

Annual cycle and inter-annual variation in the haul-out pattern of an increasing southern elephant seal colony

M. LEWIS^{1*}, C. CAMPAGNA¹ and J. ZAVATTI²

¹ Centro Nacional Patagónico (CONICET), 9120 Puerto Madryn, Argentina

² Universidad Nacional de la Patagonia San Juan Bosco, Puerto Madryn, Chubut 9120, Argentina

*Corresponding author: lewis@cenpat.edu.ar

Abstract: The study describes the annual cycle of southern elephant seals for the increasing colony of Península Valdés, and compares it to the haul-out pattern reported for stable or decreasing sub-Antarctic colonies of the species. Data were collected during censuses of the entire colony (nine breeding seasons, two moulting seasons and one autumn–winter haul-out), monthly surveys of coastline and mark-recapture of pups. Pup production during the study period grew from 12 113 to 14 621 animals (1995–2003). Most relevant events of the cycle were similar for all colonies studied, independent of the geographical location, size or population trend. Compared with other locations where southern elephant seals breed and moult, distinct features for Península Valdés were: i) breeding occurs earlier in the spring, and ii) most adult females reproduce and moult in the same colony. The increasing number of animals ashore was correlated with the expansion in pup production. Population trends and stability of demographic events could be related to a consistent physical environment (ocean fronts) during foraging phases of the annual cycle.

Received 27 May 2003, accepted 16 February 2004

Key words: breeding and moulting cycle, demography, *Mirounga leonina*, ocean fronts, Península Valdés, population size

Introduction

The annual cycle in seals integrates functional, behavioural and ecological aspects of the life history of a species at the population level (Ling 1969). Adult elephant seals, *Mirounga* sp. have an annual cycle characterized by two well-defined pelagic phases at sea between moult and reproduction (Le Boeuf & Laws 1994). The breeding phase of the adult cycle has been thoroughly described for several populations of both species of elephant seals (e.g. Le Boeuf *et al.* 1974 for the northern species, *M. angustirostris*, and Carrick *et al.* 1962a, Skinner & van Aarde 1983, McCann 1985, Guinet *et al.* 1992, Campagna *et al.* 1993, Galimberti & Boitani 1999 for the southern species, *M. leonina*). Much less is known about the annual haul-out pattern of younger age categories. Juveniles haul-out to moult once per year but also come ashore at other times for unknown reasons (Carrick *et al.* 1962b, Hindell & Burton 1988, Kirkman *et al.* 2001).

Despite integrating across many life history variables, the annual cycle seems to differ little as a function of population size and colony latitude. Small colonies, such as that on Marion Island (Condy 1979), show a similar pattern of events to medium-sized or large colonies, such as Heard (Slip & Burton 1999) and Macquarie islands (Hindell & Burton 1988), which are at similar latitudes. Latitude may have an effect on the date of peak number of breeding females (Condy 1979, Campagna *et al.* 1993, Galimberti & Boitani 1999) via a physiological response to daylength. The photoperiod is likely to influence implantation of the

blastocyst and therefore the synchronization of breeding (Daniel 1981, Boyd 1991).

Besides size and latitude, southern elephant seal colonies vary in their population trends. The Patagonian population of Península Valdés (Argentina) is the only one of the 14 described breeding localities where the elephant seal population has increased in size consistently over the last three decades (Campagna & Lewis 1992, Lewis *et al.* 1998). The largest population of the species, located on the island of South Georgia, has apparently been stable, with an estimated 113 000 pups born per year (Boyd *et al.* 1996). All other major colonies declined during the last decades of the twentieth century (Hindell & Burton 1987, Guinet *et al.* 1992, Bester & Wilkinson 1994). The recent period of rapid declines appears to have ended for most populations of the Indian and Pacific sectors of the Southern Ocean (Guinet *et al.* 1999, Pistorius *et al.* 1999, Slip & Burton 1999).

The Península Valdés colony also differs in other respects. It is continental, rather than sub-Antarctic, and occurs at a temperate latitude (Laws 1994). Space is not a limiting factor for the aggregation of animals and seals are distributed along c. 200 km of coastline, which results in unusually low density conditions for the species (Campagna & Lewis 1992, Baldi *et al.* 1996). When leaving the Patagonian coast to forage at sea, this deep diving seal has to cross the largest continental shelf in the Southern Hemisphere (Campagna *et al.* 1995, 2000). Adults forage in the south-west Atlantic and apparently do not reach the Antarctic Polar Front (Campagna *et al.* 1998, 1999), where

seals from more southerly rookeries often forage (Hindell *et al.* 1991, McConnell *et al.* 1992). Despite these differences from other colonies, the behaviour on land and at sea, and the demographic variables that had been described for Valdés are similar to stable and declining populations (Campagna & Lewis 1992, Campagna *et al.* 1993, 1995, 1998, Lewis *et al.* 1998).

This study is the first description of the annual cycle for a growing population of southern elephant seals. We report monthly changes in the number of animals ashore, discriminating sex and age categories. If the annual cycle integrates aspects of life history strategies at the population level, we hypothesize that colonies with different population trends may have distinct cycles. Moreover, if an accurately timed and synchronized breeding–moulting cycle is under the strict control of environmental factors, as suggested by Carrick *et al.* (1962b), then the terrestrial portion of the annual cycle may be linked to seasonal food supplies (Ling 1969). A comparison between colonies may then point towards causes behind different trends in population numbers. We expect for Península Valdés, compared with other sites:

- i) greater inter-annual regularity of the haul-out pattern for various age and sex classes, and
- ii) greater synchronization of haul-out of the population.

Results are discussed in the context of major seasonal ocean fronts that determine oceanographic regimes and productivity in the south-west Atlantic Ocean.

Materials and methods

Elephant seals reproduce along the coast of Patagonia only at Península Valdés (Fig. 1). Seals are found along the open ocean coastline of the Península, from Punta Buenos Aires to Morro Nuevo (*c.* 200 km); a small proportion of the population extends south of Valdés and across the mouth of the Nuevo Gulf. Demographic data were collected during partial counts and censuses of the entire colony. Particular consideration was devoted to the breeding haul-out, when

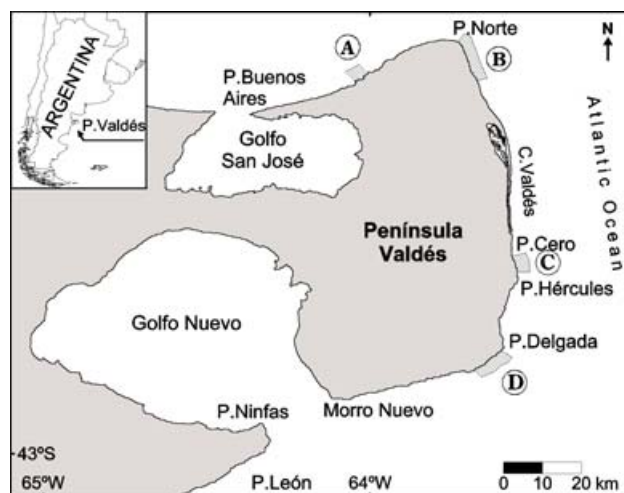


Fig. 1. Geographic location of the Valdés colony of southern elephant seals. Animals are distributed in the outer coast of the Península, from Punta Buenos Aires to Morro Nuevo (198 km) and further south, from Punta Ninfas to Punta León (36 km). The distribution area was surveyed during censuses conducted at the peak of the breeding and moulting seasons. The location of four smaller sampled areas is also indicated (total of 32 km; A–D, see also Table I).

the colony was surveyed on foot during the peak of nine reproductive seasons (first week of October, 1995–2003). Censuses of the entire colony also took place in 1998 and 1999 moulting seasons (December) and during the autumn–winter haul-out, in June 1998. In addition to censusing the colony, we conducted periodic counts of part of the breeding area every 3–7 days during eight seasons (1998–2003). The target sector was a stretch of about 12 km of coastline with high density groups, around Punta Delgada. Partial counts of four sample areas (Fig. 1) were also conducted at monthly intervals, from September 1995 to December 1997. The latter areas were spread along the coast and represented the dominant topographies of the study area (steep pebble beaches, open sandy beaches, sandy beaches limited by high cliffs and a combination of sandy and pebble places). The four areas covered 32 km of

Table 1. Sampling areas where monthly surveys were conducted during 1995–97. Habitable coastline indicates beaches that could be accessed by seals. A to D refers to the geographic location of these areas as shown in Fig. 1.

Area	Location	Lat S/ Long W	Area surveyed (km)	Topography	Shoreline (km) with similar habitat	Habitable coastline (%)	Moult density (individuals km ⁻¹)	Breeding density (individuals km ⁻¹)
A	La Armonía	42°05'45" 63°54'35"	4.2	Close sandy beaches bordered by cliffs	50.2	75.5	86	158
B	Punta Norte	42°04'40" 63°45'27"	11.1	Long beaches of fine pebbles with gentle slope	106.9	100	15	55
C	Punta Hércules	42°33'15" 63°36'3"	4.4	Long beaches with mild slopes	28.7	100	233	390
D	Punta Delgada	42°45'57" 63°38'16"	12	Sandy and pebble beaches extended by rocky shelf	12.2	98	287	426
Total			31.7		198	-	-	-

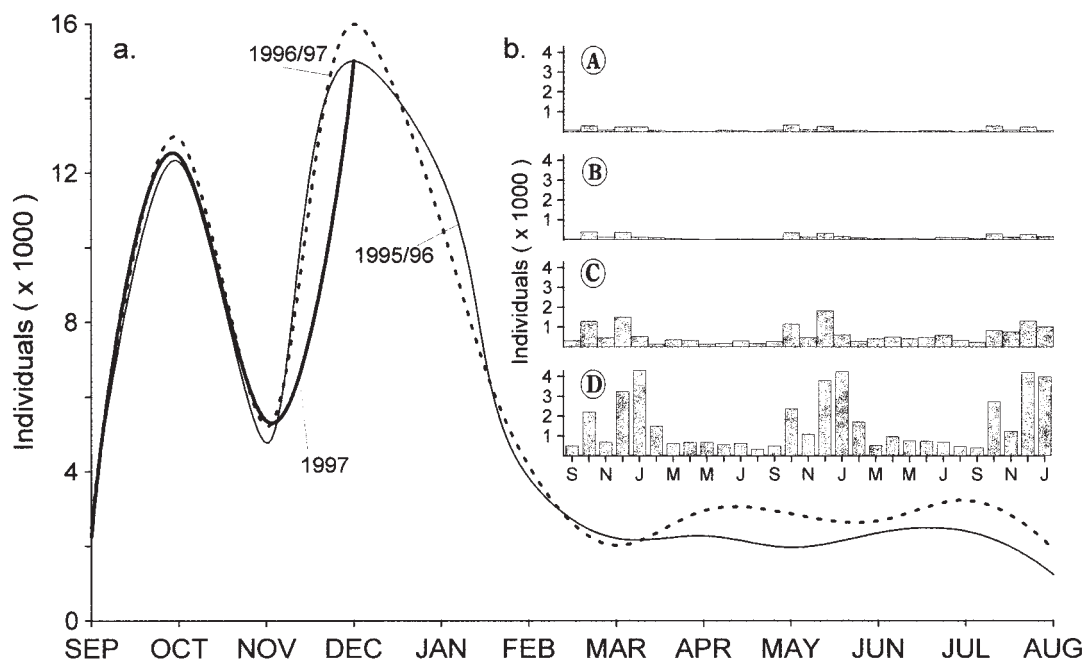


Fig. 2. The annual cycle as described by the monthly variation in the total number of elephant seals ashore during three years. **a.** Smoothed curves represent the total population of Península Valdés (individuals >1 year old) for the period 1995–97 based on counts conducted in four sample areas (A–D in Fig. 1 and part b of this figure). **b.** Histograms with the actual number of animals for the sampled areas (A–D) from which smoothed curves were derived. Data points were connected by lines for graphical purposes and should not imply interpolation. See Methods regarding differential coefficients used to estimate total numbers.

coastline in 1995 and 1996 (18% of the used coast of Península Valdés; Table I). The extension was increased to 59 km in 1997.

The number of animals recorded in the sampled areas (A–D in Fig. 1) was then extrapolated to the total coastline. We multiplied the counts per area by a factor that reflected how representative the area was for the entire colony in terms of density and topography (Table I). Variance around the percent difference between the sub-sampled areas and the complete counts for areas of low (A–B) and high (C–D) density were 2.6 and 1.4, respectively. The total number of animals estimated could then be compared with those observed during regular surveys of the entire coast that occurred during peak breeding and moult seasons, and an occasional survey during June 1998.

Pup production was estimated based on the number of adult females at the peak of the season, plus the number of weaned and a correction factor (4% of the females present) to account for females arrived after the peak (Campagna *et al.* 1993). The rate of change in pup production was calculated following Caughley (1977), a standard procedure also applied in other population studies for the species (van Aarde 1980, Pistorius *et al.* 1999).

Counts were conducted together with a categorization of every animal recorded according to the following general classification: underyearlings, yearlings and 1–3 year old juveniles, 4–6 years old juveniles and adults. To describe the haul-out pattern, all individuals ≤ 6 years old were

considered juveniles whilst weanlings and pups were excluded. A more accurate estimate of age classes was obtained from 718 resights of known-age, tagged animals between 1990 and 2000. Juvenile sex ratio was estimated from direct recording of the sex of individuals.

The total number of animals during the moult and breeding seasons for different areas was compared with a Wilcoxon matched pairs test. Coefficients of variation (CV) obtained for the date of occurrence (Julian day) of key events of the breeding season were used to support inter-annual synchronicity. Events were: maximum number of breeding females ashore, stabilization in the number and maximum number of harems and intersection of the growth curves of the number of nursing pups and weanlings (an indicator that integrates synchronicity of births with duration of lactation).

Statistical analyses were performed with data analysis software (StatSoft Inc 2001). A non-parametric test for independent samples (Siegel & Castellan 1995) was conducted to compare the distribution of age-class categories at different time of the annual cycle.

Results

Description of the annual cycle

There were seals ashore all year around, with two peaks in the number of adults during the first week of October (breeding season) and from early December to mid-January

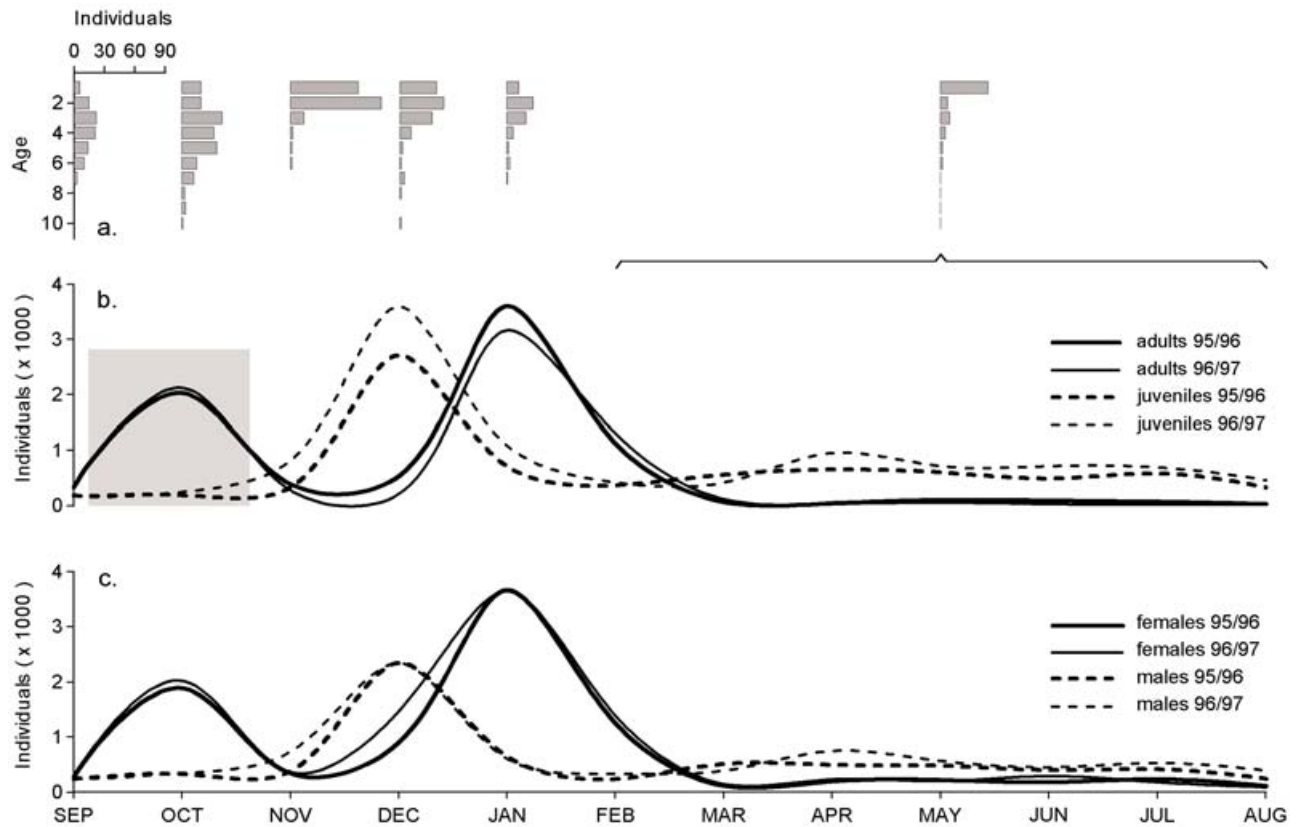


Fig. 3. The annual cycle as described by the monthly number of seals ashore for the Punta Delgada area (12 km of coastline). **a.** Age distribution of known-age individuals resighted during counts. **b.** Comparisons of adults and juveniles. The shadowed area indicates the interval of the breeding season surveyed periodically (see Fig. 4b). **c.** Comparisons of males and females (all age classes) for two consecutive years.

(moult of adult females; Fig. 2a). The reproductive period was indicated by a gradual increase in the number of adults of both sexes starting in early September, a brief peak by the end of the first week of October and a gradual decline extended up to mid-November (see Figs 3b & 4b for more detail). During breeding, 85% of 13 075 animals ashore (SD = 697 animals, $n = 6$ seasons) were adult females ranging from 2–10 years of age ($n = 149$; Fig. 3a).

The smallest number of adults ashore occurred in mid-November and coincided with the maximum number of moulting juveniles (Fig. 3b). 58% of the seals hauled-out at this time were 1–4 years old (mean age = 1.7 ± 0.7 years). The sex ratio of moulting juveniles was not different from 50:50 (44 vs 56 $\chi^2 = 1.5$, $n = 174$, $P > 0.05$).

The first adult females arrived to moult during early December, a time that coincided with the largest number of animals ashore in the year ($14\,991 \pm 691$ vs $13\,075 \pm 697$ seals for the breeding season). At this time, juveniles were still the most abundant group on the beaches (84%). The age of these seals increased compared to the November mean to 2.5 ± 1.6 years ($\chi^2 = 41.3$, $df = 8$, $P_{0.01} = 20.1$). The remainder of December was dominated by moulting juveniles (81%), subadult males (5%) and adult females (14% of 7570 animals recorded on 15 December 1998). The

proportion of adult females ashore increased significantly during January (56%) and declined to 42% in February.

The age and sex composition of animals ashore changed from mid to late summer (February–March). Adult and subadult males started to moult in late February and up to April. By mid-March, 78% of 2049 animals were males and at least 39% were potentially breeders. The sex ratio started to be male biased in March and this continued up to August (66% males, $\chi^2 = 5.3$, $P < 0.05$). Most individuals ashore during early autumn and winter (March–August) were young juveniles (mean age: 1.8 ± 1.3 years, $n = 72$, $\chi^2 = 42.3$, $df = 30$, $P_{0.05} = 43.8$). From March to August the total number of animals ashore was no more than 3000 individuals. The lowest number of seals ashore was recorded in August.

A few local differences within the distribution range were found in the haul-out pattern related to the two main peaks of the cycle. Punta Delgada had 31% more animals moulting than breeding (Wilcoxon z-test = 2.02, $n = 0\,6$, $P < 0.05$) while in the northern coast of the distribution range (Punta Norte and La Armonía) the number of moulting animals was 18% lower than those hauling-out to breed.

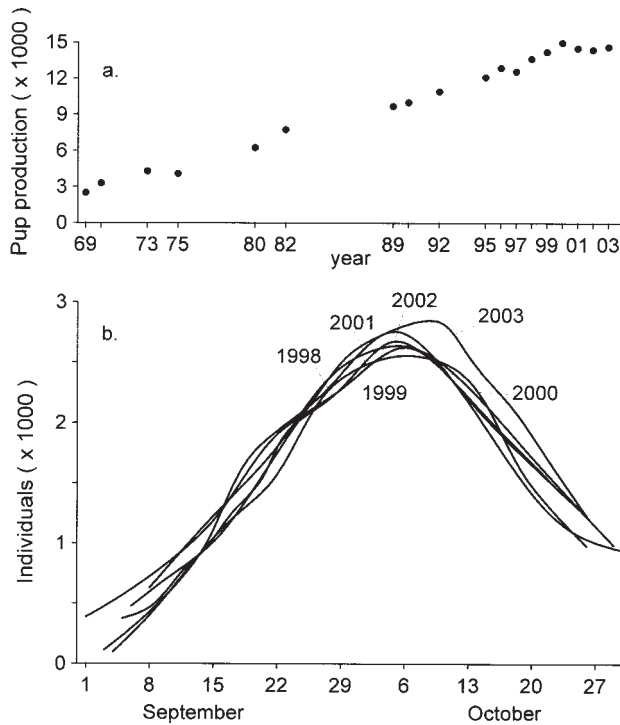


Fig. 4. a. Trend in the number of pups born during the last three decades. Records before 1990 were published in Campagna & Lewis (1992), and records between 1992–97 in Lewis *et al.* (1998). Annual rate of increase was estimated as 5% births per year from 1969–2003. **b.** Elephant seals ashore during six breeding seasons at Punta Delgada between 1998 and 2003 based on counts every 3–7 days. The data points are connected by lines to aid the reader and should not imply interpolation.

Regularity and synchronicity of the haul-out

Dates of arrival, peak numbers and departure of various age and sex classes remained similar between years for the entire colony, and within and between years for the sampled areas (Fig. 2a & Fig. 3a–c). Likewise, adult departure and juvenile arrival were both synchronous and regular phenomena (Fig. 3b).

The general haul-out pattern of reproductive animals were highly synchronous, and remained similar during at least six consecutive seasons. Counts at Punta Delgada showed that

84% of reproductive animals arrived during a period of three to four weeks (Fig. 4b, Table II). Virtually all births occurred within 10 weeks, from late August to the first week of November. Ninety percent of the pups were born during a period of 45–59 days from the beginning of the season, depending on the years. Harems were established during six weeks; this interval was regular between years ($F_{(5,39)} = 0.28$; $P > 0.05$). The peak of females occurred on 6 October (mean Julian day 279; SD = 1.9). The date of intersection of the growth curves of pups and weanlings occurred during the third week of October (mean Julian day = 291, SD = 1.5).

Annual cycle and population trend

The size of the Valdés population continued to expand during this study. Total pup production for the period 1995–2003 grew from 12 113 to 14 621 individuals (Fig. 4a). Likewise, the total number of animals of both sexes (mostly adults) at the peak of breeding, increased for the same period at a rate of 2% per year (from 12 307 to 14 443 individuals).

At the coarse-scale of the available data, the increase in the number of animals in the population (Fig. 4a) did not apparently affect the regularity and synchronicity of the main events of the annual cycle. We tested this generalization focusing on Punta Delgada study area (D in Fig. 1). The similarities among breeding seasons suggested by the shape of the curves in Fig. 4b was reflected in the low coefficient of variation (CV) for the date of occurrence (Julian day) of the following variables:

- i) number of breeding females ashore (CV = 0.7),
- ii) stabilization in the number of harems (CV = 1.3), and
- iii) intersection of the growth curves of the number of pups and weanlings (CV = 0.5).

Discussion

The annual haul-out pattern of the Patagonian population of southern elephant seals is similar to that of other populations, such as Macquarie (Carrick *et al.* 1962b

Table II. Demographic parameters for the breeding season at Punta Delgada for the period 1998–2003. Total males are the mean number (± 1 SD) of seals counted between 14 September and 28 October. Total males included harem males, adults and subadults in the area. Maximum number of pups born per year was estimated as the sum of adult females, weaned pups and dead pups (Slip & Burton 1999). Dates are shown in Julian days.

Males	1998	1999	2000	2001	2002	2003
Alpha males in harem	44 \pm 8.1	42 \pm 4.1	47 \pm 5.6	48 \pm 6.3	40 \pm 9.1	46 \pm 6.4
(n)	(7)	(6)	(7)	(6)	(9)	(11)
Total males	377 \pm 118	376 \pm 51	322 \pm 98	315 \pm 66	323 \pm 50	352 \pm 63
Females at peak	2279	2230	2225	2380	2358	2433
(date)	(293)	(287)	(292)	(284)	(281)	(295)
Pups born	2685	2828	2640	2710	2664	2942
Intersection of no. of pups and weanlings (date)	290	292	289	290	291	293

Hindell & Burton 1988), Heard (Slip & Burton 1999), Marion (Condy 1979), Signy and South Georgia (Laws 1956; only breeding and moulting seasons for South Georgia). These populations have been decreasing in numbers, except for South Georgia (Boyd *et al.* 1996). The cycle of the latter was studied at a time when males were being harvested (Laws 1994). The annual cycle of the southern elephant seal is broadly similar to that of the northern species.

Regular counts made throughout the year have been reported for selected studied areas at Marion (Condy 1979), Macquarie (Hindell & Burton 1988) and Heard Islands (Slip & Burton 1999). Cycles described for these colonies show virtually the same events found at Península Valdés: a major peak for adults of both sexes related to reproduction, several peaks related to the moult of adult females, adult males and juveniles (when most adults are at sea), and a haul-out of juveniles during the autumn and winter months (April to August).

However, breeding occurs earlier at Península Valdés than at other colonies, and most adult females that reproduce in Valdés return to the colony to moult. The total number of animals ashore also increased with time, consistent with the expansion in pup production.

Clinal gradation of breeding

A remarkable synchrony in the timing of the haul-out of breeding females was described for all major southern elephant seal populations (in addition to previous references on the cycle, see: Skinner & van Aarde 1983, McCann 1985, Guinet *et al.* 1992, Le Boeuf & Laws 1994, Galimberti & Boitani 1999). But when colonies are compared with respect to specific events of the season, there is a clinal pattern (Pearson $r = 0.8$, $P < 0.05$, $n = 10$), with reproduction starting about two weeks earlier at Península Valdés than at other places. This clinal gradation at peak breeding season was proposed for populations with a wide latitudinal range of distribution (Ling 1969) and has been confirmed for southern elephant seals (see also: Carrick *et al.* (1962b, table 2), Condy (1979, table 5), Campagna *et al.* (1993, fig. 7), Galimberti & Boitani (1999, table 3).

From a proximate perspective, differences in the timing of the annual cycle have been linked to the effect of the photoperiod on breeding and moulting (Ling 1969, Condy 1979, Boyd 1991). The effect of the daylength on implantation was proposed as a determinant cause of the seasonal timing and sequence of the entire cycle in adults (Condy 1979, Campagna *et al.* 1993, Galimberti & Boitani 1999). Besides daylength, the thermal environment could also have an effect on the annual cycle (Condy 1979). Península Valdés is close to the northern limit of distribution for the species; only the colony at Gough Island is at a lower latitude (Bester 1990), but the oceanic environment of this island reduces the temperature ranges.

Air temperatures by the end of the breeding season (November) and during most of the adult moult at Valdés often range above 30°C. Most days are free of clouds and solar radiation is intense (Lewis & Campagna 1998). Comparatively, in sub-Antarctic colonies, air temperatures for the same time of the year are below 0°C (Laws 1956). Differences are even more dramatic during the summer haul-out. As the thermal environment affects the behaviour of females and pups in southern and northern elephant seals (White & Odell 1971, Lewis & Campagna 1998) and others phocids (Whittow 1987), the extension of the breeding haul-out may be limited by high temperatures (Lewis & Campagna 1998).

Longer breeding haul-outs

The breeding haul-out is longer for Valdés than for colonies closer to the Antarctic Convergence. A similar methodology used to define the length of the breeding season allows comparisons at least with the populations of Macquarie, Possession, Falkland and South Georgia islands. The length of the parturition period is 70 days for Valdés, compared to a range of 60–50 days for other colonies (Carrick *et al.* 1962b, McCann 1985, Guinet *et al.* 1992, Campagna *et al.* 1993, Galimberti & Boitani 1999). There is no evidence of a clinal gradation in the length of the breeding period as a function of latitude.

The moult haul-out is more difficult to compare than the breeding season, as the onset and end of the former period are defined less accurately and there is no clear peak in the number of animals. During the moulting season, adult females are present at Valdés for a period of at least nine weeks, from early to mid-December up to early February. A similar duration of the moult haul-out (eight weeks) has been reported for Marion Island (Condy 1979). Shorter seasons (seven weeks) were described for South Georgia and Macquarie colonies (Laws 1956, Hindell & Burton 1988). As the interval between breeding and moult (indicated by the duration of the post-reproductive foraging trip) is similar for all colonies (68–73 days), the moult also occurs earlier at Valdés than at other places.

Annual cycle and population trend

This study suggests that the population trend does not affect the general shape of the annual cycle. Hindell & Burton (1988) concluded that little change had occurred in the order and duration of the haul-out pattern at Macquarie Island from the 1950s up to 1985, a period during which the size of the colony was decreasing (Hindell & Burton 1987). The annual cycle was studied at Marion Island during 1973 to 1976 (Condy 1979), a period during which the population was decreasing (Skinner & van Aarde 1983). Despite the variation in the number of females on land each year, there was no apparent change in the haul-out pattern. Similar

conclusions are drawn for the expanding Península Valdés population, for which cycles were virtually identical during consecutive years (Fig. 2a).

Correlations limited to the reproductive season best illustrate that the effect of population changes in size are quantitative (number of animals ashore), but do not change the general shape of the cycle. Curves for six breeding seasons for a sampled area at Península Valdés reflect an increase in number of reproductive animals with a constant timing of events (Fig. 4b). During these six seasons, the total breeding female population increased by one thousand animals (from 13 116 to 14 155).

Inter-colony comparisons suggest that different population sizes do not apparently affect the pattern of events of the annual cycle. The Valdés population, has a similar pattern of events to that of the Macquarie colony (77 800 animals) or the Marion Island population (2000 animals; Le Boeuf & Laws 1994). If comparisons are limited to the reproductive season, the above generalization extends to populations of a few hundred animals, such as that of Falkland-Malvinas Islands (Galimberti & Boitani 1999).

Oceanographic correlates

The sustained increase in pup production and the regularity of the events in the haul-out pattern described for Península Valdés could be related to productivity-driven oceanographic phenomena affecting foraging success.

Satellite-determined locations at sea, correlated with the dive pattern and temperature of the water column, were reported for adults of both sexes breeding and moulting at Valdés (Campagna *et al.* 1995, 1998, 1999, 2000). Results suggest that adult males and post-breeding females forage along the border of the continental shelf, an area under the effects of productive ocean fronts.

A general circulation scheme for the south-west Atlantic has two pivotal components, the Brazil and the Falkland-Malvinas (F-M) currents. The dynamics of these currents associated to bathymetric features, most relevant of which are the shallow (< 100 m) continental shelf and the steep shelf slope, generate thermal frontal regions with climate and biological effects both within and beyond the area (Podestá *et al.* 1991, Brandini *et al.* 2000, Saraceno *et al.* in press). Depth-driven fronts such as the shelf-Brazil, shelf F-M and the core of the Brazil/F-M collision are consistent in location, being seasonality the most relevant source of variability.

Thermal fronts drive ocean productivity (Podestá *et al.* 1991, Carreto *et al.* 1995) and it was suggested that regions visited by elephant seals during the foraging phase of the annual cycle would be characterized by a higher productivity potential (Bradshaw *et al.* in press). It has been also reported that elephant seals tend to revisit the same areas of the ocean despite high variation in annual foraging

success (Bradshaw *et al.* in press). Therefore, constancy and predictability in productivity would result in increased foraging success, individual survival and population growth.

Acknowledgements

We thank Dr Ian Boyd and an anonymous reviewer for helpful and constructive comments of a previous version of the paper, Drs A. Piola, G. Podestá, A. Rivas and A. Gagliardini for their advice regarding the oceanographic aspects of this work, M.R. Marin for assistance in data analysis, V. Falabella, F. Quintana and R. Vera for field assistance, as well as the many technicians, students and volunteers that participated in the annual censuses. Logistical support was provided by Centro Nacional Patagónico (National Research Council of Argentina, CONICET), Estancia Rincón Chico and Establecimiento Faro Punta Delgada. The Dirección de Fauna and Secretaría Provincial de Turismo de Chubut issued the permits to conduct research at Península Valdés. The project received partial support by CONICET (PEI N° 0307/97); the Wildlife Conservation Society, EcoCentro Puerto Madryn and the Minority International Research Training Program (PI. Dr. C. L. Ortiz, University of California, Santa Cruz).

References

- BALDI, R.C., CAMPAGNA, C., PEDRAZA, S. & LE BOEUF, B.J. 1996. Social effects of space availability on the breeding behaviour of elephant seal in Patagonia. *Animal Behaviour*, **51**, 717–724.
- BESTER, M.N. 1990. Population trends of subantarctic fur seals and southern elephant seals at Gough Island. *South African Journal of Antarctic Research*, **20**, 9–12.
- BESTER, M.N. & WILKINSON, I.S. 1994. Population ecology of southern elephant seals at Marion Island. In LE BOEUF, B.J. & LAWS, R.M., eds. *Elephant seals: population ecology, behavior and physiology*. Berkeley: University of California Press, 85–97.
- BOYD, I.L. 1991. Environmental and physiological factors controlling the reproductive cycle of pinnipeds. *Canadian Journal of Zoology*, **69**, 1135–1148.
- BOYD, I.L., WALKER, T.R. & PONCET, J. 1996. Status of southern elephant seals at South Georgia. *Antarctic Science*, **8**, 237–244.
- BRADSHAW, C.J.A., HINDELL, M.A., SUMNER, M.D. & MICHAEL, K.J. In press. Loyalty pays: life-history consequences of fidelity to marine foraging regions by elephant seals. *Animal Behaviour*.
- BRANDINI, F.P., BOLTOVSKOY, D., PIOLA, A., KOCMUR, S., ROTTGERS, R., ABREU, P.C. & LOPES, R.M. 2000. Multiannual trends in fronts and distribution of nutrients and chlorophyll in the southwestern Atlantic (30–62°S). *Deep-Sea Research I*, **47**, 1015–1033.
- CAMPAGNA, C. & LEWIS, M. 1992. Growth and distribution of a southern elephant seal colony. *Marine Mammal Science*, **8**, 387–396.
- CAMPAGNA, C., LEWIS, M. & BALDI, R. 1993. Breeding biology of southern elephant seals in Patagonia. *Marine Mammal Science*, **9**, 34–47.
- CAMPAGNA, C., LE BOEUF, B.J., BLACKWELL, S., CROCKER, D.E. & QUINTANA, F. 1995. Diving behaviour and foraging location of female southern elephant seals from Patagonia. *Journal of Zoology*, **236**, 55–71.
- CAMPAGNA, C., QUINTANA, F., LE BOEUF, B.J., BLACKWELL, S. & CROCKER, D.E. 1998. Diving behaviour and foraging ecology of female southern elephant seals from Patagonia. *Aquatic Mammals*, **4**, 1–11.

- CAMPAGNA, C., FEDAK, M.A. & MCCONNELL, B.J. 1999. Post-breeding distribution and diving behaviour of adult male southern elephant seals from Patagonia. *Journal of Mammalogy*, **4**, 1341–1352.
- CAMPAGNA, C., RIVAS, A.L. & MARIN, M.R. 2000. Temperature and depth profiles recorded during dives of elephant seals reflect distinct ocean environments. *Journal of Marine Systems*, **24**, 299–312.
- CARRETO, J.I., LUTZ, V.A., CARIGNAN, M.O., CUCCHI COLLEONI, A.D. & DE MARCO, S.G. 1995. Hydrography and chlorophyll a in the transect from the coast to the shelf break in the Argentinean Sea. *Continental Shelf Research*, **15**, 315–336.
- CARRICK, R., CSORDAS, S.E. & INGHAM, S.E. 1962a. Studies of the southern elephant seal, *Mirounga leonina* (L.) IV. Breeding and development. *CSIRO Wildlife Research*, **7**, 161–197.
- CARRICK, R., CSORDAS, S.E., INGHAM, S.E. & KEITH, K. 1962b. Studies of the southern elephant seal, *Mirounga leonina* (L.) III. The annual cycle in relation to age and sex. *CSIRO Wildlife Research*, **7**, 119–160.
- CAUGHLEY, G. 1977. *Analysis of vertebrate populations*. London: Wiley, 234 pp.
- CONDY, P.R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Zoology*, **14**, 95–102.
- DANIEL, J.C. 1981. Delayed implantation in the northern fur seal (*Callorhinus ursinus*) and other pinnipeds. *Journal of Reproduction and Fertility*, Supplement **29**, 35–10.
- GALIMBERTI, F. & BOITANI, L. 1999. Demography and breeding biology of a small, localized population of southern elephant seals (*Mirounga leonina*). *Marine Mammal Science*, **15**, 159–178.
- GUINET, C., JOUVENTIN, P. & WEIMERSKIRCH, H. 1992. Population changes, movements of southern elephant seals on Crozet and Kerguelen archipelagos in the last decades. *Polar Biology*, **12**, 349–356.
- GUINET, C., JOUVENTIN, P. & WEIMERSKIRCH, H. 1999. Recent population change of the southern elephant seal at Îles Crozet and Îles Kerguelen: the end of the decrease? *Antarctic Science*, **11**, 193–197.
- HINDELL, M.A. & BURTON, H.R. 1987. Past and present status of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. *Journal of Zoology*, **213**, 365–380.
- HINDELL, M.A. & BURTON, H.R. 1988. Seasonal haul-out patterns of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. *Journal of Mammalogy*, **69**, 81–88.
- HINDELL, M.A., BURTON, H. & SLIP, D. 1991. Foraging areas of southern elephant seals, *Mirounga leonina*, as inferred from water temperature data. *Australian Journal of Marine and Freshwater Research*, **42**, 115–128.
- KIRKMAN, S.P., BESTER, M.N., PISTORIUS, P.A., HOFMEYER, G.J.G., OWEN, R. & MECENERO, S. 2001. Participation in the winter haul-out by southern elephant seals (*Mirounga leonina*). *Antarctic Science*, **13**, 380–384.
- LAWS, R.M. 1956. The elephant seal (*Mirounga leonina* Linn.) II. General, social and reproductive behaviour. *Falkland Islands Dependencies Survey Scientific Reports*, No. 13, 1–88.
- LAWS, R.M. 1994. History and present status of southern elephant seal populations. In LE BOEUF, B.J. & LAWS, R.M., eds. *Elephant seals: population ecology, behavior and physiology*. Berkeley: University of California Press, 49–65.
- LE BOEUF, B.J., AINLEY, D.G. & LEWIS, T.J. 1974. Elephant seals on the Farallones: population structure of an incipient breeding colony. *Journal of Mammalogy*, **55**, 370–384.
- LE BOEUF, B.J. & LAWS, R.M. 1994. Elephant seals: an introduction to the genus. In LE BOEUF, B.J. & LAWS, R.M., eds. *Elephant seals: population ecology, behavior and physiology*. Berkeley: University of California Press, 1–26.
- LEWIS, M. & CAMPAGNA, C. 1998. Flipping sand in elephant seals. *Aquatic Mammals*, **24**, 85–90.
- 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**, 29–40.
- LING, J.K. 1969. A review of ecological factors affecting the annual cycle in island populations of seals. *Pacific Science*, **23**, 399–413.
- MCCANN, T.S. 1985. Size, status and demography of southern elephant seal (*Mirounga leonina*) populations. In LING, J.K. & BRYDEN, M.M., eds. *Sea mammals in south latitudes. Proceedings of a symposium of the 52nd ANZAAS Congress*. Adelaide: South Australian Museum, 1–17.
- MCCONNELL, B.J., CHAMBERS, C. & FEDAK, M.A. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science*, **4**, 393–398.
- PISTORIUS, P.A., BESTER, M.N. & KIRKMAN, S.P. 1999. Dynamic age distributions in a declining population of southern elephant seals. *Antarctic Science*, **11**, 445–450.
- PODESTA, G.P., BROWN, O.B. & EVANS, R.H. 1991. The annual cycle of satellite-derived sea surface temperature in the southwestern Atlantic Ocean. *American Meteorological Society*, **4**, 457–467.
- SARACENO, M., PROVOST, C., PIOLA, A.R., BAVA, J. & GAGLIARDINI, D.A. 2004. The Brazil Malvinas Frontal System as seen from nine years of advanced very high resolution radiometer data. *Journal of Geophysical Research*, **109**, C05027, doi: 10.1029/2003JC002127.
- SIEGEL, S. & CASTELLAN, N.J. 1995. *Estadística no paramétrica aplicada a las ciencias de la conducta*, 4th ed. Mexico: Trillas S.A., 437 pp.
- SKINNER, J.D. & VAN AARDE, R.J. 1983. Observations on the trend of the breeding population of southern elephant seals, *Mirounga leonina*, at Marion Island. *Journal of Applied Ecology*, **20**, 707–712.
- SLIP, D.J. & BURTON, H. 1999. Population status and seasonal haul-out patterns of the southern elephant seal (*Mirounga leonina*) at Heard Island. *Antarctic Science*, **11**, 38–47.
- STATSOFT INC. 2001. *Statistica* (data analysis software system), ver. 6. Microsoft Corp. www.statsoft.com
- VAN AARDE, R.J. 1980. Fluctuations in the population of southern elephant seal, *Mirounga leonina*, at Kerguelen Island. *South African Journal of Zoology*, **15**, 99–108.
- WHITE, F.N. & ODELL, D.K. 1971. Thermoregulatory behavior of the Northern elephant seal, *Mirounga angustirostris*. *Journal of Mammalogy*, **52**, 758–774.
- WHITTOW, G.C. 1987. Thermoregulatory adaptations in marine mammals: interacting effects of exercise and body mass. *Marine Mammal Science*, **3**, 220–241.