

# Effects of El Niño and La Niña events on the sex ratio of southern elephant seals at King George Island

Daniel F. Vergani<sup>1,\*</sup>, Zulma B. Stanganelli<sup>1</sup>, David Bilenca<sup>2</sup>

<sup>1</sup>Centro Nacional Patagónico, CENPAT-CONICET, Boulevard Almirante Brown 3500, 9120 Puerto Madryn, Chubut, Argentina

<sup>2</sup>Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón II, 4 Piso, C1428EHA Buenos Aires, Argentina

**ABSTRACT:** The response of altered sex ratio in southern elephant seals due to environmental stress was analysed. Data were collected at King George Island from 1980 to 1994. Significant retreats in the ice cover during El Niño events strongly suggest environmental stress during this period along the Bellingshausen Sea, a zone where female elephant seals from King George Island feed during their pregnancy. Randomly chosen weaning elephant seal pups ( $n = 1178$ ) were sexed at Stranger Point (King George Island, 62° 14' S, 58° 30' W) over 5 km of beach from 1985 to 1994. Adult sex ratio was also determined annually from 1980 to 1994 as the ratio between maximum number of bulls and females on land. The theoretical pup sex ratio was assumed as 1:1 according to background information. Adult sex ratio was calculated as 1:6. To define the occurrence of El Niño Southern Oscillation (ENSO) during the study period, a sea surface temperature (SST) index called 'Niño 3.4' for the region 5° N to 5° S, 120° E to 170° W was considered. Monthly SST anomalies were obtained from the Climate Prediction Center (CPC, NOAA). To provide an annual index of anomaly strength (IAS), the monthly adjusted oscillation index climatology (AOIC) was averaged. Accumulated values during the whole study period showed that during El Niño years (1987, 1991, 1992) the proportion of pups was significantly biased in favour of females ( $p < 0.01$ ). During normal years (1986, 1990, 1993, 1994) and La Niña years (1985, 1988, 1989), accumulative values showed a greater proportion of male pups to females ( $p < 0.05$ ). Using the 1:1 hypothesis, we found during El Niño years a 9% reduction in the male segment, whereas in non-El Niño years a recovery of 7% was observed (3% during normal years and 4% during La Niña years. To see the influence of accumulative values of pup sex ratio in adult sex ratio, a theoretical adult proportion was calculated as 1:6. To test this hypothesis, information on adult sex ratio taken from King George Island between 1980 and 1994 ( $n = 14$  yr) was analysed. The average adult sex ratio for King George Island was 1:7. This value seems to confirm the hypothesis that this population has had a balanced production of male and female pups in the long term. Comparisons with Pacific and Indian declining seal populations were made.

**KEY WORDS:** El Niño · ENSO · La Niña · *Mirounga leonina* · Southern elephant seals · Sex ratio · King George Island

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

The effect of the El Niño Southern Oscillation (ENSO) on regional ecosystems, both in warm (El Niño) and cold (La Niña) phases, depends on how it influences physical processes that determine ecosystem productivity. In the Eastern tropical Pacific Ocean, for example, warm ENSO events cause an overall

reduction in upwelling (Trillmich & Limberger 1985, Enfield 1987). In the Antarctic, ENSO may be associated with a variation in the extension of the seasonal pack-ice zone (Stammerjohn & Smith 1996). The recruitment success of krill (*Euphausia superba*), a major component of the Antarctic ecosystem has been linked to oscillations in sea-ice extent. That is, krill abundance may decline after winters with reduced ice

coverage. This reduction may have important consequences throughout the Southern Ocean ecosystem (Loeb et al. 1997, Brierley et al. 2002).

Cephalopods are another key component affected by the variation in sea-ice extent. While it is clear that these animals play a key role in the Southern Ocean marine ecosystem (Ainley & DeMaster 1990), their distribution in the Antarctic is poorly known due to, among other reasons, their fast swimming speed that makes them difficult to sample with conventional research trawls (Wormuth & Roper 1983). Southern elephant seals (*Mirounga leonina*) provide an interesting alternative as these Antarctic top predators seem to feed largely on cephalopods to maintain their high energy demands (Piatkowski et al. 2002).

Variation in sex ratio has been shown to occur in mammals, both in natural and controlled environments, as a consequence of nutritional stress and changes in resource availability, among other reasons (Clutton-Brock & Iason 1986, Clutton-Brock 1991). In species for which maternal investment differs between offspring sexes, it has been argued that if maternal condition favours the breeding success of male pups over female ones, mothers in superior conditions should produce more males, while mothers in poorer conditions should produce more females (Trivers & Williard 1973). Despite the intuitive appeal of this argument, it seldom has been tested. If demonstrated for specific cases, then sex proportion could offer a useful index to study the impact of drastic changes in food resources in the ecosystem due to environmental anomalies like El Niño.

Southern elephant seals (*Mirounga leonina*) provide an opportunity to test the aforementioned hypothesis for several reasons: (1) they are the most polygynous among seals (Laws 1953, 1956); (2) males may be 1 order of magnitude larger than the females with which they mate (McCann 1980); (3) during lactation, mothers fast, thus energy transferred to their pup is obtained only from stored reserves (Matthews 1929); and (4) the fasting capacity of nursing females and the mass gained by their pups represent a sensitive mechanism that not only reflects their ability to choose feeding grounds, but also the physical influences and biological factors that regulate resource ability in these areas (Vergani et al. 2001). Changes in food availability during El Niño and La Niña events seem to influence elephant seal populations on King George Island through an overall reduction in the biomass ingested by mothers (Piatkowski et al. 2002), and consequently, the weaning mass of pups (Vergani et al. 2001).

It has been suggested that southern elephant seal females need to weigh more than 300 kg if they are to breed at all, and more than 380 kg if they are to give birth to a male pup (Arnbohm et al. 1994). The proportion of mothers that can bear male pups therefore

depends on food availability in the ecosystem. In times of poor food availability such as during El Niño years, more females might be below the weight required to bear male pups; thus, the sex ratio would be biased in favour of females as mothers with a male foetus would either lose their pregnancy or would have smaller male pups with a lower chance of survival.

At King George Island, female elephant seals haul out to breed in September (mean date: 16 September; range 8 to 26 September) and reach the peak of the breeding season between 21 and 31 October (Vergani & Stanganelli 1990). After moulting in March, embryos are released from diapause and implantation occurs (Gibbney 1953). Females continue feeding until August/September in the Bellinghousen Sea, west of Alexander Island (Bornemann et al. 2000). It is during this 6 mo period that pregnant females are sensitive to changes in ENSO-related food availability (Vergani et al. 2001).

We analyse the response of southern elephant seal sex ratio to environmental stress. Data were collected from 1980 to 1994 at King George Island. Environmental stress in this period was evidenced by significant retreats in the ice cover during El Niño events along the Bellinghousen Sea (Kwok & Comiso, 2002), the region where female elephant seals from King George Island feed during their pregnancy (Bornemann et al. 2000). Comparisons with declining seal populations of the Pacific and Indian oceans were made.

## MATERIALS AND METHODS

To define the occurrence of ENSO events, a sea surface temperature (SST) index called 'Niño 3.4' for the region 5° N to 5° S, 120° E to 170° W was used. Monthly SST anomalies were obtained from the Climate Prediction Center (CPC, NOAA). Anomalies are departures from the 1971 to 2000 adjusted oscillation index climatology (AOIC) (Smith & Reynolds 1998). To analyse SSTs on an annual basis, an index of anomaly strength (IAS) was calculated as the average of the monthly AOIC.

Southern elephant seal pups were selected from weaning groups at random ( $n = 1178$ ) and were sexed at Stranger Point (King George Island, 62° 14' S, 58° 30' W) over a given 5 km beach stretch from 1985 to 1994. Adult sex ratio was determined annually from 1980 to 1994 as the ratio between the maximum numbers of bulls and females on land. Data from 1980 to 1988 were previously published in Vergani & Stanganelli (1990), and data from 1989 to 1994 were collected using the same methodology. Theoretical adult sex ratio was calculated assuming that the Atlantic population of females reach sexual maturity at Age 4 (McCann 1985) and males become sexually active at Age 8 (McCann 1981), meaning that there is a delay of

approximately 4 yr between sexes to be recruited into the reproductive population. Thus, the expected adult sex ratio, in equilibrium conditions, calculated by means of an additive calculation matrix was found to be 1:6, assuming equal mortality ratio between sexes (Table 1). This figure was verified using sex ratio time series data from King George Island.

Pup mortality was calculated annually as the percent of total number of dead pups over the total number of pups born. This was determined in the peak of females' haul out as the number of females plus all weaned and dead pups (Vergani & Stanganelli 1990). Frequently, sexing dead pups was not possible because of scavenger bird activity. As a result, pup mortality was not discriminated by sex.

Two previous studies have examined the sex ratio in southern elephant seal pup populations. The first one focused on populations at Peninsula Valdés during 3 breeding seasons (1984, 1988 and 1989) concluding that sex ratio of weanlings did not differ from unity (Campaña et al. 1992). The second study, carried out at South Georgia Island during 4 breeding seasons (1986, 1988, 1989 and 1990), showed that the male pup proportion increases rapidly with maternal mass and stabilises at a level not significantly different from parity (Arnbom et al. 1994). Taking into account these results, we assumed that the probability of being male is 0.5, and that this probability is independent among the members of the

Table 1. Additive calculation matrix to estimate the theoretical adult sex proportion of 1:6 considering an ideal population of 2 mothers producing 1 pup each year: Mother 1 gives birth to female offspring who will also have females and Mother 2 gives birth to male offspring. Sexual maturity has been considered to be at 4 yr in females (McCann 1985) and at 8 yr for males (McCann 1981)

Year:	0	1	2	Recruitment					8	Total
<b>Mother 1 offspring</b>										
F					1				1	2
	F					1				1
		F					1			1
			F					1		1
				F					1	1
					F					0
						F				0
Total adult females recruited										6
<b>Mother 2 offspring</b>										
M										1
	M									0
		M								0
			M							0
				M						0
					M					0
						M				0
Total adult males recruited										1

sample. The appropriate probability distribution is therefore the binomial for sample size  $k$ . The expected frequencies are the expansion of the binomial:

$$(p + q)^k$$

where  $p$  and  $q$  are the probabilities of being male and female, respectively. With the aid of Pascal's triangle, this expansion, representing the expected male proportion, can be expressed as:

$$\binom{k}{0}p^kq^0 + \binom{k}{1}p^{k-1}q^1 + \dots + \binom{k}{k-1}p^1q^{k-1} + \binom{k}{k}p^0q^k$$

The relative expected frequencies are the probability distribution in random samples known as the binomial distribution. The layout is shown in Table 2.

We can work out the expected frequency for any given class of  $Y$  (the number of male pups per sample) from the general formula for any term of the binomial distribution:

$$C(k, Y)p^Yq^{k-Y}$$

The expression  $C(k, Y)$  stands for the number of combinations that can be formed from  $k$  items taken  $Y$  at a time. This can be evaluated as:

$$k!/[Y!(k - Y)!]$$

where, for example,  $k!$  factorial means the product of all the integers from 1 up to and including  $k$ . The set-up is shown in Table 2 with the calculated relative expected frequencies ( $\hat{f}_{rel}$ ). (Sokal & Rohlf 1981).

Table 2. Variation in ENSO strength (IAS) and the expected binomial frequencies of male and female pups on the assumption that the sex ratio is 1:1. The first column lists the ENSO year classification as 1: El Niño, 0: normal and -1: La Niña; the second column shows the ENSO strengths; the third column includes the corresponding year; the fourth column lists the number of male pups per sample; the fifth column is the percentage of male pups referring to the total number of pups born each year; the sixth column shows the relative expected frequencies ( $\hat{f}_{rel}$ ) of the different outcomes; and the seventh column contains the levels of statistical significance of male pups proportion with respect to the 1:1 hypothesis.

\*p < 0.05: significant, \*\*p < 0.01: highly significant

ENSO	IAS	Year	Male pups		$\hat{f}_{rel}$	p
			Number	%		
1	1.43	87	15	30.0	0.002	**
1	0.75	92	29	40.8	0.029	*
1	0.74	91	63	44.1	0.024	*
0	0.50	94	107	52.2	0.046	*
0	0.47	93	60	53.6	0.057	
0	0.25	90	39	56.5	0.054	
0	0.21	86	49	49.5	0.080	
-1	-0.61	85	53	55.8	0.043	*
-1	-0.71	89	68	49.3	0.067	
-1	-1.00	88	110	56.1	0.013	*

## RESULTS

According to the calculated IAS values, ENSO strength varied between +1.43 and  $-0.61^{\circ}\text{C}$ . Years with SST anomaly values greater than  $+0.5^{\circ}\text{C}$  were identified as El Niño years. Years with anomaly values between  $+0.5$  and  $-0.5^{\circ}\text{C}$  were classified as normal, whereas La Niña years were classified as those with anomaly values less than  $-0.5^{\circ}\text{C}$ . The percentage of male pups in a given study year varied between 30 and 56%. For years with anomaly values above  $1.0^{\circ}\text{C}$  (1987), the sex proportion was negatively biased for male pups (30%;  $p < 0.01$ ). For years with values between 1.0 and  $0.7^{\circ}\text{C}$  (1991 and 1992), the proportion was negatively biased for male pups at 41 and 44%, respectively ( $p < 0.05$ ). For anomaly values between 0.5 and  $-1.0^{\circ}\text{C}$  (1986, 1989, 1990 and 1993), the sex proportion was not homogeneous (it varied in this data set from equal to significantly different;  $p < 0.05$ ), although certain years showed a positive bias for male pups (1985, 1988 and 1994) (Table 2). The relationship between these variables was fitted to a curvilinear regression expressed as a quadratic polynomial function ( $R^2 = 0.82$ ) (Fig. 1).

Data pooled over the entire study period show that during El Niño years (1987, 1991 and 1992), the pup sex ratio was significantly biased in favour of females (59% of the cohort was female;  $p < 0.01$ ). During normal years (1986, 1990, 1993 and 1994) and La Niña years (1985, 1988 and 1989), combined values show a proportion of male pups from 53 to 54%, significantly higher than the female proportion ( $p < 0.05$ ) (Table 3). Taking into account the 1:1 hypothesis, we found, during El Niño years, an overall reduction of 9% in the male segment, while in years other than El Niño, a recovery of the male segment of 7% was estimated. As

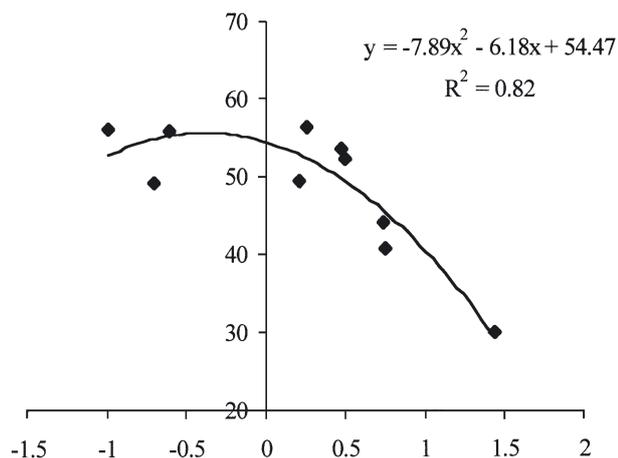


Fig. 1. *Mirounga leonina*. Relationship between ENSO strength and male pup percentage

Table 3. Combined values of Sex Ratio during ENSO occurrence in the study period. 0: normal, 1: El Niño, -1: La Niña. \*\* $p < 0.01$ : highly significant; \* $p < 0.05$ : significant

ENSO	Males		$\hat{f}_{rel}$	p
	Number	%		
1	107	41	0.000	**
0	255	53	0.019	*
-1	231	54	0.011	*

Table 4. Variation in ENSO strength (IAS) and pup mortality. 1: El Niño, 0: normal, -1: La Niña

ENSO	IAS	Year	Dead pups	Total born	%
1	1.43	1987	25	623	4.0
1	0.75	1992	19	625	3.0
1	0.74	1991	38	699	5.4
0	0.50	1994	28	423	6.6
0	0.47	1993	17	504	3.4
0	0.25	1990	8	554	1.4
0	0.21	1986	30	737	4.1
-1	-0.61	1985	26	603	4.3
-1	-0.71	1989	14	559	2.5
-1	-1.00	1988	10	583	1.7

Table 5. Combined values of mortality during ENSO occurrence in the study period. 1: El Niño, 0: normal, -1: La Niña

ENSO	Total born	Death	%
1	1947	82	4.2
0	2218	83	3.7
-1	1745	50	2.9

the overall difference between these results is only 2%, and considering that the El Niño cohort was smaller than that in normal and La Niña years, the sex ratio in pup population on King George Island seems to be balanced during the study period.

Pup mortality varied between 4.0 and 5.4% during El Niño years and between 1.7 and 4.3% during La Niña years (Table 4). Combined values during the whole study period show 4.2% (2.9%) mortality during El Niño (La Niña) years (Table 5).

To explore the influence of combined values of pup sex ratio on adult sex ratio, a theoretical adult proportion was calculated as 1:6 (Table 1). To test this hypothesis, information on adult sex ratio taken from King George Island between 1980 and 1994 ( $n = 14$ ; Table 6). The average adult sex ratio for King George Island between 1980 and 1994 was 1:7. This value seems to confirm the hypothesis that this population has had a balanced production of male and female pups in the long term.

Table 6. Adult sex proportion variation in southern elephant seals at King George Island

Year	Males	Females	Male:Female
1980	94	825	1:9
1982	84	464	1:6
1983	93	489	1:5
1984	93	585	1:6
1985	95	603	1:6
1986	108	737	1:7
1987	68	623	1:9
1988	96	583	1:6
1989	83	559	1:7
1990	63	554	1:9
1991	77	577	1:7
1992	94	625	1:7
1993	79	504	1:6
1994	72	423	1:6
Total	1199	8151	1:7

## DISCUSSION

Annual sea-ice dynamics affect both ocean structure and circulation. For example, sea-ice growth during autumn/winter causes salt to be released from the underlying ocean, leading to an increase in seawater density, and occasionally, to deep-ocean convection and bottom-water formation.

Many studies have suggested that Antarctic ice extent is influenced by the Southern Oscillation (Carleton 1988, Jacobs & Comiso 1993, 1997, Gloersen 1995, Simmonds & Jacka 1995, Ledley & Huang 1997, Watkins & Simmonds 2000). White & Peterson (1996) found coupled anomalies that propagate eastward with the Antarctic Circumpolar Current during a period of 4 to 5 yr while taking 8 to 10 yr to encircle Antarctica. It was suggested that this Antarctic Circumpolar Wave (ACW) is associated with ENSO-related activities in the equatorial Pacific, possibly through an atmospheric teleconnection with higher southern latitudes. Yuan & Martison (2000) explored possible relationships between records of Antarctic sea-ice extent (1978 to 1996) and global climate variability. Their analysis shows a strong link between anomalies in the location of the sea-ice edge (Amundsen, Bellinghausen and Weddell seas) and the extrapolar climate.

Anomalies in these polar processes may therefore have complex consequences in the Southern Ocean ecosystem. As of yet, there is no information regarding ENSO impacts on Atlantic southern elephant seal populations other than possibly that of King George Island. In foraging areas of elephant seals from Peninsula Valdés (Campagna et al. 1998), the abundance of a Cephalopod, *Illex argentinus*, has been correlated to

SST. A SST increase at the hatching grounds of the northern patagonian shelf, particularly during June/July, was negatively correlated with fishery catches the following season. Positive SST anomalies appear to be transferred from the Pacific to the Atlantic in El Niño years via the Antarctic Circumpolar Current and equator-ward via the Atlantic circulation (Waluda et al. 1999, 2001a,b).

In South Georgia, Vergani & Stanganelli (1990) pointed out that the effects on top predators of the 1982 to 1983 El Niño event affected both South Georgia and King George Island populations. This seems to be explained, at least for the southern elephant seal population, by the fact that part of South Georgia's females migrate to the West Antarctic Peninsula (WAP) region to feed (McConnell et al. 1992, McConnell & Fedak 1996), the same feeding area selected by King George Island females (Borne-mann et al. 2000). Piatkowski et al. (2002) reported that the amount of *Psychroteuthis glacialis* obtained through stomach lavage of southern elephant seals from King George Island during the study period was higher during La Niña years and lower during El Niño ones. According to the information provided by Rodhouse et al. (1992), the same phenomenon has been observed on South Georgia (Piatkowski et al. 2002).

Although time-series of adult elephant seal sex ratios on South Georgia are not available, information from Peninsula Valdés (Table 7) suggests an adult sex ratio of 1:6, similar to the value found in King George Island populations. Assuming that the South Georgia female southern elephant seal population is stable (Boyd et al. 1996), we can conclude that the entire Atlantic population sex ratio is stable at approximately 1:6.

According to Kwok & Comiso (2002), the Bellinghausen and Amundsen seas show an association with the Southern Oscillation unique to the Antarctic region. The ENSO influence seems to reach the West

Table 7. Adult sex proportion variation in the southern elephant seal Atlantic Ocean population according to Campagna &amp; Lewis (1992) (Ref. 1), Lewis et al. (1997) (Ref. 2)

Year	Ref.	Península Valdés		Male:Female
		Male	Female	
1982	1	1016	6400	1:6
1989	1	1000	7323	1:7
1990	1	1159	8688	1:7
1992	2	1309	9277	1:7
1995	2	1749	10 706	1:6
1996	2	1839	11 233	1:6
1997	2	1728	10 844	1:6
Total		9800	64 471	1:7

Table 8. Adult sex proportion variation in the southern elephant seal Indian Ocean population according to Pascal (1979) (Ref. 1), van Aarde (1980) (Ref. 2), Bester & Lengart (1982) (Ref. 3), Guinet et al. (1992) (Ref. 4) and Skinner & van Aarde (1983) (Ref. 5)

Year	Kerguelen Island				Marion Island				Possession Island			
	Ref.	Male	Female	Male:Female	Ref.	Male	Female	Male:Female	Ref.	Male	Female	Male:Female
1970	1	4435	55252	1:12								
1973					5	31	431	1:14				
1974					5	24	371	1:15				
1975					5	15	299	1:20				
1976					5	25	234	1:09				
1977	2	2497	42420	1:17	5	18	252	1:14				
1979	3	2993	42784	1:14	5	12	240	1:20				
1980					5	16	217	1:14				
1981					5	19	219	1:12				
1982					5	6	188	1:31				
1984	4	2573	37404	1:15					4	48	900	1:19
1985									4	43	885	1:21
1986	4	2719	39704	1:15					4	56	735	1:13
1987									4	43	653	1:15
1988									4	34	696	1:20
1989	4	2677	41102	1:15					4	31	612	1:20
Total		17894	258666	1:14		166	2451	1:15		255	4481	1:18

Antarctic Peninsula Region, where elephant seals from South Georgia and King George Island feed. This area of influence quite possibly reaches the Patagonian shelf via the Antarctic Circumpolar Current (Waluda et al. 1999, 2001a,b).

The question however remains: Are these effects adverse to the Atlantic population of southern elephant seals? Comparison with elephant seal populations that feed outside areas potentially affected by ENSO may provide an answer. Two such populations, found

respectively in the Indian and Pacific oceans have both been declining for at least 3 decades (SCAR 1991). The decline of such a major vertebrate predator has been regarded as a cause for concern that other components of the ecosystem are also changing in as yet unknown ways (Hindell et al. 1994).

Adult sex ratios for southern elephant seal populations from the Indian Ocean vary between 1:15 and 1:18 (Table 8), whereas the Pacific Ocean population shows a sex ratio of 1:11 (Table 9). These values differ significantly from the 1:6 ratio observed in the Atlantic Ocean population, suggesting an unbalanced production of male pups in the Pacific and Indian areas. Weaning mass shows similar results: when populations from the 3 oceans are compared, Indian and Pacific populations show a lower male pup weaning mass (Burton et al. 1997). Furthermore, the mean male weaning mass from Marion

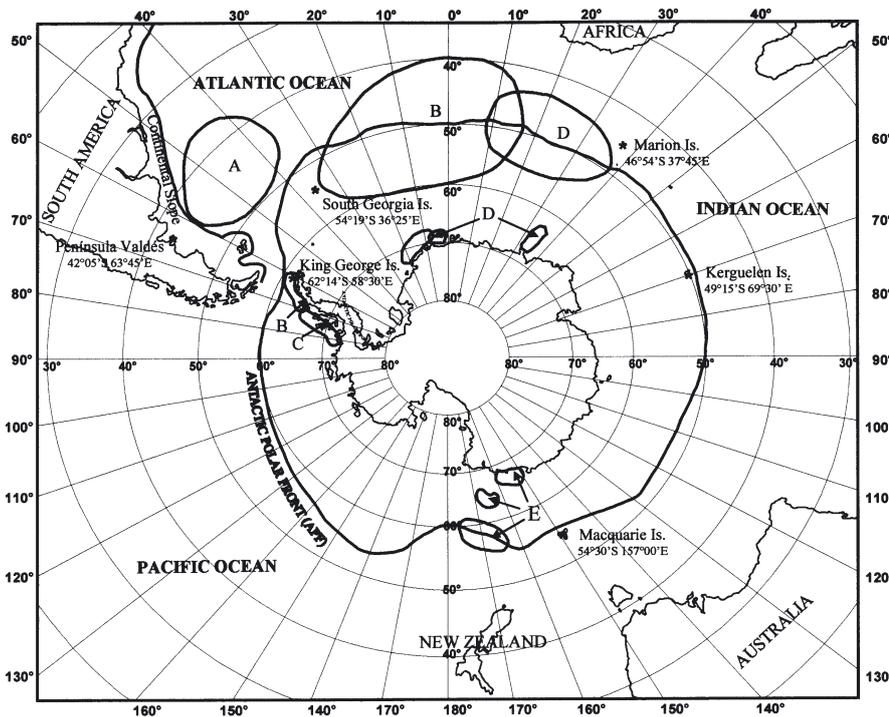


Fig. 2. *Mirounga leonina*. Female elephant seal post-moulting feeding areas. A: Peninsula Valdés (Campagna et al. 1998); B: South Georgia (McConnell & Fedak 1996); C: King George (Bornemann et al. 2000); D: Marion (Jonker & Bester 1998); E: Macquarie (Hindell et al. 1991a,b)

Table 9. Adult sex proportion variation in southern elephant seal Pacific Ocean population according to Hindell & Burton (1987)

Year	Males	Females	Male:Female
1950	465	4791	1:10
1951	414	5244	1:12
1952	464	5588	1:12
1954	512	6542	1:13
1956	506	6000	1:12
1957	469	5179	1:11
1958	502	6028	1:12
1959	705	4828	1:07
1960	412	5896	1:14
1985	248	2897	1:12
Total	4697	52993	1:11

Island (Indian Ocean population) was 119 kg ( $\pm 21$ ), whereas for Macquarie (Pacific Ocean Population), it was 123 ( $\pm 22$ ) (Burton et al. 1997). Both values are below 135 ( $\pm 21$ ), the minimum weaning male mass measured on King George Island in 1987, the strongest El Niño year registered during the study period (1985 to 1994) (Vergani et al. 2001). It is therefore not surprising that the Pacific and Indian populations exhibit such an imbalanced sex ratio.

The influence of climate anomalies in tropical areas on Antarctica remains controversial among climatologists and oceanographers, let alone ecologists. Population variables for southern elephant seal appear to be a useful tool to assess the impact of these environmental parameters. Examples of such variables include weaning mass (Vergani et al. 2001) and diet (Piatkowsky et al. 2002). In this study, pup sex ratio was used to assess variation between El Niño, La Niña and normal years, whereas the adult sex ratio was used to study long-term trends. Short-term changes in adult sex ratio appear to be buffered by the fact that it takes 8 yr for a male seal to become sexually active. Comparing the variation in the adult sex ratio in both space and time with the observed feeding areas for the 3 populations (Fig. 2), we can assess whether they would be governed by very different oceanographic parameters. El Niño-La Niña events may play an important role in maintaining stability in the Atlantic population, possibly by increasing nutrient cycling and mixing processes. Further analysis of climatic and oceanographic variables are needed to understand these links. Nevertheless, elephant seal population variables have been shown to be both useful and reliable in studying this phenomenon.

**Acknowledgements.** Information presented in this paper was taken from a long-term program on elephant seals conducted

by Daniel Vergani and Zulma Stanganelli. Logistic support was received from Dirección Nacional del Antártico, Ministerio de Defensa, Argentina, in the frame of the Cooperation Agreement between CONICET-DNA 'Projecto CNP-IAA Proyecto Cooperativo para el Estudio de Aves y Mamíferos Marinos'. We would like to thank Marc Dunn, Guillermo Podestá, Phil N. Trathan and anonymous referees for comments and revision which helped to improve this manuscript.

#### LITERATURE CITED

- Ainley DG, DeMaster DP (1990) The upper trophic levels in polar marine ecosystems. In: Smith WO Jr (ed) Polar oceanography. Chemistry, biology and geology, Part B. Academic Press, San Diego, p 599–630
- Arnbom T, Fedak MA, Rothery P (1994) Offspring sex ratio in relation to female size in the southern elephant seals, *Mirounga leonina*. Behav Ecol Sociobiol 35:373–378
- Bester MN, Lenglar PY (1982) An analysis of the southern elephant seal *Mirounga leonina* breeding population at Kerguelen. S Afr J Antarct Res 2:11–16
- Bornemann H, Kreyscher M, Ramdohr S, Martin T, Carlini A, Sellmann L, Plötz J (2000) Southern elephant movements and Antarctic sea ice. Antarct Sci 12:3–15
- Boyd IL, Walker TR, Poncet J (1996) Status of southern elephant seals at South Georgia. Antarct Sci 8:237–244
- Brierley AS, Fernandes PG, Brandon MA, Armstrong F and 8 others (2002) Antarctic Krill under sea ice: elevated abundance in a narrow band just south of ice edge. Science 295:1890–1892
- Burton HR, Arnbom T, Boyd IL, Bester M, Vergani DF, Wilkinson Y (1997) Significant differences in weaning mass of southern elephant seals from five sub-Antarctic islands in relation to population declines. In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic communities species, structure and survival. Cambridge University Press, Cambridge, p 335–338
- Campagna C, Lewis M (1992) Growth and distribution of southern elephant seal colony. Mar Mamm Sci 8(4): 387–396
- Campagna C, Le Boeuf BJ, Lewis M, Bisioli C (1992) Equal investment in male and female offspring in southern elephant seals. J Zool (Lond) 226:551–561
- Campagna C, Quintana F, Le Boeuf BJ, Blackwell S, Crocker DE (1998) Diving behaviour and foraging ecology of female southern elephant seals from Patagonia. Aquat Mamm 24(1):1–11
- Carleton AM (1988) Sea ice-atmosphere signal of the Southern Oscillation in the Weddell Sea, Antarctica. J Clim 1: 379–388
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton, NJ
- Clutton-Brock TH, Iason GR (1986) Sex ratio variation in mammals. Q Rev Biol 61:339–374
- Enfield DB (1987) Progress in understanding El Niño. Endeavour, New Series 11(84):197–204
- Gibney L (1953) Delayed implantation in the elephant seal. Nature 17:590–591
- Gloersen P (1995) Modulation of hemispheric sea ice cover by ENSO events. Nature 373:503–506
- Guinet C, Jouventin P, Weimerskirch H (1992) Population changes, movements of southern elephant seals on Crozet and Kerguelen archipelagos in the last decades. Polar Biol 12:349–356
- Hindell MA, Burton HR (1987) Past and present status of the southern elephant seal (*Mirounga leonina*) at Macquarie

- Island. *J Zool (Lond)* 213:365–380
- Hindell MA, Burton HR, Slip DJ (1991a) Foraging areas of southern elephant seals, *Mirounga leonina*, as inferred from water temperature data. *Aust J Mar Freshw Res* 42: 115–128
- Hindell MA, Slip DJ, Burton HR (1991b) The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia:Phocidae). *Aust J Zool* 39: 595–619
- Hindell MA, Slip DJ, Burton HR (1994) Possible causes of the decline of southern elephant seal populations in the southern Pacific and southern Indian Oceans. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals—population ecology, behavior, and physiology*. University of California Press, Berkeley, CA, p 85–97
- Jacobs SS, Comiso JC (1993) A recent sea-ice retreat west of the Antarctic Peninsula. *Geophys Res Lett* 20:1171–1174
- Jacobs SS, Comiso JC (1997) Climate variability in the Amundsen and Bellingshausen seas. *J Clim* 10:697–709
- Jonker FC, Bester MN (1998) Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarct Sci* 10(1): 21–30
- Kwok R, Comiso JC (2002) Southern ocean climate and sea ice anomalies associated with the Southern Oscillation. *J Clim* 15:487–501
- Laws RM (1953) The elephant seal (*Mirounga leonina* Linn.) I. Growth and age. *FIDS. Sci Rep* 8:1–67
- Laws RM (1956) Growth and sexual maturity in aquatic mammals. *Nature* 178:193–194
- Ledley TS, Huang Z (1997) A possible ENSO signal in the Ross Sea. *Geophys Res Lett* 24:3253–3256
- Lewis M, Campagna C, Quintana F, Falabella V (1998) Estado actual y distribución de la población del elefante marino del sur en la Península Valdés, Argentina. *Mastozoología Neotropical* 5(1):29–40 (with English Abstract)
- Loeb V, Siegel V, Holm Hansen O, Hewitt R, Fraser W, Trivelpiece W, Trivelpiece S (1997) Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387:897–900
- Matthews LH (1929) The natural history of the elephant seal. *Discovery Rep* 1:233–256
- McCann TS (1980) Population structure and social organisation of southern elephant seals, *Mirounga leonina*. *Biol J Linn Soc* 14:133–150
- McCann TS (1981) Aggression and sexual activity of male southern elephant seals, *Mirounga leonina*. *J Zool (Lond)* 195:295–310
- McCann TS (1985) Size, status and demography of southern elephant seal (*Mirounga leonina*) population. In: Ling JK, Bryden MM. (eds) *Studies of sea mammals in south latitudes*. South Australian Museum, Adelaide, p 1–17
- McConnell BJ, Fedak MA (1996) Movements of southern elephant seals. *Can J Zool* 74:1485–1496
- McConnell BJ, Chambers C, Fedak MA (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarct Sci* 4(4):393–398
- Pascal M (1979) Essai de dénombrement de la population d'éléphants de mer (*Mirounga leonina*) des îles Kerguelen (49° S, 69° E). *Mammalia* 43(2):147–159
- Piatkowski W, Vergani DF, Stanganelli ZB (2002) Changes in the cephalopod diet of southern elephant seal females at King George Island, during 'El Niño-La Niña' events. *J Mar Biol Assoc UK* 82:3972–3977
- Rodhouse PG, Arnbom TR, Fedak MA, Yeatman J, Murray AWA (1992) Cephalopod prey of the southern elephant seal, *Mirounga leonina* L. *Can J Zool* 70:1007–1015
- SCAR (Scientific Committee on Antarctic Research) (1991) Report of the workshop on southern elephant seals, Monterey (USA). Report no. SC-CAMLR-X/BG/3. CCAMLR, Hobart
- Simmonds I, Jacka TH (1995) Relationships between the interannual variability of Antarctic sea ice and the Southern Oscillation. *J Clim* 8:637–647
- Skinner JD, van Aarde RJ (1983) Observations on the trend of the breeding population of southern elephant seals, *Mirounga leonina*, at Marion Island. *J Appl Ecol* 20: 707–712
- Smith TM, Reynolds RW (1998) A high-resolution global sea surface temperature climatology for the 1961–1990 base period. *J Clim* 11:3320–3323
- Sokal RR, Rohlf FJ (1981) *Biometry: the principles and practice of statistics in biological research*, 2nd edn. WH Freeman, New York
- Stammerjohn SE, Smith RC (1996) Spatial and temporal variability of western Antarctic peninsula sea ice coverage. *Foundations for Ecological Research West of the Antarctic Peninsula*. *Antarct Res Ser* 70:81–104
- Trillmich F, Limberger D (1985) Drastic effects of El Niño on Galapagos pinnipeds. *Oecologia* 67:19–22
- Trivers RL, Williard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90–92
- van Aarde RJ (1980) Fluctuations in the population of southern elephants seals *Mirounga leonina* at Kerguelen Island. *S Afr J Zool* 15:99–106
- Vergani DF, Stanganelli ZB (1990) Fluctuations in breeding populations of elephant seals *Mirounga leonina* at Stranger Point, King George Island 1980–1988. In: Kerry KR, Hempel G (eds) *Antarctic ecosystem. Ecological change and conservation*. Springer-Verlag, Berlin, p 241–245
- Vergani DF, Stanganelli ZB, Bilencia D (2001) Weaning mass variation of southern elephant seals at King George Island and its possible relationship with 'El Niño' and 'La Niña' events. *Antarct Sci* 13:37–40
- Waluda CM, Trathan PN, Rodhouse PG (1999) Influence of oceanographic variability on recruitment in the *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the South Atlantic. *Mar Ecol Prog Ser* 183:159–167
- Waluda CM, Rodhouse PG, Podestá GP, Trathan PN, Pierce GJ (2001a) Surface oceanography of the inferred hatching grounds of *Illex argentinus* (Cephalopoda: Ommastrephidae) and influences on recruitment variability. *Mar Biol* 139:671–679
- Waluda CM, Rodhouse PG, Trathan PN, Pierce GJ (2001b) Remotely sensed mesoscale oceanography and the distribution of *Illex argentinus* in the South Atlantic. *Fish Oceanogr* 10(2):207–216
- Watkins AB, Simmonds I (2000) Current trends in Antarctic sea ice. The 1990s impact on a short climatology. *J Clim* 13:4441–4451
- White WB, Peterson RG (1996) Antarctic circumpolar wave in surface pressure, wind temperature and sea ice extent. *Nature* 380:699–702
- Wormuth JH, Roper CFE (1983) Quantitative sampling of oceanic cephalopods by nets: problems and recommendations. *Biol Oceanogr* 2:357–377
- Yuan X, Martison DG (2000) Antarctic sea ice extent variability and its global connectivity. *J Clim* 13:1797–1817