e.g., DeLong & Antonelis 1991, Francis & Heath 1991, Guinet *et al.* 1994, Lunn & Boyd 1993a, b, Trillmich 1985, Trillmich & Limberger 1985, Trillmich *et al.* 1991). However, the strength of the relationship between the abundance of prey and changes in the reproductive ecology of otariids due to drastic and stochastic fluctuations in the marine environment has not yet been investigated.

The goal of my thesis was to determine the effects of stochastic environmental changes on the reproductive success of the South American sea lions in Peru. I also wanted to assess whether their diet and maternal attendance patterns may indicate major changes in the abundance and distribution of prey. By examining the relationship between environmental change and reproductive parameters of South American sea lions, I sought to gain insights into the adaptive responses of females to cope with prey uncertainty and ensure pup survival.

Overview

My thesis has two principal chapters. The first (Chapter 2) explores how changes in the abundance of prey due to major environmental disturbances can affect the timing of births as well as current and future reproductive success of South American sea lions in Peru. The second (Chapter 3) considers whether some parameters of the reproductive ecology of South American sea lions (such as diet and maternal attendance) may reflect changes in the abundance and distribution of prey in the unpredictable Peruvian marine ecosystem.

Chapters 2 and 3 were written as independent manuscripts, and therefore contain some redundancies since both relate different behavioural measurements of South American sea lions to the abundance and distribution of prey.

Chapter 2: The Effects of Prey Abundance on Pup Mortality and the Timing of Birth

Introduction

Changes in the abundance or availability of prey may shape breeding, maternal patterns and survival, and compromise the future reproductive success and population dynamics of apex predators. Such changes have been noted among such species as Humboldt penguins (*Spheniscus humboldti*; Paredes and Zavalaga 1998), southern fulmars (*Fulmarus glacialis*; Jenouvier *et al.* 2003), Galapagos fur seals (*Arctocephalus galapagoensis*; Trillmich & Ono 1991), water rats (*Nectomys squamipes*; Bergallo & Magnusson 1999), wild boars (*Sus scrofa*; Massei *et al.* 1996), and fat dormouse (*Myoxus glis*; Bieber 1998). Among pinnipeds, the effects of prey shortages have been noted to increase the length of foraging trips taken by lactating females (Boyd *et al.* 1994, Costa *et al.* 1989, Georges *et al.* 2000a, Georges *et al.* 2000b, Heath *et al.* 1991, Lunn & Boyd 1993b, McCafferty *et al.* 1998, Trillmich & Ono 1991). They have also been seen to affect the timing of implantation (Boyd 1984, Boyd 1996), decrease the growth rate of pups (Lunn *et al.* 1994, Trillmich *et al.* 1991) and increase pup mortality (DeLong & Antonelis 1991, Francis & Heath 1991, Le Boeuf & Reiter 1991, Lunn & Boyd 1993b, Majluf 1991, Roux 1997, Trillmich & Dellinger 1991). Other effects of prey shortage include reducing pup production, delaying the timing of births, and extending the length of breeding cycles (Boyd 1996, Guinet *et al.* 1998, Lunn & Boyd 1993a, Ono *et al.* 1987, Pomeroy & Duck 2000, Trillmich 1985, Trites & Donnelly 2003).

The Peruvian upwelling system is one of the most unpredictable but productive marine ecosystems in the world. As a consequence, pinnipeds and sea birds inhabiting the south eastern Pacific coast have to endure interannual fluctuations of their food supply (Trillmich & Ono 1991). One of the largest predators in this ecosystem is the South American sea lion (*Otaria flavescens*). How stochastic changes in the marine ecosystem affect the reproductive ecology of this species is unknown.

From 1997-2002 I investigated how changes in prey abundance affected the reproductive success of South American sea lions. I was particularly interested in determining how this apex predator copes with the highly unpredictable Peruvian marine ecosystem. My study encompassed one major El Niño and one La Niña event. An El Niño event results in a deep

thermocline, with warm sea surface temperatures, less upwelling and a decrease in primary marine productivity (Barber & Chavez 1986, Fiedler 2002, Trillmich 1993). This causes a severe shortage of anchovy (*Engraulis ringes*) and other prey for apex predators, such as sea lions. During an El Niño, anchovy, the most important prey of South American sea lions (Arias-Schreiber 2003) tend to be of poor quality, in low numbers and at deeper depths than normal (Alamo & Espinoza 1998, Arntz *et al.* 1991, Barber & Chavez 1986, Santander & Zuzunaga 1984, Trillmich 1993). In contrast, a shallow thermocline, cool sea surface temperature and high marine productivity characterize a La Niña event as occurred from 1998-2001 (Fiedler 2002).

South American sea lions breed during the austral summer starting in mid-December. Duration of the breeding season is affected by latitude (Campagna 1985, Soto 1999), with longer seasons occurring at low latitudes and shorter seasons occurring further south at high latitudes (Soto 1999). Pregnant females give birth to a single pup and remain onshore to nurse for approximately seven days (the perinatal period) before copulating and undertaking regular feeding trips (Campagna & Le Boeuf 1988). Lactation can last up to three years (Soto 1999), but little is known about the timing of weaning or when dependent young may supplement their milk diet with fish. Lactating females have limited body reserves and are therefore dependent on the abundance of prey near the rookery to produce the milk needed to care for their pups. Reduced prey abundance may result in a mother only acquiring enough energy to meet her metabolic needs, and may leave her unable to adequately provision her pup. Thus, a shortage of prey can directly affect pup survival.

The following examines whether fluctuations of prey influence pup survival and the timing of births of South American sea lions. Data were obtained from 1997-2002 at the Ballestas Islands, Peru (Fig. 2.1) and span one El Niño and one La Niña event. They provide insights into the female adaptive responses when faced with prey shortages and document the behavioural changes associated with prey abundance that may affect pup survival. These behavioural observations are also the first to systematically describe the effects of the El Niño on future reproductive success.

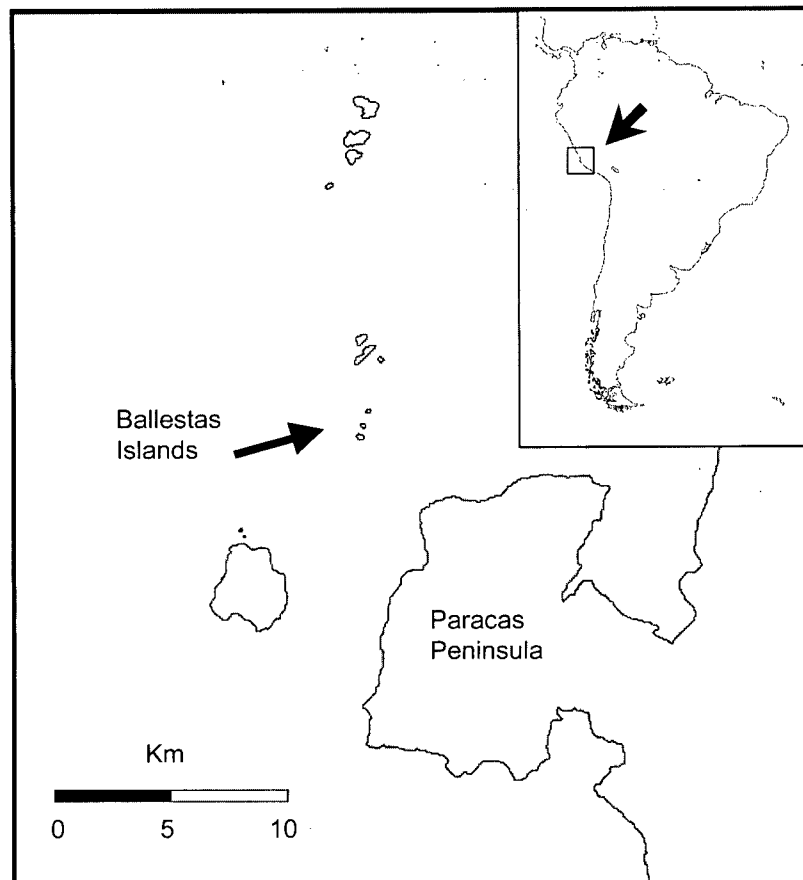


Fig. 2.1 The study site “La Maternidad” located at the North Ballestas Island, Peru.

Materials and methods

Study site

The Ballestas Islands ($13^{\circ}44'S$ $76^{\circ}24'W$) are located 250 km south of Lima (Fig. 2.1). Data were collected for 27 consecutive months from January 1997 to March 1999, and from 04 January to 10 March for three additional years (2000 - 2002). In all, the study encompassed six consecutive breeding seasons. The Ballestas Islands constitute a representative group of reproductive colonies of South American sea lions and is one of the largest breeding concentrations in Peru (Arias-Schreiber & Rivas 1998). These Islands are protected by the Peruvian Government as a guano bird reserve and are an important tourist

attraction, where sea lions are the primary draw. The main study area, La Maternidad or "The Maternity", is a narrow stretch of open pebble beach without pools or shaded areas. It is bounded to the north by open ocean, to the south by a rocky cliff, and by small caves to the east and west. I divided La Maternidad into 5 zones to facilitate the daily mapping of births and deaths (denotated as Cave, C1, C2, C3 and C4). Conspicuous rocks marked the boundaries between zones.

Births and mortality

The number of pups born each year and the mean number of females onshore (estimated from daily counts at 06:00 hrs.) were determined by two observers during day light hours (06:00 to 18:00 hrs). Parturitions occurring at night were estimated by counting fresh placentas each morning. The estimated number of pups born each day equalled the pups born during daylight hours plus the total number of placentas seen early in the morning.

The number of pups that died each day was estimated from counts of fresh carcasses. Each dead pup was noted on a map to avoid double counts. Four categories of pup mortality were distinguished: male harassment, female harassment, stillborn and unknown reasons. Unknown reasons were designated when a pup was found dead and could not be placed in any of the other categories. The low density of sea lions and the open flat topography of the study beach, as well as the low number of scavengers and small tides meant that few if any carcasses (or placentas) were missed.

The median dates of pupping and pup mortality were computed as the point during the breeding season when 50% of the total estimated births or deaths had occurred respectively. This was assumed to be a better measure of central tendency than the mean because of the large differences in the start date of the breeding season among years.

Prey abundance

Data on abundance of prey (anchovy) was obtained from the Peruvian Marine Research Institute (IMARPE) and included anchovy biomass and monthly catches from commercial fisheries along the Peruvian coast. Anchovy biomass was estimated from hydroacoustic surveys conducted once each year (between January and April) to determine the abundance of pelagic resources along the Peruvian coast. Anchovy catches represent where the fishery was concentrated and may not have reflected all of the places where anchovy were available to sea lions. Catches were also affected by partial or total closed seasons enacted by the Peruvian Government to protect spawning anchovy. This typically occurred twice per year (normally between February - March and August - September). Duration of the closed seasons differed between years and may therefore have affected the annual amount of anchovy caught for interannual comparisons.

Anchovy catch data were standardized using the catch per unit effort index (CPUE) because total catch figures were influenced by many variable factors (e.g., number of holds, trips with catch, searching time, storage capacity in the ship, etc.). CPUE was estimated by month by IMARPE and was used to compare with pup production and mortality to test for possible relationships with prey abundance.

Results

Numbers of pups born and timing of births

The number of pups born at La Maternidad fell from 1249 in 1997 to only 50 during the 1997-98 El Niño (Fig. 2.2, Table 2.1). All 50 of these pups died. Pup production in subsequent years increased from 406 in 1999 to 799 in 2002. Biomass of anchovy, like pup production, dropped during the 1997-98 El Niño, and increased over the next four years (Fig. 2). Birth rates (expressed as the ratio of pups born to the mean number of females counted on shore) were positively correlated with prey abundance (anchovy biomass) during the breeding season (Pearson $r = 0.868$, $p = 0.025$, $n = 6$; Fig. 2.3). In non El Niño years, distributions of

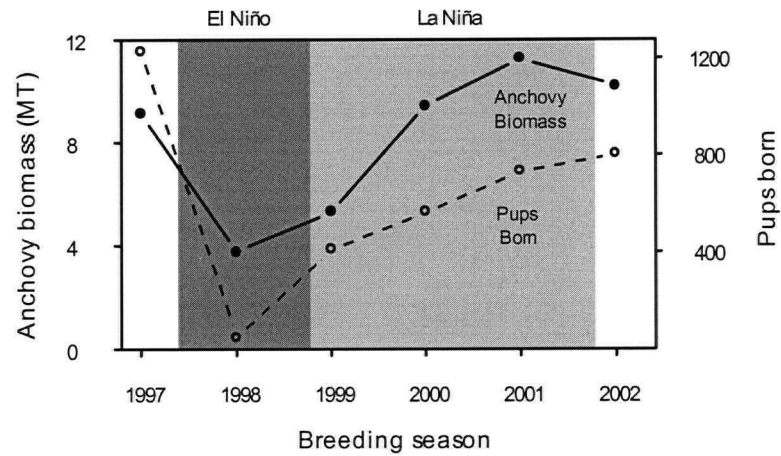


Fig. 2.2 Numbers of pups born (dashed line) and the estimated biomass of prey (anchovy; solid line) during the 1997- 2002 breeding seasons. Shaded regions denote the periods of El Niño and La Niña. Anchovy biomass is measured in millions of tons (MT).

Table 2.1 Characteristics of the breeding season from 1997-2002 at the Ballestas Islands showing the percent of pups that died, numbers of pups born, numbers of abortions, the mean number of females counted onshore, and median dates of birth and death.

Years	Pup mortality	Pups born	Abortions	Females onshore	Median birth date	Median death rate
1997	13.3	1229	no data	885	31-Jan	09-Feb
1998 El Niño	100	50	~1000	72	22-Jan	10-Feb
1999 La Niña	26.4	406	16	548	06-Feb	02-Feb
2000 La Niña	32.6	561	no data	470	22-Jan	22-Jan
2001 La Niña	11.4	729	no data	458	23-Jan	20-Jan
2002	15.1	799	>100	390	29-Jan	30-Jan

births varied between years (Kruskal-Wallis $\chi^2_4 = 65.24, p < 0.001$; Fig. 2.4). Although pupping started at different dates each year, there was general synchrony in the timing and frequency of the total number of pups born (Fig. 2.4).

Numbers of pups born were correlated with the mean numbers of females counted on the beach each year (Pearson $r = 0.860, p = 0.028, n = 6$). As with pups, mean number of females onshore varied significantly during the study period (Kruskal-Wallis $\chi^2_5 = 172.5, p < 0.001$) and decreased by 90% during the 1997-98 El Niño, and by 30% from 1999 to 2002 (Table 2.1).

The median birth date differed among years by as much as 16 days between the earliest peak of pupping (22 January 2000) and the latest (06 February 1999) (Median test, $\chi^2_4 = 262.9, p < 0.001$; Fig. 2.4). Individually recognizable females from previous breeding seasons ($n = 8$ females) varied their pupping dates – giving birth later in the season in 1999 and earlier in 2000 and 2001. Their timing of birth was consistent with the overall pattern observed from other females. In all years the peak of pup mortality occurred around the peak of pupping (measured as median dates, Fig. 2.4).

A strong negative relationship was found between the median birth date and the assumed abundance of prey during the previous year (as measured by the amount of anchovy caught per unit of commercial fishing effort CPUE; Fig. 2.5). Median birth dates tended to be later following a year of low catches, and were earlier when catches had been high (Fig. 2.5). Similar significant negative relationships were found between timing of birth and other indexes of CPUE such as anchovy catch per total hours of trip (Pearson $r = -0.959, p = 0.003, n = 6$), anchovy caught per trip ($r = -0.934, p = 0.006$), catch per register of brute tonnage estimated from total hours of trips ($r = -0.918, p = 0.01$), catch per total hold ($r = -0.972, p = 0.001$) and catch per hold with fish ($r = -0.979, p = 0.001$).

Although the numbers of pups born per unit of area within the five zones of the La Maternidad beach were equally distributed each year, individual females appeared to have a

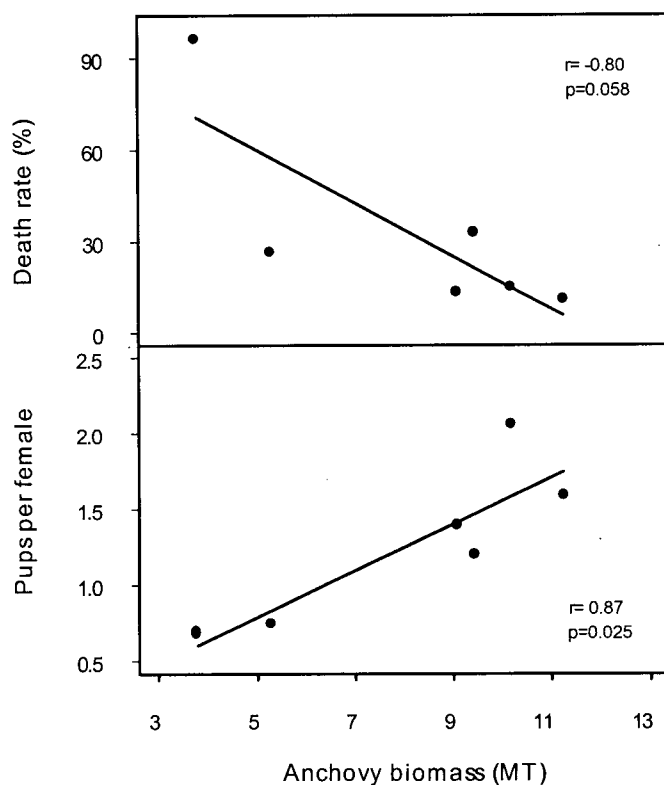


Fig. 2.3 Relationship between anchovy biomass (MT) and annual death rates of pups (top panel), and the numbers of pups born per females counted onshore (an index of birth rate) from 1997-2002 (bottom panel).

preference for where they gave birth. The Cave was the first zone where females gave birth each year. It differed from the other zones by having shade and lacking intraspecific attacks by subadult males.

El Niño

The 1997-1998 El Niño started in May 1997, after the breeding season ended. Abortions were first noted in late July 1997, and continued progressively until late October. Foetuses seen after October were classified as premature births based on their size and their different

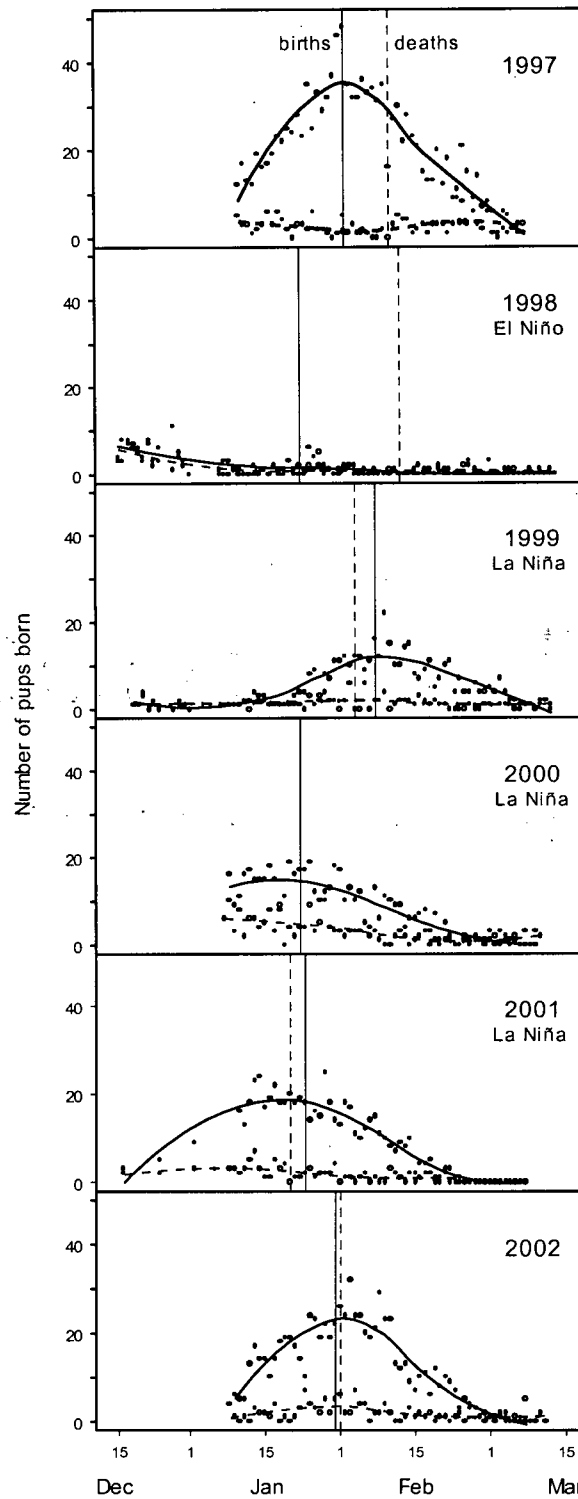


Fig. 2.4 Distributions of daily numbers of pups that were born or had died during the breeding season from 1997 to 2002. Data were fit with loess curves. The vertical lines indicate the median dates of births (solid) and deaths (dashed).

pelage colour. The frequency of premature births increased dramatically in early November at a rate of approximately 25 per day (Julian Uribe, pers. comm.) and peaked in mid November (Fig. 2.6). In all, 175 abortions and 440 premature births were observed in 1998 during the non-breeding season. Assuming 25 premature births occurred on each of the 15 days we were not present, the total number of reproductive failures numbered about 1000. High numbers of premature pups occurred at other rookeries in Peru during the 1997-1998 El Niño, but no systematic data of the daily rate are available.

During the 1997-1998 El Niño breeding season (January - March), only 50 pups were born (~5% of the expected total pup production) (Figs. 2.4 & 2.6). Most of these pups were abandoned on the beach by their mothers, who were visibly emaciated. In contrast to the El Niño, only 16 premature births were noted during La Niña (April-November 1998).

A second El Niño of moderate intensity occurred in 2002-2003 after we had completed our intensive observations, and again resulted in an increase in abortions (at a rate of 3 per day between September and November 2002). No data were recorded before or after these months. Sexually mature females in 2002 appeared to be older, in better condition, and were probably more experienced than those seen at the peak of the first El Niño (inferred by their large size). There was no evidence from other rookeries that massive abortions occurred during the 2002-2003 El Niño as seen during the 1997-1998 El Niño.

Unusual maternal behaviours were observed during the 1997-1998 El Niño when a few females (n=5) abandoned the beach as they were giving birth (the pup was emerging from the mother). Parturition was probably completed at sea where the pup would have drowned. A number of other females arrived on the beach (n=28) with newborns in their mouths. Of these 28 pups, 39% were alive (n=11), 46% were dead (n=13), and 7% were undetermined (n=2). The umbilical cord and remains of placenta were seen in all cases. Two other females arrived at the beach without a pup, but expelled their placenta minutes later. A few other females took their pups to sea after giving birth (n=7 live pups, and n=1 dead pup).

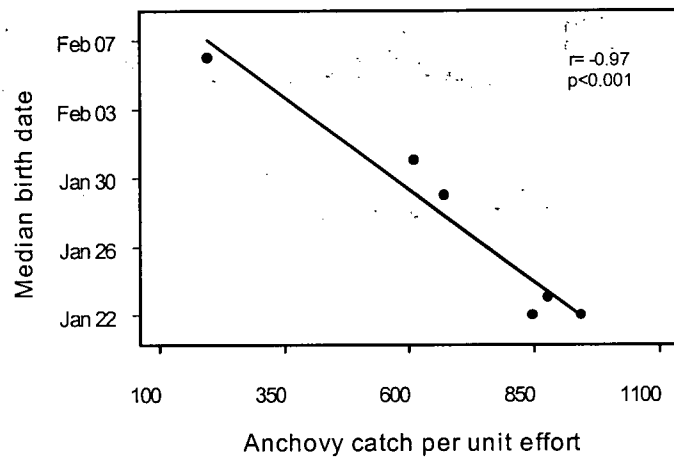


Fig. 2.5 The relationship between median dates of birth (1997-2002) and the abundance of prey in the previous year (1996-2001). Prey abundance was assumed to be proportional to the amount of anchovy caught per unit of commercial fishing effort. Data were fit with a linear regression ($r = -0.97$, $p < 0.01$).

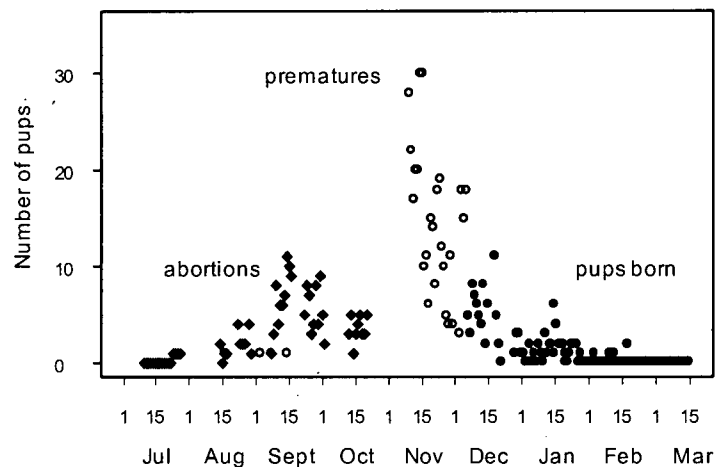


Fig. 2.6 Distribution of daily abortions, premature births and full term births during the 1997-1998 El Niño.

During the 1998 El Niño breeding season, yearlings were observed trying to take milk from unrelated females (n=17). Only six were successful (35%) and three of the 17 (18%) were injured by the females. All individuals (yearlings and adult females) showed signs of severe undernourishment. Pups were also observed trying to take milk (n=39), but only 39% of them were successful. Pups were rejected frequently and 5% were injured through their persistence. Pups in groups of up to four individuals were observed following and trying to take milk insistently from mothers arriving on the beach. Although not quantified, pups were also seen trying to take milk during the 2002-2003 El Niño breeding season. However, the frequencies appeared to be much lower than during the 1997-98 El Niño. Such behaviour was not observed in other years. Pups appeared to be undernourished during the 2002-2003 El Niño breeding season as a result of infrequent nursing associated with longer maternal feeding trips (Chapter 3.). Pups often pursued their mothers to the shoreline as they prepared to leave on a foraging trip, and tried unsuccessfully to continue suckling.

During the 1997-1998 El Niño, 100% mortality of yearlings and juveniles (individuals of approximately two years old) occurred. No individuals of these cohorts were observed at the end of this El Niño at the study site or other important rookeries. During the 1999 breeding season, only adults were on the beach. Overall, approximately 60% adult mortality was estimated from monthly counts before, during and after the El Niño.

Although carcasses were uncommon at the study beach during the non-El Niño years, emaciated carcasses of 73 yearlings, 41 females, and 35 juveniles were counted during El Niño. Yearlings were the first cohort affected by the El Niño food shortage beginning two months after its onset.

Pup mortality

The number of dead pups differed significantly among years and ranged from as few as 13% before El Niño to 100% during El Niño (Chi-square test $\chi^2 = 159.8, p < 0.001$; Fig. 2.7, Table 1). Pup mortality after El Niño also differed significantly among years (Chi-square test

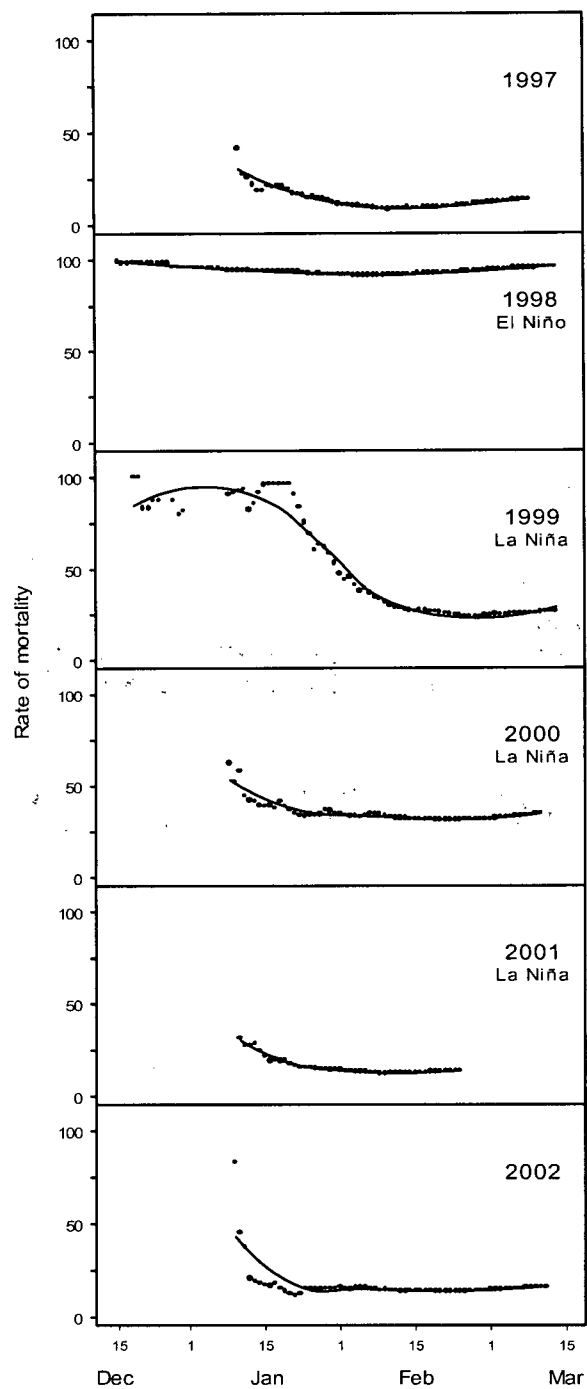


Fig. 2.7 Running rate of pup mortality through the breeding season from December to March (1997 to 2002). The rate of mortality for any given date equaled the total number of dead pups (since the first day of observation) divided by the total number of pups born over this time period.

$\chi^2_3 = 17.6, p < 0.01$). There was a strong negative correlation between the death rate of pups and prey abundance as measured by catch per unit of effort. These indices of abundance included tons of anchovy caught per trip (Pearson $r = -0.82, p = 0.04, n = 6$), catch per total hours of trip ($r = -0.87, p = 0.02$), catch per total hold ($r = -0.86, p = 0.02$), catch per hold with fish ($r = -0.84, p = 0.03$) and catch per brute tonnage register estimated from total hours of trip ($r = -0.89, p = 0.01$). There was also negative correlation between death rate and anchovy biomass during the breeding season (Pearson $r = -0.80, p = 0.058, n = 6$; Fig. 2.3). Higher rates of mortality were associated with lower estimates of anchovy biomass.

Pup mortality was consistently high throughout the breeding season in all years (Fig. 2.7), but the distribution of deaths differed among years (Kruskal-Wallis $\chi^2_4 = 22.57, p < 0.001$; Fig. 2.4). Pup mortality was independent of the number of pups born and of the number of females on the beach. The only significant correlation between births and deaths occurred during the El Niño (Pearson $r = 0.93, p < 0.001, n = 6$; Fig 2.7). Pup starvation was evident during the El Niño breeding season when only 1% of the total pups born were still alive at the end of the season. One month later, only one pup was observed alive on the entire beach.

The median dates of death differed by as much as 22 days between the earliest peak of pup mortality (20 January 2000) and the latest (10 February 1998) (Median test $\chi^2_4 = 50.5, p < 0.001$; Fig. 2.4). Numbers of pups were evenly distributed (per unit of area) over the five study zones in all years. Although the 2000 La Niña breeding season could be considered as optimal and favourable for the reproductive success of the South American sea lions (based on the high abundance of anchovy reflected in the landings and stocks assessments), pup mortality was at its highest compared with other non-El Niño years.

Aberrant behaviour

Pup mortality was caused by several factors that varied in importance among years. Most noteworthy was the aberrant behaviour observed particularly during the 1999-breeding season (a year after the peak of El Niño). Females in groups ranging from 4 to 6 animals were seen

taking and killing unrelated newborn pups. This behaviour accounted for 2.5 to 8.4% of total pup mortality. In most cases, females killed a pup by physical trauma while trying to keep it aggressively away from other females. Sub-adult males sometimes took pups to the sea from a group of disputing females. Aberrant maternal behaviour was first observed after the 1998 El Niño breeding season and continued during the rest of the study years in a lower frequency.

Discussion

An important finding of my study is that the reproductive success of South American sea lions in Peru is directly linked to fluctuations of prey availability. The 1997-1998 El Niño was the strongest on record and resulted in severe short-term effects on their reproductive ecology. My study suggests that South American sea lions face highly contrasting episodes of prey abundance — yet can evoke strategies that enable them to adapt to stochastic changes in their ecosystem and recover under favourable environmental conditions.

Pup mortality

Interannual changes in the Peruvian upwelling system can significantly affect the distribution and abundance of pelagic resources and the reproductive performance of species such as the South American sea lions that depend upon them. The strongest 1997-98 El Niño on record caused 100% of the few pups that were born that year to starve. Females returned infrequently to the beach to nurse their pups during the period of acute prey reduction (Chapter 3), and probably did not have sufficient milk to adequately nourish their pups. The acute prey shortage resulted in high adult mortality (approximately 60%) and the loss of entire young cohorts (ages zero, one and two years old). High number of carcasses recorded during annual censuses along the Peruvian coast confirms high mortality rates (Arias-Schreiber, unpubl.). Stillbirths were observed in low numbers and accounted for an average of 2.3% of the total mortality in all years.

In contrast to El Niño, high abundance of prey should have been available to sea lions during the 1999-2001 La Niña. However, the sea lions did not appear to have been able to

fully capitalize on this change in events due to the lagged effects of the acute prey shortages experienced the previous year (1997-1998 El Niño). High pup mortality recorded during the 1999-2001 La Niña breeding seasons seem to have been an indirect consequence of three different but related factors associated with short-term effects of the 1997-98 El Niño: 1) high mortality of territorial males, 2) high incidence of intraspecific aggressions and 3) aberrant female behaviour.

Only 60% of the territorial males that attempted to breed before the El Niño was alive to breed after this event (Soto 1999). The high mortality of bulls allowed for increased intraspecific aggressions by subadult males on pups. The low numbers of territorial males present after the El Niño was insufficient to defend the relatively large breeding beach (and indirectly protect the pups). As a consequence, injuries resulting from intraspecific aggressions by the higher proportion of subadult males that appeared on the beach during the 2000 La Niña breeding season caused up to 50% of the total pup mortality. Aberrant female behaviour, whereby females took and killed pups that were not their own, also contributed to the increased pup mortality. This aberrant behaviour seemed to be related to a low pregnancy rate and low numbers of females pupping successfully after the El Niño; and appeared to abate in subsequent years as more females successfully gave birth.

Pup production

My data showed that the ratio of pups born to the number of females present each year declined as the anchovy abundance dropped during the breeding season. This ratio is effectively an index of birth rates. Most mature females return to the rookery even if they do not give birth. Thus, it appears that birth rates dropped as the abundance of prey declined. Increases in pup production have been noted in some otariids following a year of high food availability (see Lunn & Boyd 1993a). Indeed, during La Niña, we observed a doubling in the number of pups born (from 1999 to 2002). Although environmental conditions were not equal during all La Niña years, there was increased pupping during 2000 and 2001 when food abundance was higher than other years.

It is important for animals to detect environmental signals that permit them to coordinate or possibly adapt the physiological events of reproduction with changes in their food supply (Boyd 1991). The 1997-1998 El Niño started soon after the end of the breeding season when females would have had high energetic demands placed on them by their suckling young. Poor body condition probably increases the frequency with which South American sea lion abort their foetuses during years when nutritional stress becomes acute. Although the cost of producing a full term foetus is likely to be small (see Winship *et al.* 2002), the cost of caring for a pup is not (Clutton-Brock 1991). Thus a female would have to continue to nurse a pup for one or more years to ensure its survival and future reproductive success. High incidence of abortions when food is scarce has also been reported in species such as the South African fur seal, *Arctocephalus pusillus* (Roux 1997) and the California sea lion, *Zalophus californianus* (Trillmich *et al.* 1991). Abortions tended to be associated with females in significantly poorer body condition compared to females that maintained pregnancies to parturition (Guinet *et al.* 1998).

High mortality of females during the 1997-1998 El Niño combined with the low pregnancy rates probably explain the low number of births that followed the El Niño year. Although pinnipeds are capable of ovulating and conceiving when prey is restricted (Lunn & Boyd 1993a, b, Trites & Donnelly 2003), it seems improbable that high numbers of females whose blastocysts successfully implanted, failed to carry foetuses to parturition under the favourable environmental conditions that followed the 1998 El Niño breeding season. Scarce numbers of abortions observed in my study area and other important rookeries preceding this event support this hypothesis. The reduced number of copulations and the abandonment of breeding areas I observed during the peak of the El Niño may be additional factors accounting for the low recruitment we noted after the El Niño breeding season.

Duration of the breeding cycle (from oestrus to parturition) varies according to the food availability (Boyd 1996) and may reflect the timing of implantation (Lunn & Boyd, 1993a) or changes in the fetal growth rate (Guinet *et al.* 1998). Although birth synchrony is maintained and high precision in the peak of pupping from year to year is observed in several species (Boulva 1975, Campagna 1985, Coulson 1981, Duck 1990, Jemison & Kelly 2001, Majluf

1991, Pitcher *et al.* 2001, Trites 1992), the South American sea lions appear to have considerable flexibility in the start and duration of their breeding season according to the abundance of prey. Thus, females tended to give birth later in the season after a year of low prey abundance, and earlier when prey abundance was high.

Birth synchrony

The peak of pup mortality occurred around the peak of pupping in all years. This differs from other South American sea lion rookeries on the Atlantic coast (see Campagna *et al.* 1992), and with other pinnipeds such as the Weddell seal (Thomas & DeMaster 1983). Food availability, suitable weather, and environmental cues acting together or independently may be the primary factors that determine the timing of births and enhance the reproductive success of females (Boness *et al.* 1995, Boyd 1991, Ims 1990, Lunn & Boyd 1993a, Majluf 1992, Pitcher *et al.* 2001). Additionally, females should give birth when the probability of offspring mortality is the lowest in order to maximize their fitness (Clutton-Brock 1988, Ritcher 1999, Trites & Antonelis 1994). However, the distribution of pupping dates for all breeding female South American sea lions within a season tended to be consistent across all years, despite differences in risk of losing their pups.

In general, older females tend to be more experienced and in better condition than younger females. A number of pinniped studies have documented that such females also tend to give birth earlier in the season compared with young mothers – thereby increasing the survival of their pups (Boyd & McCann 1989, Duck 1990, Reiter *et al.* 1981, York & Scheffer 1997). Although there is no evidence to indicate whether most dead pups belonged to young or inexperienced sea lion females before the 1997-98 El Niño, there were few young females left alive after this event and pup mortality remained at its highest around the peak of pupping. Although a bias towards older females giving birth earlier in the season was expected after the El Niño, the distribution of observed births did not change. Distribution of births during the breeding season may be independent of the age of females in South American sea lions.

The closeness of the median dates of births and deaths (Fig. 4) may be related to a concomitant rise in copulations that lead to higher incidences of male-male interactions (Soto, unpubl.). Although most pups died from unknown causes, intraspecific attacks were the main documented cause of direct pup mortality at the peak of births. These intraspecific attacks resulted from peripheral males that succeeded in evading the territorial males and entering the beach. Male interactions may also have contributed to mother-pup separations as have been observed elsewhere (Campagna *et al.* 1992, Pistorius *et al.* 2001).

The degree of polygyny appeared higher in Peru as indicated by the mean ratio of males to females (1:30) compared to the ratio (1:4) at rookeries on the Atlantic coast (see Campagna, 1985). My study site also appears to have had a shortage of suitable territories that may have affected male behaviour and lead to intense male competition and a high incidence of intraspecific attacks on pups. An absence of pools or shady areas (necessary to reduce thermal stress due to intense solar radiation) favours territories along the water edge and restricts the number of territories. This in turn increases intraspecific competition, and favours a reproductive system where few males defend shoreline territories and have access to most copulations. This suggests that having more territories with thermoregulatory advantages besides the shoreline, would have lessened male competition and would have lowered pup mortality. Although further studies are necessary to test this hypothesis, topographies that are suitable for reproduction and enhance thermoregulation are scarce in Peru. Thus, sea lions tend to be concentrated in large numbers on relatively few rookeries that have limited access by humans.

Prey abundance

I found a strong relationship between reproductive success (current and future) of the South American sea lion and the abundance of prey in the Peruvian upwelling ecosystem. The impact that fluctuations in the abundance of prey may have on the sea lion reproductive ecology will depend on the intensity and timing of such changes relative to the timing of the breeding cycle. Prey shortage during El Niño events may result in higher numbers of

abortions and reproductive failures in subsequent years. In contrast, high abundance of prey during La Niña can favour reproductive success and an increase in pup production.

Timing of births and pup mortality

The timing of births and pup mortality were strongly related to the interannual fluctuations in the abundance of prey. Births occurred later in the season after years of low prey abundance and earlier in the season after a year of high prey abundance. Pup mortality reached its highest when prey scarcity was acute because mothers were unable to adequately supply energy resources to their pups. Moreover, high numbers of abortions were observed during years when prey abundance appeared to be low. This may have been a physiological response of pregnant females that negated future energetic costs under adverse conditions. In contrast, when resources were abundant, the numbers of pups born rapidly increased. However, rates of pup mortality remained high during the years of high prey abundance as an indirect consequence of altered population dynamics and maternal behaviour caused by the previous severe food shortages that sea lions experienced during El Niño.

Global warming models predict stronger and more frequent future El Niños events along the Peruvian coast. This does not bode well for South American sea lions if the lagged aberrant behaviours associated with high adult mortality further impact their reproductive success. As such, the direct and indirect effects of the drastic and stochastic changes in the upwelling ecosystem on births and pup mortality may endanger the South American sea lions in Peru.

Summary

Pup mortality and the timing of birth of South American sea lions were investigated to determine the possible relationship between fluctuations in prey abundance in the Peruvian upwelling ecosystem and current and future reproductive success during six consecutive breeding seasons. My study from 1997 to 2002 encompassed the strongest El Niño on record and one La Niña event. Pup mortality ranged from 13% before El Niño to 100% during El

Niño, and was negatively correlated with prey abundance. Abortions were also more frequent when prey abundance was low. However, pup mortality remained high following El Niño due to its short-term effects on population dynamics and subsequent maternal behaviour. Births occurred later in the season after years of low prey abundance and earlier following years of high prey abundance. The peak of pupping occurred around the peak of mortality in all years, and may have been the product of intensive competition between bulls at the peak of the breeding. Stronger and more frequent El Niños appears to be occurring along the Peruvian coast and could produce significant stochastic changes in births and pup mortality that place the vulnerable South American sea lion population in Peru at great risk.

Chapter 3: Diet and Maternal Attendance as Indicators of Prey Abundance and Changes in the Marine Environment

Introduction

In theory, changes in ocean productivity directly affect the abundance and distribution of prey species, which in turn affect the reproductive and foraging ecology of their predators (Bester & Van Jaarstveld 1997, Boyd & Murray 2001, Georges *et al.* 2000a, Guinet *et al.* 2001, McCann 1987, Trillmich & Ono 1991). A number of studies have related changes in the foraging behaviour of such apex marine predators as pinnipeds, whales and sea birds to the abundance of prey they feed upon (e.g., Boyd 1999, Boyd *et al.* 1994, Boyd *et al.* 2002, Costa *et al.* 1989, Georges *et al.* 2000a, Lunn *et al.* 1994, McCafferty *et al.* 1998). However, only a few studies have attempted to validate the relationship between prey and foraging behaviour by assessing oceanographic conditions or the distribution and abundance of prey due to the difficulty and costs of conducting such research (e.g., Boehlert *et al.* 2001, Boyd & Arnborn 1991, Boyd & Murray 2001, Campagna *et al.* 2000, Hakoyama *et al.* 1994, Hooker & Boyd 2003, Lea & Dubroca 2003, Lydersen *et al.* 2003, McCafferty *et al.* 1999, Wilson *et al.* 1994).

The degree to which behavioural responses of apex predators are proxies for changes in the marine environment is not clear. A better understanding of this relationship would help guide the use of apex predators as indicators of marine environmental change. It might also help to assess the consequences of fishing on the foraging ecology of apex predators and the potential for competition to occur with humans for marine resources.

Female South American sea lions offer a unique opportunity to evaluate the strength of the relationship between fluctuations in the marine ecosystem and the reproductive ecology of apex predators. These sea lions inhabit the productive but unpredictable Peruvian upwelling ecosystem (Ryther 1969), and are exposed to interannual and stochastic fluctuations in the distribution and abundance of their principal prey — the anchovy (Arias-Schreiber 2003). The distribution and abundance of anchovy, as well as the effects of reduced ocean productivity on its life history have been well documented due to the economic importance of

anchovy to the Peruvian fishing industry (Barber & Chavez 1986, Muck *et al.* 1987, Ñiquen & Bouchon 2002, Pauly & Palomares 1987, Pauly & Tsukayama 1987, Senocak *et al.* 1987). Similarly, considerable knowledge has been gathered on the foraging, reproduction and diet for the sea lions throughout their distributional range along the Atlantic and Pacific coasts of South America (Campagna *et al.* 1992, Campagna & Le Boeuf 1988, Campagna *et al.* 2001, Koen Alonso *et al.* 2000, Soto 1999, Thompson *et al.* 1998, Werner & Campagna 1995). Females are easy to monitor since they give birth on land and alternate intermittent trips at sea to feed (foraging trips) with visits onshore to nurse their pups during the austral summer (Campagna & Le Boeuf 1988). Female sea lions also provide all the nutritional resources needed to rear their pups, and do not rely on fat reserves stored before parturition (Trillmich *et al.* 1991). Thus, stochastic fluctuations of the marine environment should directly affect the maternal performance and future reproductive success in this species.

The goal of my study was to determine whether behavioural measurements from apex predators reflect physical changes in the marine environment and alterations in the abundance and distribution of prey. Sea lion diets and behavioural observations of maternal attendance patterns were assessed at the Ballestas Islands, Peru, over 5 consecutive breeding seasons of contrasting prey abundance that included the strongest El Niño on record (1997-1998, McPhaden 1999) and a moderate La Niña (1999-2001). I investigated the reproductive ecology (maternal attendance and dietary habits of South American sea lions) and its relationship with oceanographic variables (sea temperature anomalies) and marine prey resources (distribution and abundance of anchovy) at matching spatial and temporal scales. The strength of these relationships were expected to reveal the extent to which South American sea lions could be used as indicators of abundance and distribution of prey in the unpredictable Peruvian marine ecosystem. My results also provided valuable information about the effects of prey fluctuations on the reproductive ecology and behaviour of sea lions for better understanding the ecology of other marine mammals and their adaptative responses to cope with marine environmental change.

Materials and methods

Study site

Data were collected on the Ballestas Islands ($13^{\circ}44'S$ $76^{\circ}24'W$), Pisco, Peru, which are home to one of the largest breeding concentrations of South American sea lions in Peru (Arias-Schreiber & Rivas 1998). The islands are protected by the Peruvian Government as a guano bird reserve. The main study area, La Maternidad ("The Maternity"), is an open pebble beach without pools or shaded areas that allows for all of the sea lions using the rookery to be observed. It is bounded to the north by open ocean, to the south by a rocky cliff, and by small caves to the east and west.

Diet

Diet was determined from scats collected by IMARPE at San Gallan Island ($13^{\circ}51'S$, $76^{\circ}26'W$), a nearby breeding rookery that was approximately 7 km from my study site. The topography of my behavioural study site at La Maternidad prevented access to the beach to collect scats. Numbers of scats collected at San Gallan Island varied between years ($n = 139$ scats in January and March 1998; 81 scats in January and March 1999; 50 in April 2000; 21 in January 2001 and 84 samples in January and February 2002). Hard parts that could be identified to species were recovered in all scats, except 60 in 1998 (El Niño), 8 in 1999 (La Niña) and 10 in 2002 that contained no identifiable hard parts.

Scats were frozen after collection, then later thawed and washed using a series of sieves with mesh sizes of 2.0, 0.425 and 0.25 mm (U.S.A. Standard Test, Tyler). Fish otoliths, cephalopod beaks and crustacean remains were separated. Otoliths were identified to the lowest taxonomic level using the reference collections of the Peruvian Marine Research Institute (IMARPE) and the identification guide of García-Godos (2001). Cephalopod beaks were not identified to species and crustacean remains did not accurately reflect the number of individuals in each sample due to their advanced stage of digestion. Thus, only the frequency of occurrence (defined as the number of scats in which a given prey occurred, Dellinger & Trillmich 1988) for each taxonomic group was included in the analysis.

Maternal attendance

Observations were made during 5 consecutive breeding seasons (Jan 4–Mar 10) from 1998 to 2002. Maternal attendance was estimated by measuring the duration of individual female attendance cycles (time spent at sea foraging and time spent onshore nursing their pups). Females were marked with paint pellets fired from a CO₂ gun (Nel-Spot Company), and with paint-filled-eggs thrown up to 35 m from the animals. Females were marked on their day of parturition or during the interval between parturition and a mother's first departure to sea (the perinatal period) (1998: n = 45; 1999: n = 80; 2000: n = 100; 2001: n = 144; 2002: n = 103). The small sample size during the 1998 El Niño breeding season resulted from the low numbers of females using the study beach, given most females with pups were marked that season. Paint markings and natural scarring were drawn on animal identification cards. Marks lasted from two to three weeks. Some females were remarked depending on the quality of the initial mark.

Female attendance was recorded using focal sampling methodology (at 10 minute intervals) during day light hours (06:00 to 18:00 hrs) from a cliff that was about 70 meters above the colony and 100 meters distant. The duration of the perinatal period, foraging trips and visits onshore were recorded for each marked female. Females that lost their pups were removed from the sample. If a female was recorded at the beach at the end of the day and was not found the next morning, her time of departure was assumed to have occurred at midnight (the midpoint between when observations stopped and began again). Females whose date of pupping were unknown and had remained onshore with their pups for more than 3 days after being marked were assumed to have not made their first post-partum trip to sea. First feeding trips and first visits onshore were analyzed independently from the rest of the data because the maternal investment is known to be high during the perinatal period. Sample sizes represented the number of females rather than the numbers of trips and visits onshore. Thus, only mean durations of trips and visits onshore for each female were included in the analysis. Daily counts of females were conducted at 06:00, 12:00 and 18:00 hrs each year.

Prey abundance and oceanographic conditions

Interannual oceanographic and biological fluctuations occurred during my study from 1998 to 2002. The strong 1997-1998 El Niño, resulted in increased sea surface temperatures and the deepening of the thermocline, which drastically reduced the primary marine productivity (Fiedler 2002, McPhaden 1999). This in turn affected the distribution and abundance of anchovy and other potential prey for the sea lions. In contrast, the moderate 1999-2001 La Niña was characterized by cold surface temperatures, shallow thermoclines and high marine productivity (Fiedler 2002), which in turn resulted in favourable prey conditions for the sea lions. The 2002 breeding season took place during the early stages of the moderate 2002 El Niño (Moron 2002, Ñiquen & Bouchon 2002).

Data on prey abundance and the distribution of pelagic resources were obtained from IMARPE. These included CPUE (catch per unit of effort) indexes from catches of anchovy from commercial fisheries and, abundance and distribution of Peruvian anchovy derived from hydroacoustic surveys along the Peruvian coast. Hydroacoustic surveys encompassed the area between shore and 100-120 nm and were carried out using the echo sounding SIMRAD EK-500 and EY-500. Abundance of anchovy from hydroacoustic surveys was estimated using echo integration techniques (see MacLennan & Simmonds 1992). CPUE is often used as a measurement of relative abundance for anchovy (Bouchon *et al.* 2002, Ñiquen & Bouchon 2002, Santojanni *et al.* 2003), and was compared with the duration of the foraging trips and visits onshore to test for possible relationships. CPUE indexes included the catch of anchovy per hours of trip, per hold with fish, per registered brute tonnage, and per registered brute tonnage estimated from hours of trip. According to IMARPE (M. Ñiquen unpubl.) the anchovy catch per hours of trip has showed the strongest correlation with the assessments of anchovy biomass from hydroacoustic surveys.

Oceanographic conditions were assessed from sea surface temperatures recorded daily by the IMARPE, at the Coastal Laboratory of Pisco. Temperature anomalies were calculated from data collected since 1976 by IMARPE. Since sea surface temperatures can be used as an index of environmental uncertainty (Gentry & Kooyman 1986) and have been associated with changes in the abundance of the Peruvian anchovy (Barber & Chavez 1986) and maternal

performance in otariids (Francis *et al.* 1998, Lea 2002), I analyzed these oceanographic features to test for possible relationships with the maternal attendance pattern. The occurrence of principal prey species in the diet and the potential link to their distribution and abundance close to the breeding area was also explored.

Results

Diet

A total of 1719 otoliths were found in 307 scats. All but 1.8% of the otoliths ($n=31$) could be identified. The main prey items consumed were fish (76.7% frequency of occurrence), crustaceans (88.3%) and cephalopods (17.9%; Table 3.1), with the highest numbers of prey species occurring in 2002 (17 spp.) and during the 1997-98 El Niño (12 spp.). An average of 8 species were found in the scats during La Niña (1999 to 2001).

Significant differences were found in the occurrences of principal prey among and within years. Only anchovy (*Engraulis ringes*) and squid (*Loligo sp.*) occurred in all years. However, consumption of anchovy differed among years (logistic regression deviance test — with year as a categorical variable: $\chi^2_4 = 32.86$, $p < 0.001$) as did consumption of squid ($\chi^2_4 = 23.20$, $p < 0.001$).

No differences were found in the relative occurrences of anchovy within a season in any year. Occurrences of anchovy represented an average of 75% of the total fish identified in the scats (excluding the El Niño year when anchovy was scarce and other fish species were consumed). Including the El Niño year resulted in anchovy making up 68% of all fish occurrences. The only year that squid varied within a season was 1999 (logistic regression deviance test: $\chi^2_1 = 4.73$, $p = 0.03$). The pelagic squat lobster (*Pleuroncodes monodon*) was found in all years except during the 1997-1998 El Niño and in February 2002. Its occurrence differed between years (logistic regression deviance test — with year as a categorical variable: $\chi^2_3 = 36.61$, $p < 0.001$), but only differed within a season in 2002 when no remains were found in the scats collected in February of that year (early stages of the 2002 El Niño, see Table 3.1).

Table 3.1 Frequencies of occurrences (%) of the principal prey of South American sea lions during the breeding season from 1998 to 2002 at San Gallan Island. Mean values excluded the 1998 El Niño.

(*) Occurrences of crustaceans in 2002 correspond to percentages for January 2002 only since no crustacean remains were found in the scats during February 2002.

Years	Fish (%)	Crustaceans (%)	Cephalopods (%)
1998 El Niño	97.5	0.0	5.1
1999 La Niña	41.1	83.6	27.4
2000 La Niña	86.0	96.0	6.0
2001 La Niña	100.0	76.2	28.6
2002	79.7	97.5*	9.5
1999-2002 Mean	76.7	88.3	17.9

Important demersal species for commercial fisheries occurred in most years. These included the lumptail searobin (*Prionotus stephanophrys*, mean = 21.6%), Peruvian hake (*Merluccius gayi*, 8.2%) and camotillo (*Normanichthys crockeri*, 29.2%). However, differences in their occurrences were found among years (lumptail searobin, Logistic regression deviance test $\chi^2_3 = 57.43$, $p = 0.027$; Peruvian hake, $\chi^2_3 = 8.82$, $p = 0.032$; and camotillo $\chi^2_3 = 9.09$, $p = 0.028$). Only during the 1997-1998 El Niño did the demersal cachema (*Cynoscion analis*) occur in high percentages (22.2%).

Maternal attendance

The duration of foraging trips (Kruskal-Wallis, $\chi^2_4 = 133.1$, $p < 0.001$) and visits onshore (Kruskal-Wallis, $\chi^2_4 = 18.7$, $p < 0.001$) differed significantly among years, even after removing the El Niño year (trips: $\chi^2_3 = 121.97$, $p < 0.001$; visits: $\chi^2_3 = 8.87$, $p = 0.031$; Fig. 3.1; Table 3.2.). Pairwise comparisons showed that the foraging trips recorded during the

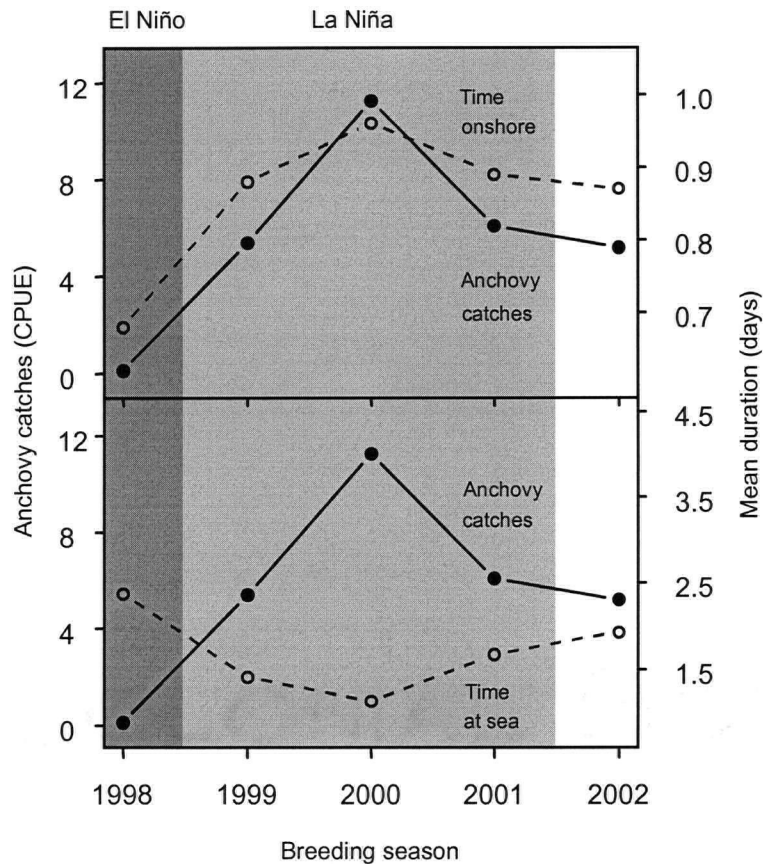


Fig. 3.1 Mean time that females spent at sea and onshore during the breeding season 1998-2002 contrasted with an index of prey abundance (anchovy catches, CPUE).

1998 El Niño did not differ significantly from those in 2001 (Dunnett, $p = 0.93$) and 2002 (Dunnett, $p = 0.60$). The lack of difference may reflect the small sample size or the high variability in foraging times during the 1998 El Niño.

Duration of visits onshore was similar between all years except between 2000 and 2002 (Dunnett, $p = 0.031$). Mean duration of foraging trips and visits onshore were inversely related, with the longest foraging trips and shortest visits onshore occurring during El Niño. Similarly, duration of foraging trips were the shortest during the 2000 La Niña, while the visits onshore were the longest (Fig. 3.1). During El Niño, foraging trips were twice the mean duration of trips in subsequent years (Table 3.2).

Duration of the first trip and visit onshore after parturition were longer than all other trips and visits in all years (Table 3.3) and also varied significantly among years (trips: Kruskal-Wallis $\chi^2_4 = 91.75$, $p < 0.001$, visits: Kruskal-Wallis, $\chi^2_4 = 17.35$, $p = 0.002$).

The perinatal period averaged 7.46 days over the 5 years of study (Table 3.3), and varied significantly among years (Kruskal-Wallis $\chi^2_4 = 38.61$, $p < 0.001$), with the shortest period occurring during the 1998 El Niño and the longest perinatal period during the 2000 La Niña. Between year comparisons revealed significant differences in the duration of the perinatal period between 2000 and 2001 (Dunnett, $p = 0.025$), and 2000 and 2002 (Dunnett, $p = 0.049$). During La Niña, the perinatal period was about 2 days longer than during El Niño.

Of the 42 females marked during the 1997-98 El Niño breeding season, 22% ($n = 10$) did not return to the beach after the first feeding trip, and another 22% abandoned their pups after the second feeding trip. Removing females that lost their pups from the samples in all years (see Methods) resulted in numbers of recorded foraging trips being lower during El Niño compared to other years (Fig. 3.2) since most pups died before the end of the breeding season (Chapter 2). During El Niño, no trend was observed in the mean time that females spent at sea, until the 5th trip, when mean time at sea began decreasing with each subsequent trip (Fig. 3.2). In 1999, the first season after El Niño, no trend was detected for the mean time spent at sea. However, mean times at sea increased over the breeding season in 2000 and 2002, and decreased in 2001 (Fig. 3.2). No trends were found during El Niño in the time spent onshore. However, for all other years (1999 to 2002) the mean time onshore decreased, as the pups grew older (Fig. 3.2).

The proportion of time that females spent at sea per attendance cycle differed among years (Kruskal-Wallis, $\chi^2_4 = 132.05$, $p < 0.001$), and was the greatest during the 1998 El Niño (71%) and the lowest during La Niña (53%). Differences were also noted among years for the proportion of time females spent at sea during the first trip after parturition (Kruskal-Wallis, $\chi^2_4 = 102.25$, $p < 0.001$).

Table 3.2 Mean duration \pm SE (in days) of foraging trips and visits onshore, and mean number of females onshore during the 1998 to 2002 breeding seasons. Sample sizes in parentheses indicate the number of counts and the number of females per trip and per visit each breeding season included in the analysis.

Breeding Season	Mean trip at sea	Mean visit onshore	Mean number females
1998 El Niño	2.37 \pm 0.23 (22)	0.68 \pm 0.04 (22)	72.11 \pm 6.15 (54)
range	0.45 - 4.41	0.43 - 1.21	13 - 154
1999 La Niña	1.40 \pm 0.04 (92)	0.88 \pm 0.03 (88)	548.04 \pm 18.64 (63)
range	0.49 - 2.88	0.28 - 1.62	287 - 1113
2000 La Niña	1.12 \pm 0.03 (122)	0.96 \pm 0.02 (119)	470.15 \pm 7.22 (60)
range	0.45 - 2.08	0.54 - 1.66	311 - 596
2001 La Niña	1.66 \pm 0.07 (117)	0.89 \pm 0.08 (112)	457.90 \pm 7.43 (43)
range	0.36 - 3.36	0.34 - 1.62	321 - 536
2002	1.92 \pm 0.06 (107)	0.87 \pm 0.02 (103)	390.19 \pm 12.01 (47)
range	0.57 - 3.60	0.36 - 1.64	205 - 519
1998-2002 Mean	1.56 \pm 0.07	0.90 \pm 0.04	470.06 \pm 14.56

There was considerable variability in the duration of foraging trips between females within a year. Variability in time spent at sea was highest during the 1998 El Niño ($CV = 45.15\%$) and lowest during the 2000 La Niña (25.89%). Such variability was statistically consistent among years ($CV = 32.3\%$ for all years combined). However, the lack of statistical significance may be related to a small sample size during the 1998 El Niño and the lower number of female foraging trips recorded that year due to pup mortality (see Fig. 3.2). Variability observed in the duration of visits onshore was similar among years (26.94%).

Table 3.3 Mean duration \pm SE (in days) of the perinatal period, first foraging trip and first visit onshore during the 1998-2002 breeding seasons at the Ballestas Islands. Sample sizes are in parentheses and indicate the number of females included in the analysis each breeding season.

Breeding season	Perinatal period	First trip	First visit
1998 El Niño	5.72 \pm 0.36 (26)	2.98 \pm 0.29 (32)	1.01 \pm 0.11 (32)
range	1.26 - 7.24	0.83 - 8.29	0.27 - 2.43
1999 La Niña	7.54 \pm 0.10 (114)	1.56 \pm 0.07 (113)	1.25 \pm 0.05 (101)
range	3.65 - 12.00	0.30 - 4.00	0.32 - 3.37
2000 La Niña	7.69 \pm 0.10 (104)	1.32 \pm 0.05 (143)	1.23 \pm 0.04 (128)
range	4.43 - 10.34	0.33 - 3.72	0.30 - 2.66
2001 La Niña	7.23 \pm 0.11 (80)	1.69 \pm 0.06 (117)	1.11 \pm 0.04 (113)
range	5.00 - 10.00	0.28 - 3.74	0.30 - 3.00
2002	7.21 \pm 0.14 (65)	2.21 \pm 0.98 (104)	1.03 \pm 0.04 (96)
range	4.75 - 10.71	0.49 - 5.74	0.28 - 2.45
1998-2002 Mean	7.46 \pm 0.39	1.66 \pm 0.08	1.16 \pm 0.06

The proportion of time that females spent at sea was significantly correlated with the duration of attendance cycles each year (1998 El Niño: Pearson $r = 0.742$, $p < 0.001$, $n = 22$; 1999: $r = 0.372$, $p < 0.001$, $n = 91$; 2001: $r = 0.548$, $p < 0.001$, $n = 111$; 2002: $r = 0.492$, $p < 0.001$, $n = 103$) except in 2000 when the foraging trips were the shortest ($r = 0.097$, $p = 0.292$, $n = 119$). Females tended to spend a greater proportion of their time at sea in years when they made longer foraging cycles. No relationship was detected between the time spent at sea and the preceding or subsequent time spent onshore each year.

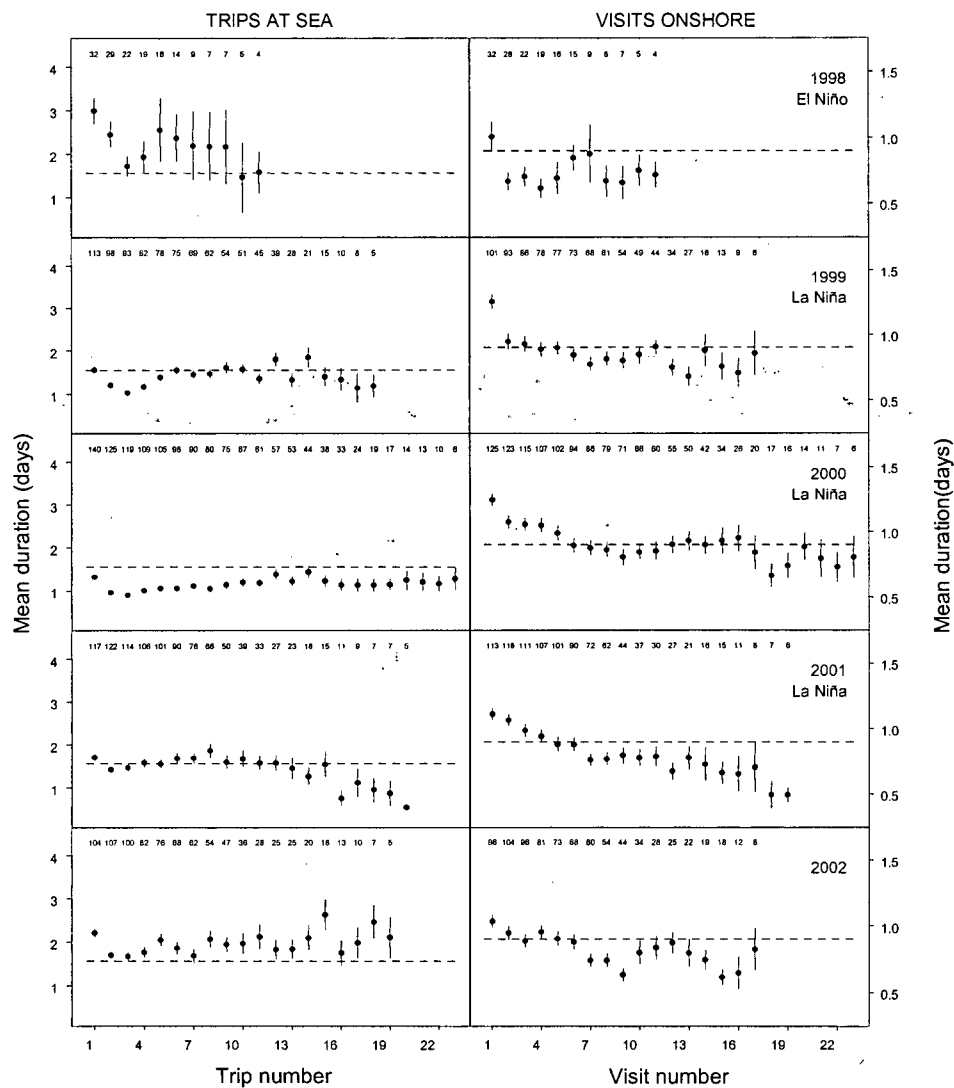


Fig. 3.2 Mean duration \pm SE (days) of female trips at sea and visits onshore over the breeding seasons from 1998 to 2002. Sample sizes (number of individual females) are shown at the top of each panel. Dashed lines represent the grand mean of trips and visits respectively excluding the El Niño year. Trip numbers show the trips that females made after parturition from their first to their 23rd trip, while visits indicate the time spent onshore.

Arrivals

Time of arrival onshore varied significantly among years ($\chi^2_{12} = 112.9, p < 0.001$), but did not differ significantly among the La Niña years (1999-2001). The time of arrival during La Niña was not random during the hours of observation (06:00 to 18:00 hrs) (pooled data: $\chi^2_3 = 310.7, p < 0.001$; Fig. 3.3). In general, most females arrived after midday in all years except during the 1998 El Niño, when they arrived more frequently before midday. Arrivals during La Niña occurred mostly at night and dawn rather than during the day (2000: $\chi^2_1 = 29.43, p < 0.001$, 57.14%; 2001: $\chi^2_1 = 4.15, p = 0.042$, 53.14%) except in 1999 and 2002 when no differences were found. In contrast, most females arrived during the daytime during the 1998 El Niño rather than at night and dawn ($\chi^2_1 = 13.26, p < 0.001$).

Departures

Timing of departures from land varied significantly among years ($\chi^2_{12} = 148.2, p < 0.001$). Significant differences were also found during La Niña years ($\chi^2_6 = 19.55, p = 0.003$). In general, most females departed in the morning in all years except during El Niño when most females departed at the end of the day (Fig 3.3).

Most departures occurred at night and dawn than during the day light from 1998 to 2002 (mean \pm SE: 72.2 ± 3.7 % and 27.7 ± 3.7 % respectively). Departures outnumbered arrivals at night and dawn in all years (72 ± 3.7 % and 48 ± 3.5 % respectively).

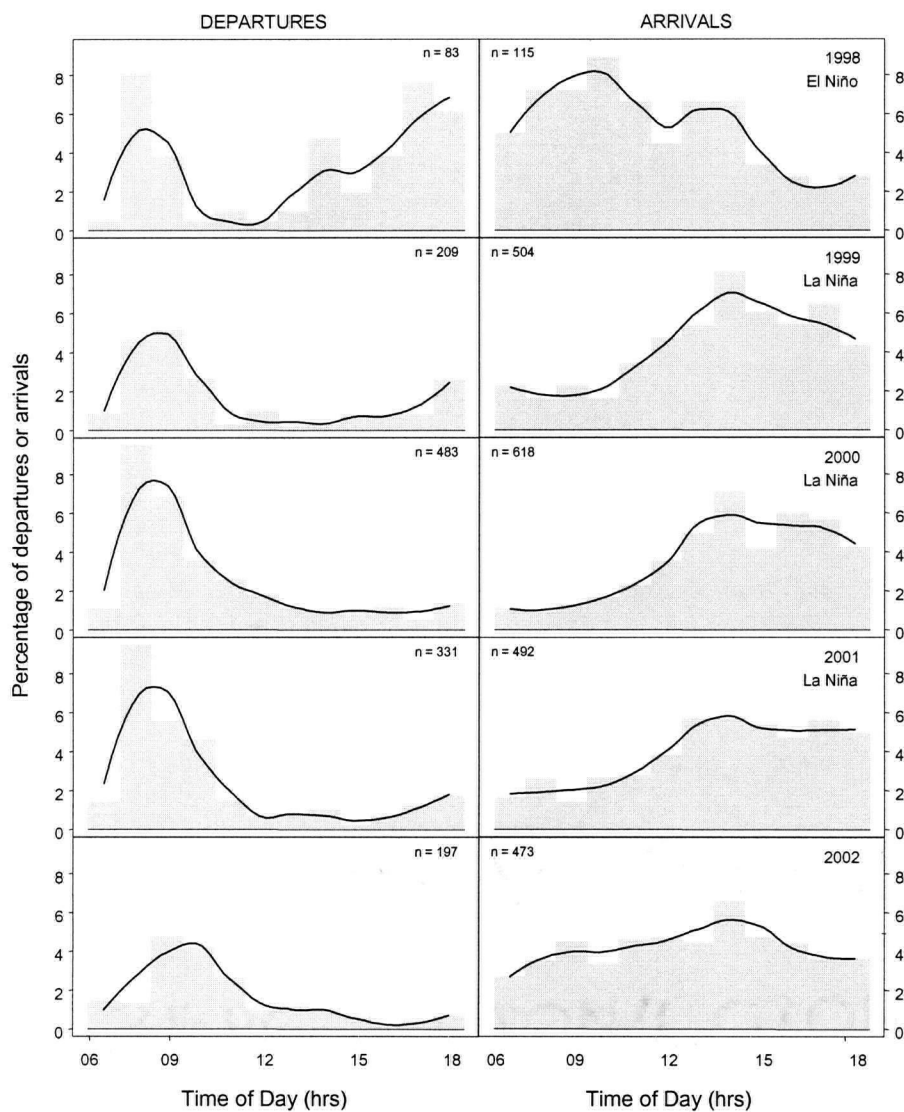


Fig. 3.3 Timing of arrivals and departures of lactating females observed during day light hours from 1998 to 2002 at the Ballestas Islands. Percentages were calculated as number of arrival (or departures) each hour as a percent of total (day and night) arrivals (or departures). Data were smoothed with Loess curves (solid lines). Total numbers of documented arrivals and departures are indicated in each panel.

Numbers of females onshore

Mean numbers of females that were onshore during the breeding season (based on counts at 06:00 hrs) varied significantly among years (Kruskal-Wallis $\chi^2_4 = 159.71, p < 0.001$). Numbers fell from a mean of 885 females before the 1997-98 El Niño (Chapter 2) to 72 during the El Niño, and decreased again from 548 females after El Niño in 1999, to 390 in 2002 (Table 3.2). One major difference during El Niño (as opposed to other years such as the 2000 La Niña shown in Fig. 3.4) was the low numbers of females that were onshore during the breeding season due to drastic abandonment of the breeding beaches. Numbers of females onshore during non-El Niño years did not vary significantly before or after the breeding season (K. Soto pers. obs.).

Mean numbers of females onshore during the day (based on counts at 06:00, 12:00 and 18:00 hrs) varied significantly each year (Kruskal-Wallis: 1999: $\chi^2_2 = 56.40, p < 0.001$; 2000: $\chi^2_2 = 114.16, p < 0.001$; 2001: $\chi^2_2 = 48.31, p < 0.001$; 2002: $\chi^2_2 = 26.59, p < 0.001$). In general, numbers tended to be high early in the morning, dropping to a minimum around midday, and increasing to a maximum towards the end of the day when most of the arrivals were recorded (Fig. 3.3). Each morning, most of the females and their pups moved towards the water's edge to occupy the shoreline, presumably to avoid overheating as soon as the sunlight fell on the beach (at approximately 07:30 hrs.). Other females abandoned the beach at this time, as noted by the high number of recorded departures. Females did not make such movements during cloudy days. Instead, the animals tended to increase the spacing between them. Although no significant differences were found in the number of females onshore throughout the day, during El Niño, the highest numbers of females were counted at midday with lower numbers registered at the end of the day, and minimum numbers in the morning. Differences between the mean numbers of females at the end of the day (18:00 hrs) and following morning (06:00 hrs) indicated that most females departed at night, which is consistent with my observations that the highest numbers of marked females departed over night.

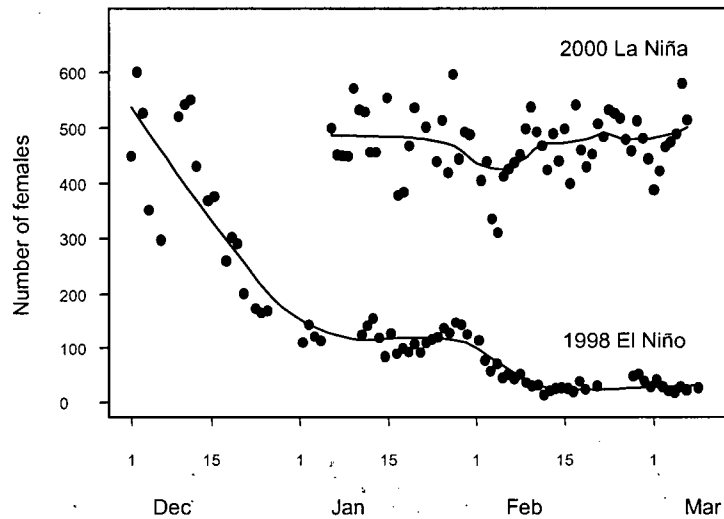


Fig. 3.4 Daily number of females onshore (based on counts at 06:00 hrs) during the 1997-98 El Niño contrasted with the 2000 La Niña (which was similar to other non El Niño years). Data during Dec 1999 were not collected, but would have been in the range of values collected from Jan - Mar 2000 based on observations in other years. Data were smoothed with Loess curves.

Prey abundance, oceanographic conditions and maternal attendance patterns

Females appeared to adjust their attendance cycles in response to changes in prey abundance (Fig. 3.1), as shown by the inverse relationship between the time spent at sea and the abundance of prey (measured as the amount of anchovy caught per unit of commercial fishing effort, CPUE, as is shown in Table 3.4). Conversely, females spent more time onshore as abundance of prey increased (measured using CPUE indexes shown in Table 3.4).

Durations of foraging trips were positively correlated with the sea surface temperature anomalies (Pearson: $r = 0.896$, $p = 0.039$, $n = 5$; Fig. 5). In contrast, durations of visits onshore were inversely correlated with the temperature anomalies ($r = -0.877$, $p = 0.051$, $n = 5$; Fig 3.5). Therefore, foraging trips were longer and visits onshore were shorter when anomalies were positive (such as during El Niño) and foraging trips were shorter and visits onshore were longer when anomalies were negative (as during La Niña).

Table 3.4 Relationship between an index of prey abundance (anchovy catches from commercial fisheries, CPUE) and the duration of the maternal attendance cycle (time at sea and time onshore). (* estimated from total hours of trip).

Anchovy CPUE	Time at sea			Time onshore		
	<i>r</i>	<i>p</i>	<i>n</i>	<i>r</i>	<i>p</i>	<i>n</i>
Catch per total hours of trip	-0.946	0.015	5	0.820	0.080	5
Catch per hold with fish	-0.832	0.081	5	0.874	0.052	5
Catch per registered brute tonnage capacity	-0.990	0.001	5	0.897	0.039	5
Catch per registered brute tonnage capacity*	-0.955	0.011	5	0.815	0.093	5

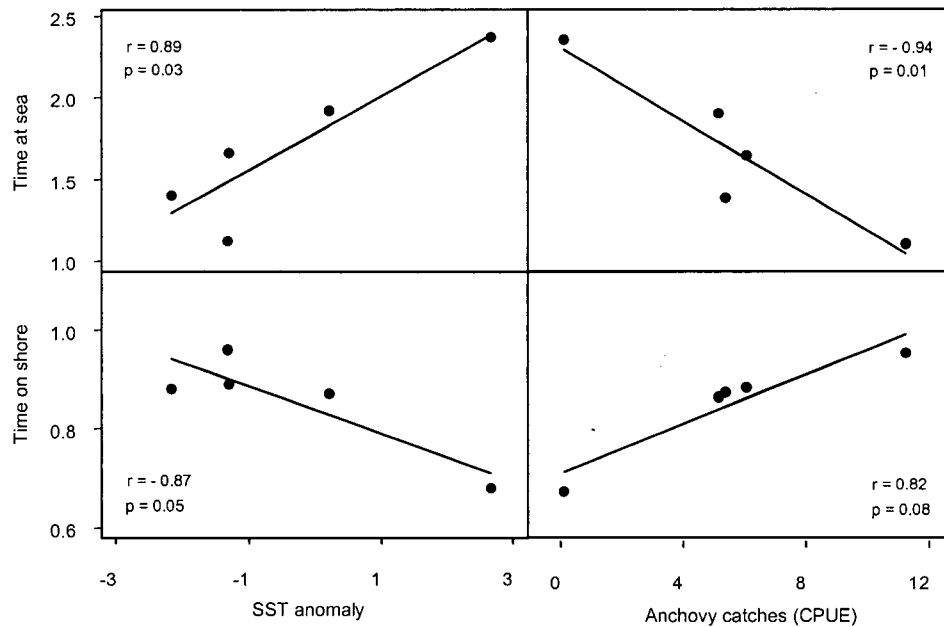


Fig. 3.5 Relationship between the time that females spent at sea and onshore during the breeding seasons (1998-2002) and sea surface temperature anomaly (left panels) and an index of prey abundance (anchovy catches, CPUE: Catch per total hours of trip; right panels).

Discussion

There appears to be a strong relationship between diet and the maternal attendance pattern, and the prey that was available to South American sea lions in the Peruvian marine ecosystem. The types and proportions of prey consumed as well as the maternal attendance cycles changed according to year to year shifts in the abundance and distribution of fish and crustaceans. However, maternal flexibility was insufficient during the 1997-1998 El Niño conditions to compensate for acute prey shortages, resulting in females spending prolonged times at sea that exceeded the fasting abilities of their pups and caused high mortalities due to starvation.

Diet

South American sea lions fed mainly on fish, crustaceans and cephalopods, but the frequency of occurrence of each differed between and within seasons. Anchovy and the pelagic squat lobster were the main prey consumed by sea lions during La Niña. However, their spatial distribution and concentration with respect to the breeding rookery varied in those years (despite being close to the surface, Fig. 3.6). Interestingly, occurrence of anchovy and squat lobster in the diets increased as prey became more abundant close to the rookery (IMARPE 1999, 2000, 2001, 2002; Fig. 3.6).

Sea lions fed on a variety of prey when their principal prey were scarce as occurred during the 1997-98 El Niño and in 2002. High occurrences of demersal species in the diet during these years suggest that sea lions foraged at deeper depths than normal. The only time the pelagic squat lobster was not found in the diet was during the 1997-98 El Niño and in February 2002 (during the early stages of the moderate El Niño 2002). This was probably due to the preference of squat lobsters for colder waters (Paredes & Elliot 1997), and is consistent with the observation that squat lobsters were scarce near the breeding rookery based on hydroacoustic surveys conducted during warm episodes (see IMARPE 2002).

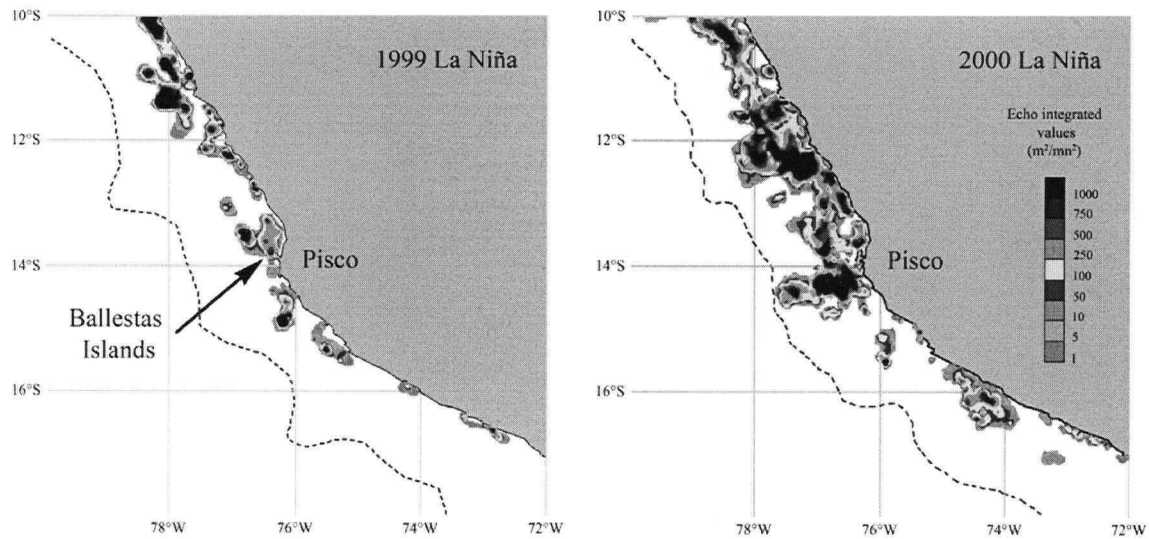


Fig. 3.6 Distribution and abundance of anchovy around the Ballestas Islands. Data from hydroacoustic surveys during the 1999 La Niña (left panel) and 2000 La Niña (right panel). Dashed lines indicate the limits of the surveys. Adapted from IMARPE (1999, 2000).

Sea lions appear to have foraged on their preferred prey according to its relative abundance in the marine environment. They showed strong prey preferences that were reflected in the dominant occurrences of these resources in their diets. Scarcity of resources in the marine ecosystem was also reflected by low occurrences in their diet as well. The apparent relationship between diet and the distribution and abundance of their principal prey (obtained from hydroacoustic surveys and commercial catches) suggests that the South American sea lion diet is a good indicator of the distribution and abundance of marine resources in the Peruvian marine ecosystem.

Maternal attendance patterns and prey abundance

Perinatal Period. Duration of the perinatal period has been proposed to be directly linked to the availability of prey and the energy reserves acquired before parturition (Bowen 1991). In my study, the mean duration of the perinatal period during years when prey was not restricted did not differ from the results of other studies along the Atlantic coast of South America (Campagna & Le Boeuf 1988, Cappozzo et al. 1991, Werner & Campagna 1995), nor did it differ from the findings for other species of sea lions (Heath et al. 1991, Higgins et al. 1988, Higgins & Gass 1993, Milette & Trites 2003, Ono et al. 1987, Trillmich 1986).

The short perinatal period observed during the El Niño implies that initial female body condition was significantly reduced compared to other years, and probably led to a faster depletion of scarce maternal fat reserves to critical values. A reduced perinatal period might have significantly decreased the chances of pups surviving if they did not initially gain enough energy reserves to survive the initial fast while their mothers were foraging at sea. Similar reductions in perinatal attendance have been reported for other otariids due to changes in the abundance of prey (see Lunn *et al.* 1993, Ono *et al.* 1987).

Gentry et al. (1986) proposed that depletion of fat stores regulates the time spent onshore after a foraging trip. Similarly, the length of the perinatal period is probably determined by the rate that female fat reserves are depleted to produce milk and adequately nourish their pups. The length of the perinatal period must also be limited by the maximum energy a female can store before parturition, which might be related to the size of the female and the abundance of key prey species. This limit is probably easily attained under favourable oceanographic conditions (such as during La Niña). Consequently, the length of the perinatal period might not increase significantly during years when prey is abundant due to inherent physical and physiological constraints placed on the female.

Time at sea. Females appear to have modified the duration of their foraging trips to compensate for changes in prey quality and abundance (Fig. 3.1). The deepening of the thermocline during the 1998 El Niño (by more than 100 m; Pizarro 1997, Sánchez et al. 2000) would have meant that females had to dive to greater depths than normal. Also, they may have had to travel longer distances from the rookery to follow the migrating anchovy to cooler areas of southern Peru (Ñiquen & Bouchon 2002).

Females in my study responded to the acute prey shortage during the 1997-98 El Niño by increasing the length of their foraging trips. In contrast, females spent shorter times at sea during the favourable conditions of La Niña. Increased times at sea due to reductions of prey have also been reported for several otariid species (Boyd 1999, Costa *et al.* 1991, DeLong & Antonelis 1991, Heath *et al.* 1991, Limberger *et al.* 1983, Majluf 1991, McCafferty *et al.* 1998, Ono *et al.* 1987, Trillmich & Dellinger 1991, Trillmich *et al.* 1986).

Although favourable oceanographic conditions (in terms of sea lion prey) were observed along the Peruvian coast during La Niña years, the spatial distribution and abundance of pelagic resources differed between years (see IMARPE 1999, 2000, 2001, 2002). These apparent differences in the accessibility of prey close to the rookery might explain the differences in foraging trip duration during La Niña, since shorter foraging trips corresponded to higher abundances of prey close to the breeding area (IMARPE 2000; Fig. 3.6), and longer foraging trips corresponded to a mid- to high-abundance of prey located further away from the breeding beaches (IMARPE 1999; 2001; Fig. 3.6).

During the 1997-98 El Niño breeding season, no assessments of pelagic resources by hydroacoustic surveys were conducted by IMARPE. However, data from landings of commercial fisheries indicated that anchovy catches were minimal at that time because of the deepening of the thermocline (Ñiquen & Bouchon 2002). Interestingly, the longest foraging trips were also observed at that time.

The poor body condition I observed during El Niño indicated that females were unable to gain enough resources to meet their own energy requirements. As a consequence, females were apparently unable to sustain normal rates of energy delivery to their pups or compensate

adequately by increasing foraging effort because the prey shortage was extreme. Females appear to have had no alternative but to abandon their pups or maintain lactation with milk of low quality and quantity after spending long periods at sea. Insufficiently replenished body reserves may have forced females to continue foraging for longer periods.

Long trips did not appear to result in an increase in energy gained or milk transferred to pups. Emaciated females and severely undernourished pups confirmed the failure of foraging and the severity of this event. Although most females abandoned their pups, it did not ensure their own survival. High numbers of visibly emaciated females died during the peak of El Niño in February 1998 at several rookeries along the Peruvian coast (K. Soto per.obs.). Similarly, many pups were unable to successfully fast between the infrequent visits onshore, and subsequently starved to death (Chapter 2). One emaciated pup attempted to continuously take milk from other females, but died after waiting 9 days for his mother. She returned 2 days later and was also visibly emaciated.

While prey shortages would have resulted in females increasing their foraging effort for a reduced rate of foraging success, the energy content of anchovy was also lower during El Niño (Alamo & Espinoza 1998). This would have resulted in reduced energy intake per unit of prey caught by the sea lions. The concentration of low quality and reduced prey abundance at deeper depths than normal would have also caused the sea lions to expend more energy per unit of prey consumed. Moreover, poor body condition may have reduced female diving abilities and further decreased foraging success.

A longer first foraging trip after parturition seems to reflect the time needed for females to replenish the fat reserves they depleted during the perinatal period. However, when faced with prey restrictions, longer trips might also have reflected lower foraging success. Although other otariids are known to increase diving effort near their rookery when prey is limited (Feldkamp *et al.* 1991, Lea *et al.* 2002), it is unknown whether the longer foraging trips of South American sea lions noted during El Niño were due to increased foraging effort associated with swimming greater distances from the rookery and/or increasing the rate of diving closer to the rookery. Nevertheless, it is apparent that none of these foraging behaviours were sufficient to compensate for acute prey reduction. Long distances were

apparently traveled since a number of known females who abandoned their pups were sighted as far as 250 km south of the breeding rookery (K. Soto per.obs.).

Boyd *et al.* (1991) considered two factors that might set the duration of female foraging trips. One was that females need to attain a minimum amount of energy before returning onshore to nurse their pups. The second was that the time spent away must not exceed the ability of the pups to fast, regardless of the energy gained. If the former factor occurs, females may return before or after a determined time limit depending on the availability of prey (Lunn *et al.* 1993). However, if a minimum of energy is gained before the time limit, females may continue foraging until they reach the set time limit or their maximum storage capacity (Lunn *et al.* 1993).

The length of foraging trips for female South American sea lions seems to be mainly determined by their storage capacity than by a set time limit. During the 2000 La Niña, when prey abundance was the highest, females presumably reached their storage capacities faster than in other years based on the shortness of their trips. If trip durations were time limited, trips would have been expected to be of similar durations during good years such as the La Niña years. Instead, average trip durations correlated with the abundance and distribution of prey, such that time at sea was reduced as prey became more abundant (Figs. 3.5 and 3.6).

The flexibility in the duration of maternal foraging trips observed in the South American sea lions seems to depend on a combination of environmental, physical and physiological constraints. Females presumably require a minimum time at sea to replenish their resources and/or satisfy a minimum gain of energy. Such a restriction is probably determined by physiological and physical constraints (Boyd *et al.* 1991, Thompson *et al.* 1998) as well as by prey abundance. Similarly, there must also be a maximum time spent at sea before pups starve, which must be a function of the fasting abilities of pups, the female storage capacity and the abundance of prey. However, extreme restrictions in the availability of prey (such as during the 1997-98 El Niño), presumably results in females extending the time they spend at sea to ensure their own survival, which must ultimately depend on their physiological foraging capabilities and their foraging success.

The duration of foraging trips recorded during years when prey was not restricted were similar to values obtained for the South American sea lions at the Falkland Islands (Thompson *et al.* 1998). However, South American sea lions from Argentina (Campagna & Le Boeuf 1988, Campagna *et al.* 2001, Cappozzo *et al.* 1991, Werner & Campagna 1995) spent as much as twice the time foraging as did the sea lions I observed. Since distance to the foraging grounds is an important component of trip duration (Boyd 1999, Merrick & Loughlin 1997), and time at sea increases with travel distance (Bonadonna *et al.* 2000, Boyd 1999), these long trip durations may indicate that longer distances are traveled or longer times are spent foraging in Argentina to satisfy prey energy requirements.

Time onshore. The time that females spent onshore after foraging also varied according to the abundance of prey (Figs. 3.1 & 3.5). Shorter visits onshore occurred when prey abundance was lower as observed during the 1997-98 El Niño – and longer visits occurred when prey was not restricted (as during La Niña). In several otariid species, the time that females spent onshore has been less sensitive to prey reductions than the time spent at sea. Although shorter times onshore have been observed in several species during shortages of prey, they did not differ significantly from values obtained in normal years (see Ono *et al.* 1987, Heath *et al.* 1991, Majluf 1991).

Low caloric prey might have prevented the females from producing milk of high quantity and quality. Consequently, milk reserves might have been depleted faster during El Niño, thereby forcing females to depart sooner than in other years. Pup body condition deteriorated continuously during the long fasting periods and reflected the reduced foraging success of their mothers.

Arrivals and departures. Although arrivals and departures occurred throughout the day, most females arrived during daylight and departed at night and dawn (Fig. 3.3). These patterns suggest that female South American sea lions foraged mostly at night and dawn, when anchovy were closer to the surface and more accessible to the sea lions (Arntz *et al.* 1991). Such nocturnal foraging patterns have been reported for the sympatric South American fur seal (Trillmich *et al.* 1986), which also prey mainly on anchovy (Arias-Schreiber 2003).

Higher proportions of departures in the morning and arrivals after midday (Fig. 3.3) have also been observed for other otariid species (see Trillmich *et al.* 1986), and probably relate to female behavioural adaptations to avoid thermal stress, since both patterns avoid overheating during the hot midday hours. Diurnal foragers avoid the costs of overheating, although diurnal foraging might demand higher energy investment than nocturnal foraging since anchovy are located at deeper depths during the day (Arntz *et al.* 1991). In all likelihood, diurnal foragers probably compensate for higher costs of foraging if prey are abundant and easily accessible.

During El Niño, females arrived onshore before midday when higher air temperatures would have increased the risks of overheating on land. Similar pattern of arrivals and departures have been observed in the South American fur seal during El Niño 1982-83 (Trillmich *et al.* 1986). Apparently, reduced prey would have meant that the costs of foraging during the day might not have compensated for the cost of thermoregulation on land.

Species that inhabit the tropics and subtropics experience high air temperatures during the breeding seasons and incur high costs since the reduction of thermal stress is associated with behaviours that compromise reproductive success (e.g., aggressiveness, Limberger *et al.* 1986, Majluf 1987, Trillmich *et al.* 1986, Chapter 2). In such circumstances, sea lions probably avoid the costs of thermoregulation through behavioural adaptations by arriving soon after midday and departing before midday in all years, except during El Niño when maternal behaviour was altered because of reduced prey (Fig. 3.3).

Numbers of females onshore. Numbers of females onshore decreased dramatically during the 1997-98 El Niño (Fig. 3.4). Females progressively abandoned the rookery throughout the El Niño starting in November 1997, and no animals were observed at the end of the breeding season in March 1998. High adult mortality and the loss of the entire young cohorts during the El Niño (Chapter 2) accounts for the low number of survivors that remained in April 1998. Although favourable oceanographic conditions were observed after El Niño, the recovery of the South American sea lion numbers might take many years to be noticed due to the time needed for the young females to reach the age of reproduction and successfully pup. However, since favourable oceanographic conditions and high survival of young cannot be guaranteed in subsequent years, a slow increase in the sea lion population might be expected due to the unpredictability of the Peruvian upwelling ecosystem and the loss of an important part of the reproductive population. If another El Niño of strong magnitude occurs, the recovery of the remaining population of sea lions could be seriously compromised since young cohorts would be the most affected.

Conclusions

My study demonstrates that South American sea lion maternal responses and diets reflected the interannual fluctuations of the Peruvian upwelling ecosystem and suggests that South American sea lions may be good indicators of relative changes in the distribution and abundance of marine resources. Although the dramatic changes in the marine ecosystem due to the occurrence of strong El Niño and moderate La Niña events are extreme compared to fluctuations in other marine ecosystems, the responses of apex predators such as the South American sea lions reveals important insights about the behavioural adaptations and the limitations of those adaptations that might have evolved to cope with uncertainty in prey distribution and abundance, and rapid changes in the ecosystem.

The fact that behavioural measurements from apex predators may be considered good proxies of the abundance and distribution of prey as well as oceanographic features is promising and opens new windows for the implementation of research using marine mammals as data collectors. Thus, the integration of biological and oceanographic information has the

potential to provide a better understanding of the dynamics of the marine ecosystem and its influence in shaping the life history of apex predators.

Summary

The diet and maternal attendance pattern of South American sea lions in Peru were investigated during the 1998-2002 breeding seasons when drastic changes in marine productivity occurred as a consequence of the strong 1997-1998 El Niño and a moderate 1999-2001 La Niña. The goal of my study was to determine whether changes in the diet and maternal attendance pattern reflected physical changes in the marine environment and alterations in the abundance and distribution of prey. Behavioural observations conducted at the Ballestas Islands found maternal attendance patterns were strongly linked to the abundance of prey and oceanographic features close to the rookeries. Females responded to the acute prey shortage during the El Niño by increasing the length of their foraging trips and decreasing the time they spent onshore with their pups. In contrast, females spent shorter times at sea and longer times onshore during the favourable conditions of La Niña. Acute prey shortages appeared to cause high pup mortalities because females had to spend more time at sea searching for prey and did not return frequently enough to nurse their pups.

The high abundance of anchovy and squat lobster near the breeding areas during La Niña (as indicated by independent fisheries assessments) suggest that sea lions did not have to travel very far to acquire their preferred prey. However, the lower occurrence of these preferred prey species during El Niño, resulted in sea lions increasing the number of species consumed, particularly demersal fishes. Females appear to have adjusted their maternal attendance patterns and diets according to how the abundance and distribution of their prey changed from year to year. Based on these observations, diet and maternal responses appear to reflect interannual fluctuations of the unpredictable Peruvian upwelling ecosystem, and suggest that the South American sea lions may be good indicators of relative changes in the distribution and abundance of marine resources.

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