



The founding of a southern elephant seal colony

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ABSTRACT

The only large mainland colony of southern elephant seals (*Mirounga leonina*) is on Península Valdés, at 42°S, in Argentine Patagonia. Censuses of pups have been carried out regularly there since 1970, and the population grew five-fold by 2010. Here we use Bayesian modeling tools to make rigorous estimates of the rate of population growth, r , and to estimate survival and recruitment parameters that could account for the growth, incorporating observation error across different census methods. In the 1970s, $r = 8\%/yr$, but has slowed to $<1\%/yr$ over the past decade. Using explicit demographic models, we established that the high growth of the 1970s was consistent with adult and juvenile survival at the upper end of published values (0.87/yr adult female survival; 0.40 juvenile survivorship to age four); the decline in the rate of population growth from 1970 to 2010 can be described by density-dependent reductions in adult and juvenile survival that fall well within published variation. Extrapolating empirical models of population growth rate backwards illustrates that the population could have been an established colony, with 100 pups born per year, between 1915 and 1945, consistent with qualitative observations prior to 1950. We conclude that the Valdés colony was founded by a few immigrants early in the 20th century and has been growing mostly by internal recruitment, with unknown density-dependent processes causing a reduction in growth and stabilization at 15,000–16,000 pups born.

Key words: *Mirounga leonina*, southern elephant seal, population trends, Bayesian state space models.

Breeding populations of the southern elephant seal (*Mirounga leonina*) are found mostly on subantarctic islands, but there is one exceptional temperate, continental colony at Península Valdés, in coastal Patagonia, Argentina (Laws 1994). Although elephant seals were recorded along the coast of Argentina during the early 1800s (D'Orbigny 1998), the first reports of a breeding colony at Península Valdés are

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from the 1940s (Carrara 1952). Observations from the 1960s and 1970s indicated a well-established breeding aggregation, though of unknown size (Conway 1965, Le Boeuf and Petrionovich 1974). Since 1982, we have been carrying out complete censuses of pup production and observed substantial population increase (Pistorius *et al.* 2004, Ferrari *et al.* 2009); this is the only southern elephant seal colony where population increase is the general trend over several decades (McMahon *et al.* 2005).

Given the expansion of the Península Valdés colony over the past 50 yr, we developed the hypothesis that there were no elephant seals on the Península Valdés mainland prior to the 20th century. Here we evaluate this hypothesis from a demographic perspective, using Bayesian state-space models and 40 yr of census data to quantify the rate of expansion and associate population trends with published estimates of survival from other studies. We test two principal hypotheses: first that the colony could have been founded during the 20th century, and second, that growth of the colony could be due entirely to internal recruitment and density dependence, as opposed to immigration from the large colonies elsewhere.

Pinnipeds in other parts of the world have proven excellent subjects for precise demographic models, owing to their well-circumscribed populations that can be thoroughly censused by counting pups at a few locations (Stewart *et al.* 1994, Harrison *et al.* 2006). Indeed, we profit by drawing a comparison with the northern elephant seal, *Mirounga angustirostris*, which also has well-documented population growth on core island colonies and on peripheral mainland colonies (Le Boeuf *et al.* 2011). For both the Año Nuevo population of northern elephant seals and the Península Valdés population of southern elephant seals, we have the opportunity to monitor population growth from soon after founding through a phase of rapid growth to stabilization, a rare opportunity in any species. Demographic data for a species that reproduces on land but spends most of its life at sea, where it disperses widely over pelagic and benthic habitats, has conservation value vis-à-vis threats as climate-change and the expansion of fisheries in international waters.

METHODS

Census Data

During September and October, adult seals gather in harems along the Atlantic front of Península Valdés and direct counts of all individuals are possible. The number of females onshore increases steadily from early September and peaks during the first week of October (Campagna *et al.* 1993). Virtually all females give birth to a pup, spending 28 ± 2.5 d ashore. Weanling pups remain on the beach for about one month or more after adults depart to forage at sea.

Censuses were divided into three periods according to the method used:

- (1) Five partial counts from 1969 to 1980 are available from literature (Daciuk 1973, Ximenez and Scolaro 1974, Scolaro 1976, Vergani *et al.* 1987). Data were corrected for differences in the date of the census within the breeding cycle and the total area surveyed (see Campagna and Lewis 1992).
- (2) Four censuses were conducted by plane during the first week of October, the peak of the breeding season, from 1982 to 1992 (Campagna and Lewis 1992, Lewis *et al.* 1998).
- (3) Fourteen censuses were conducted by walking the entire extent of the colony during the peak of the breeding season from 1995 to 2010.

We used pup production as our metric of population size (Sibly and Hone 2002). The total pup production for a season was estimated as the sum of adult females (F) and weaned pups (W) present on the census day. When the census day was exactly midseason, which is the highest female count, F includes 90% of the females destined to use the colony and W adds 5% more (McCann and Rothery 1988, Condit *et al.* 2007). We expect a small difference between census and midseason day, thus we believe that $F + W$ consistently represents the total production within 5%.

The Modeling Approach

We described population change from year to year as a state-space model (Clark 2007). The general model is formed by two equations:

$$\begin{aligned}x_t &= f_t(x_{t-}, \mathbf{b}) + \varepsilon_t \\y_t &= x_t + w_t\end{aligned}\tag{1}$$

where x_t is the true population size in year t and y_t is the number counted; both are log-transformed. The first equation is the process model, a deterministic function $f_t(x_{t-}, \mathbf{b})$ describing how past abundance predicts x_t ; $\mathbf{b} = (b_1, \dots, b_t)$ are projection parameters, and x_{t-} represents the population prior to t . Stochasticity is added by the term ε_t that describes process error, which we assume to be a zero-mean Gaussian, $N(\varepsilon_t | 0, \sigma^2)$, σ^2 being the variance of the error. The second equation corresponds to the data model and describes sampling error; we assume that there are no systematic biases and that w_t is a zero-mean process $N(w_t | 0, \tau_t^2)$, but the observation error τ_t^2 can vary with t and with census method. A Bayesian approach to the state-space model allows us to consider both process error and census error, incorporating the differences in census procedures (Calder *et al.* 2003, Clark and Bjørnstad 2004). Years without counts (19 yr of a range of 42) were treated like missing data, and were estimated (Clark 2007).

Within the state-space Bayesian framework we evaluated models of two different types. One set comprises descriptive empirical models of population growth rate, with no demography, that allow easy backwards extrapolation of population size; and a second set of explanatory demographic models, based on estimates of elephant seal survival published elsewhere. Empirical models provide precise estimates of the rate of population growth, and rigorous tests of whether the rate changed through time. In the absence of any density-dependent regulation, population growth rate would be constant, while negative density-dependence would lead to a declining rate of population growth as population increases (McMahon *et al.* 2009). The demographic models allow explicit estimates of density-dependence in key demographic parameters: adult female survival and recruitment of juvenile females into the breeding population at age 4.

Empirical Models of Population Growth

We considered two models aimed at estimating the rate of population growth, r , and how it changed through time (Table 1). The rate r is defined by:

$$n_t = \exp(r)n_{t-1}$$

Table 1. Empirical models ($n_t = \exp(r)n_{t-1}$) were considered to estimate the rate of population growth, r .

Model	Description	Posterior estimations*		Comparison criteria	
		1970s	At present	Predictive Loss ($G_M + P_M$)	DIC (p_D)
1. Segmented regression	Several phases of exponential growth. This model considers a change in population trend not necessarily related to population regulation.† $r = b_j, j = 1, 2, \dots, k$.	$r = 0.078$ (0.044 – 0.112)	$r = 0.008$ (–0.026 – 0.043)	5.159 (0.053 + 5.106)	77.93 (12.28)
2. Logistic	Ricker logistic. This model considers intrinsic population regulation associated to a density dependence parameter (b_2). $r = b_1 - \exp(b_2)n_{t-1}$	$r = 0.082$ (0.054 – 0.112)	$r = 0.006$ (–0.026 – 0.037)	1.598 (0.078 + 1.520)	77.515 (11.78)

*Posterior median and 90% credible interval (see the text for complete prior assumptions).

†We considered segmented regression with 1, 2, 3, and 4 phases and selected the model with three phases, 1969–1982, 1982–1999, and 1999–2010, according to Predictive Loss criterion; predictive loss for 1, 2, and 4 phases models were 7.75 (1.54 + 6.21), 5.6 (0.16 + 5.44), and 5.75 (0.04 + 5.71), respectively.

where n is population size, or in its log-transformed form

$$x_t = r + x_{t-1}.$$

Model 1 was a segmented (or piecewise) regression (Lerman 1980), allowing k different phases of exponential growth, with divisions at $t = j_1, \dots, t = j_k$. Then $r = b_i$ for $j_{i-1} < t \leq j_i$, where b_i was the population growth rate in interval $i = 1, 2, \dots, k$. We considered models with 1–4 phases, and chose the one with the best fit to the data (based on criteria described below). To select the transition points, in models with 2, 3, and 4 phases, we applied segmented regression with grid search (Lerman 1980) and then fixed the selected points in the state space model. The advantages of segmented regression are that it provides precise estimates of growth rate, r , and rigorous tests of whether it changed, and when.

Model 2 was a Ricker logistic model, in which r changes continuously with n :

$$r = r_0 - \frac{r_0}{K} n_{t-1} = b_1 - \exp(b_2) n_{t-1}$$

where b_2 is the parameter associated with density dependence, $r_0 = b_1$ is the maximal rate of increase and $K = b_1 / \exp(b_2)$ the carrying capacity. The Ricker model also provides exact estimate of r , but in addition a simple, yet straightforward measure of density-dependence. Both segmented regression and the Ricker model allow easy backwards extrapolation of population size prior to the observations.

Demographic Models of Population Growth

We considered three models built from demography and population structure, with density-dependence in survival and recruitment modeled explicitly (Table 2). Based on the assumption that age at first breeding is 4 yr (Pistorius *et al.* 2004), we described population growth with the difference equation:

$$n_t = q n_{t-4} + p n_{t-1} \quad (2)$$

where p is the annual adult female survival and q the recruitment of juvenile females into the adult class. If l_4 is the probability of surviving to age 4 and m is fecundity (females born per adult female), then $q = l_4 \times m$. This allowed us to incorporate a simple population structure without an explicit matrix model, which would require many more parameters (Buckland *et al.* 2004). A density-dependence parameter b_3 was included in these lagged models, affecting only recruitment (model 3), only adult survival (model 4), or both (model 5).

Prior Assumptions and Sampling

Projection parameter priors were flat and noninformative for empirical models. For demographic models, it should be evident that parameters p and q in Equation 2 are not uniquely determined by population growth alone. Indeed, we can show that for any given growth rate r , there is an infinite set of values of p and q that fall on an exact line, all producing r . We thus used published survival data from southern elephant seals (McCann 1985, McMahan *et al.* 2003, Pistorius *et al.* 2004) to set priors on p and q . Three studies give estimates of adult female survival at 0.77–0.89,

Table 2. Demographic models ($n_t = qn_{t-4} + pn_{t-1}$) were considered to estimate female recruitment q , and adult female survival p .

Model	Description	Posterior estimations*		Comparison criteria	
		1970s	At present	Predictive Loss ($G_M + P_M$)	DIC (p_D)
3. Lagged logistic with density-dependence affecting recruitment	This model considers a simple population structure and includes a density dependence parameter (b_3) affecting q . $q = \exp(b_1 - \exp(b_3)n_{t-4})$, $p = \exp(b_2)$	$q = 0.203$ (0.138 – 0.282)	$q = 0.152$ (0.111 – 0.204)	2.585 (0.394 + 2.191)	78.634 (13.49)
4. Lagged logistic with density-dependence affecting survival	Idem Model 3 but density dependence parameter affecting p . $q = \exp(b_1)$, $p = \exp(b_2 - \exp(b_3)n_{t-1})$	$q = 0.193$ (0.134 – 0.267)	$p = 0.854$ (0.769 – 0.91)	4.693 (0.990 + 3.703)	79.565 (15)
5. Lagged logistic with density-dependence affecting recruitment and survival	Idem Model 3 but density dependence parameter affecting both p and q . $q = \exp(b_1 - \exp(b_3)n_{t-4})$, $p = \exp(b_2 - \exp(b_3)n_{t-1})$	$q = 0.21$ (0.146 – 0.288)	$q = 0.203$ (0.144 – 0.27)	3.571 (0.785 + 2.786)	79.535 (13.73)

*Posterior median and 90% credible interval. We assume priors credible intervals (0.1–0.24) for q and (0.77–0.89) for p (see the text for complete prior assumptions).

and these form our basis for the prior on p . The recruitment term, q in our model, is the product of fecundity and survivorship to age 4. McCann (1985) and McMahon *et al.* (2003) give survivorship to age 4 in the range 0.2–0.48, and other studies routinely assume fecundity is near 0.5 (one birth per year with half females), so q would be in 0.1–0.24. Thus we used normal distributions for b_1 and b_2 so that the 90% confidence intervals for p and q covered those range. We used a flat normal prior for the density dependence parameter b_3 .

We used noninformative prior distributions for initial abundances and for process error. For observation errors we took into account the three monitoring methods, we fit τ_{part}^2 for the early years with partial counts, τ_{air}^2 for the middle period with aerial censuses, and τ_{ter}^2 for the terrestrial censuses. For τ_{part}^2 we used a noninformative prior, but for the later peak breeding censuses, τ_{air}^2 and τ_{ter}^2 , we assumed 4% error in counts (Campagna and Lewis 1992, Campagna *et al.* 1993), thus defined an informative prior with mean 0.04 but unbounded variance. The *joint posterior of the state-space model* is:

$$\begin{aligned}
 & p(\{x_t\}, \sigma^2, \{\tau_t^2\}, \mathbf{b}|\{y_t\}) \\
 & \propto \overbrace{\prod_{\substack{t \text{ with} \\ \text{counts}}} N(y_t|x_t, \tau_t^2)}^{\text{data model}} \overbrace{\prod_{1969 \leq t \leq 2010} N(x_t|f_t(x_{t-}, \mathbf{b}), \sigma^2)}^{\text{process model}} \\
 & \underbrace{\prod_{t < 1969} N(x_t|\mu_{x_t}, s_{x_t}^2)}_{\text{initial abundance priors}} \underbrace{\prod_{1 \leq i \leq j} N(b_i|\mu_{b_i}, s_{b_i}^2)}_{\text{projection parameter priors}} \underbrace{IG(\sigma^2|\alpha_\sigma, \beta_\sigma)}_{\text{process error prior}} \underbrace{\prod_{\substack{t \text{ with} \\ \text{counts}}} IG(\tau_t^2|\alpha_{\tau_t}, \beta_{\tau_t})}_{\text{observation error priors}}
 \end{aligned}$$

and the following priors were used: noninformative normal for initial abundances, $x_t \sim N(0, 100^2)$, $t < 1969$; non informative inverse-gamma for process error and observation error of partial counts, $\sigma^2, \tau_{\text{part}}^2 \sim IG(0.5, 0.01)$; and informative inverse-gamma with unbounded variance for aerial and terrestrial censuses observation errors, $\tau_{\text{air}}^2, \tau_{\text{ter}}^2 \sim IG(2, 0.04)$.

We implemented a Gibbs sampler to obtain posterior draws for each parameter (Gelman *et al.* 1995, Condit *et al.* 2007). The use of conjugate-normal and inverse-gamma distributions simplifies calculations since we can sample most parameters directly from conditional distributions. For those parameters that could not be directly sampled we used a Metropolis algorithm (Carlin *et al.* 1992, Clark 2007). We implemented the sampler as a R program (R Development Core Team 2009), for each model we ran 100,000 simulations, discarded the first 10,000 as burn-in and thin the remaining by sampling every 10th, producing 9,000 posterior samples.

Model Comparison

We applied a predictive loss criterion (Gelfand and Gosh 1998) to compare models. This approach was motivated by a decision theoretic framework where predictive distributions are computed from the posterior draws. To draw a predictive distribution, we used the Gibbs posterior sample of parameters, $\mathbf{b}(g)$, $\sigma^2(g)$, $\tau_t^2(g)$ and $x_t(g)$,

creating 9,000 model predictions using

$$x_t^{\text{pred}}(g) = x_t(g) \quad \text{for } t < 1969,$$

$$x_t^{\text{pred}}(g) \sim N(x_t^{\text{pred}}(g) | f_t(x_t^{\text{pred}}(g), \mathbf{b}(g)), \sigma^2(g)) \quad \text{for } t \geq 1969,$$

and replicate observations with

$$y_t^{\text{pred}}(g) \sim N(y_t^{\text{pred}}(g) | x_t^{\text{pred}}(g), \tau_t^2(g)).$$

This produced a predictive mean, $E(y_t^{\text{pred}})$, and variance, $E(y_t^{\text{pred}})$, for every year with counts. We computed the sum of squared deviations between observations and the predictive means, G_M , and predictive variance, P_M , is a penalty term:

$$G_M = \sum (E(y_t^{\text{pred}}) - y_t)^2$$

$$P_M = \sum \text{var}(y_t^{\text{pred}}),$$

summed over all years with counts. Then predictive loss is $D_M = G_M + P_M$, and the best-fitting model is the one with the minimum D_M .

We also computed the Deviance Information Criterion (DIC, Spiegelhalter *et al.* 2002) for all models as an alternative comparison tool. The DIC is similar to Akaike Information Criterion but can be computed directly from the posterior samples. We focused DIC on the data model with parameters τ_t^2 and x_t for years with counts. The deviance is

$$D(y_t | x_t, \tau_t^2) = -2 \log \prod_t N(y_t | x_t, \tau_t^2) + C,$$

for some constant C and

$$\text{DIC} = 2\overline{D(y_t | x_t, \tau_t^2)} - D(\overline{y_t | x_t, \tau_t^2}),$$

where the overline represents posteriors mean estimates from the Gibbs sampler. The quantity $P_D = \overline{D(y_t | x_t, \tau_t^2)} - D(\overline{y_t | x_t, \tau_t^2})$ is referred to as the effective number of parameters.

RESULTS

Population Growth and Density Dependence

Population size increased from 2,400 pups in 1969 to 15,200 in 2010 (Fig. 1). The optimal piecewise regression model described this growth with three phases, 1969–1982, 1982–1999, and 1999–2010. Models with 1, 2, and 4 phases all had higher predictive loss (and thus poorer fit). According to the three-phase model, the rate of population increase from 1969 to 1982 was 0.078/yr (0.044–0.112, 90% credible interval), declining to 0.008/yr (–0.026–0.043) during 1999–2010

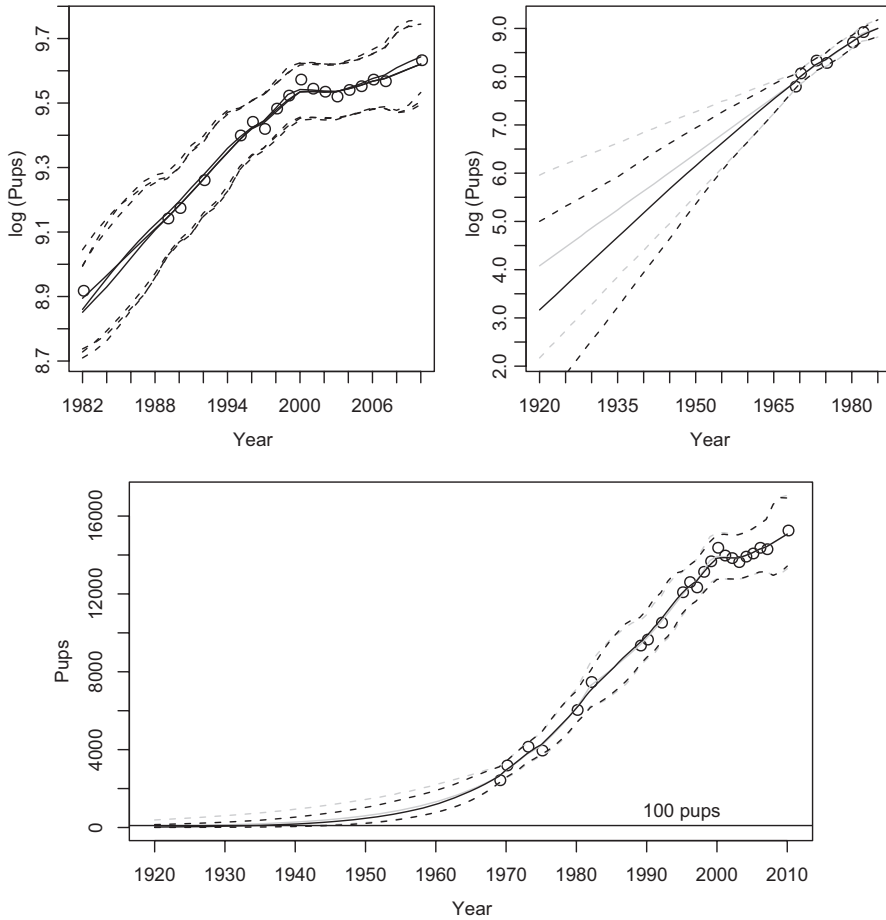


Figure 1. Estimates of annual abundance: posterior median (solid line) and 90% credible intervals (dashed lines); points correspond to observed values. Upper left panel: Log-transformed number of pups from 1982 to 2010 of models 1, 2, and 3. Upper right panel: Log-transformed backwards extrapolation of the empirical models: logistic (model 1, black) and segmented regression (model 2, gray) from 1920 to 1982. Lower panel: Overall population growth from 1920 to 2010 according to the empirical models.

(Table 1). Observation error was greater than process error and observation error posteriors were smaller for the terrestrial census period (Fig. 2, these differences were common to all the models). The logistic model and regression model produced very similar estimates for the rate of population growth and abundances during the observation period (Table 1, Fig. 1), but the logistic model had a better fit according to criteria of predictive loss and DIC (Table 1), meaning the data are better described if population trend declined smoothly with abundance. The maximal rate of increase (b_1) in the logistic model, which is the growth rate when population was very low, had posterior median 0.10/yr (0.062–0.141), and the predicted carrying capacity was 16,200 pups (12,600–31,100).

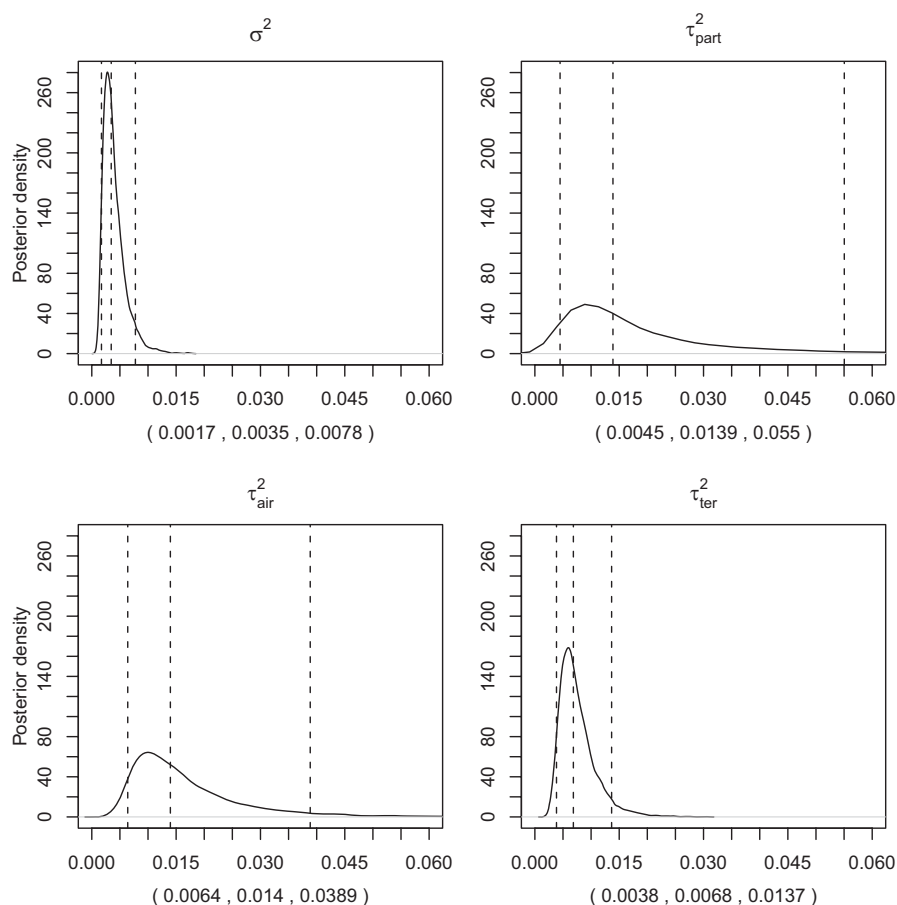


Figure 2. Posterior densities for error parameters: approximated curves were obtained with the R function density, median and 90% credible intervals are shown with vertical lines and values appear below each curve. The shown densities correspond to model 2 but estimates were similar for all models.

The models with density-dependence in adult survival (p) and recruitment (q) also accounted for the population trajectory closely (Fig. 1). The best fit was a model with density-dependence only in recruitment, in which $p = 0.87/\text{yr}$ while q declines from 0.20/yr in 1970 to 0.15/yr in 2010 (Table 2, Fig. 3). The model in which only adult survival varied, and in which both adult survival and recruitment varied, also produced good fits to the data, though with inferior predictive loss (Table 2). In all demographic models, the median p fell between 0.84 and 0.87 and the median q fell between 0.15 and 0.21 (Table 1, Fig. 3).

When Did the Population Have 100 Pups?

According to a backwards extrapolation of the logistic model, the population is most likely to have reached 100 pups in 1935, with credible intervals

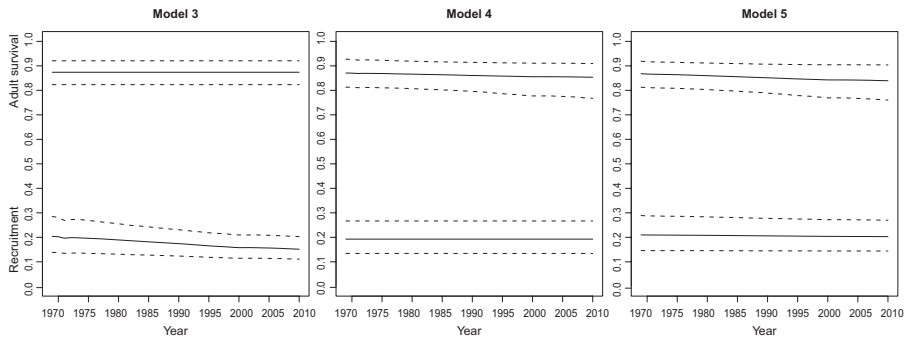


Figure 3. Recruitment and adult survival as a function of the year according to demographic models (see Table 2 for models description).

1915–1945 (Fig. 1). Alternatively, assuming that population growth was 0.078/yr—as estimated for 1969–1982 by the regression model—the population was 100 pups in 1927 (credible intervals 1895–1939).

DISCUSSION

The elephant seal population at Península Valdés increased rapidly from the mid-1960s through the 1990s, but has essentially stabilized over the past 10 yr. Piecewise regression and the Ricker model concur that the observed annual rate of population growth was 8–10%/yr prior to 1980, but <1%/yr during the past decade.

We can fit demographic models incorporating density-dependence that account for this reduction in growth. The initial rate of 8%/yr is accommodated with adult female survival of 0.87/yr and female recruitment of 0.20/yr. Both rates are within published ranges, matching closely, for example, the life table of McCann (1985), for South Georgia, but higher than rates given by McMahan *et al.* (2003) for Marion and Macquarie islands. Adult female survival at Península Valdés averaged 0.85 over 7 yr (1991–1997), but was >0.86/yr in most years (Pistorius *et al.* 2004). These comparisons serve only as illustrations, not to validate the models, since we have used these same sources to elicit prior distributions.

Density-dependent reduction in survival and recruitment that would be required to reduce population growth to near zero also falls within published ranges. For example, the model with density-dependence acting only on recruitment accounts for the stabilization of the population with the annual rate falling from 0.20 to 0.15/yr; McMahan *et al.* (2003) give the equivalent recruitment rate (half the survivorship to age 4) as low as 0.16/yr at Marion Island, but 0.23/yr at Macquarie. Alternatively, a reduction in adult survival from 0.87/yr to 0.84/yr would stabilize the population, and McMahan *et al.* (2003) and Pistorius *et al.* (2004) reported adult survival rates well below 0.84, sometimes below 0.80/yr.

Evidence for density dependence has been evaluated in other pinniped populations (McMahan *et al.* 2009, Rotella *et al.* 2009). In our study, there is no need to invoke immigration in the early years to account for high population growth, and no need to consider loss of immigration in the subsequent stabilization. The entire population trajectory since 1969 can be explained by local density-dependence in

recruitment, survival, or both. This is only a statement of plausibility: our results do not discount immigration, as we do not have enough evidence on demographic rates to test for density-dependence. But there is other evidence suggesting that interchange between the nearest large colony, South Georgia, and Península Valdés is rare. Mitochondrial DNA and morphometric characters indicate significant differentiation between the populations and, though genetic analyses suggest the possibility of some male-mediated gene flow (Hoelzel *et al.* 2001), the rate is low (Slade *et al.* 1998). Individually-tagged seals suggest little immigration from South Georgia to Patagonia (Lewis *et al.* 2006), and juveniles tracked by satellite from South Georgia have not visited Península Valdés, though the opposite has happened (Campagna *et al.* 2006). There is some interchange between Península Valdés and the much smaller Malvinas colony (Lewis *et al.* 2006), but this is unlikely to influence the population trend of Península Valdés.

Our model identified recruitment at age 4 as the most likely to account for the observed decline in population growth. Since our recruitment term subsumes fecundity with juvenile survivorship, we cannot determine which is most responsible for density-dependence. Other studies of large mammals, though, point to juvenile survivorship, since it is highly responsive to density (Gaillard *et al.* 2000, Eberhard 2002), and previous studies of elephant seals identify juvenile survivorship as highly variable (Le Boeuf *et al.* 1994, McMahon *et al.* 2005). Indeed, fecundity can never be higher than one in pinnipeds and seldom appears too much below in mature females, while juvenile survival varies more than two-fold from site to site and from cohort to cohort. On the other hand, although a small variance around the age at first breeding is unlikely to alter our general results, the model could not be applied to assess the effect of changes in age at sexual maturity, a demographic variable that could have a major impact on populations with negative growth (Pistorious *et al.* 2001, McMahon *et al.* 2003).

State space models with Bayesian estimation provide a flexible framework for modeling census data, accounting for observation and process error (Clark and Bjørnstad 2004, Buckland *et al.* 2004, Clark *et al.* 2005, Dennis *et al.* 2006). Bayesian estimation also allowed us to combine different census methods and estimate different errors for each. Although such models usually require many parameters in age-structured data, the assumption that age at first breeding is 4 yr (for virtually all females), along with informative priors, allows us to confront empirical and demographic models of population growth. We compared models using two different criteria with similar conclusions. DIC is based on penalized likelihoods and is one of the most used criteria for model selection with Bayesian estimation. However, there is no consensus on how to use DIC with missing data (Spiegelhalter *et al.* 2002, Celeux *et al.* 2006) and it provides very similar values for all models in our case. Predictive loss, on the other hand, allows us to rank the models according to their capability for predicting the actual data set.

There is no other southern elephant seal colony that compares in demographic trends with the Península Valdés population, as no other colony has been expanding continuously over decades. A better comparison can be made with the northern counterpart, as there are several recent colonies of northern elephant seals that have been growing steadily. For example, at the Año Nuevo colony, California, the annual growth rate during its early phase of growth was 12%–30%, higher than we observed at Península Valdés (Le Boeuf *et al.* 2011). Rates so high cannot be sustained by internal recruitment alone, and individually tagged seals at Año Nuevo demonstrated that there were many immigrants from large colonies to the south. Like the Península

Valdés colony, the population at Año Nuevo increased for decades before leveling off in 1995; however, the decline in population growth at Año Nuevo is most likely due to a reduction in the rate of immigration, not due to lower recruitment or survival (Le Bouef *et al.* 2011). Año Nuevo is only 200–400 km from several larger colonies to the south; in contrast, Península Valdés is isolated, with the nearest larger colony of southern elephant seals >2,000 km away at South Georgia Island and the much smaller Malvinas colony also >1,000 km distant.

The second main goal of this study was to estimate a founding date for the Península Valdés colony. Model results suggest a founding event between the turn of the century and 1940, with little subsequent immigration. As in the case of density-dependence, this is a plausibility argument, since we do not have censuses prior to 1970. There is other evidence, though, to suggest that the elephant seal colony of Península Valdés was established in the early decades of the 20th century. Naturalists from the 19th century report elephant seals in Argentina, although they do not mention Península Valdés (D'Orbigny 1998). There was a large sealing industry at the peninsula during the 1920–1960s, targeting South American sea lions, *Otaria byronia* (Crespo and Pedraza 1991). Hundreds of thousands of animals were harvested for skin and blubber. We were able to study meticulous records kept by the sealers as well as interview several of them. Very few elephant seals were present during these times, and were only killed as an exceptional practice (Sebastián Machinea, personal communication in the mid-1980s²). Since elephant seal blubber is a valuable source of oil, it seems unlikely there could have been many present, else they would have formed an important part of the hunt. The earliest published accounts of southern elephant seal pups on the Argentine coast appeared after 1950, and though none give numbers for the entire area of present distribution, they all suggest the colony was small (Carrara 1952, Conway 1965, Daciuck 1973, Le Bouef and Petrinovich 1974). Taken together, demographic models and casual observations suggest a small population early in the 20th century and a rapid increase starting in the 1960s.

Accepting the assertion that density-dependent decrease in survival or recruitment has led to the Peninsula Valdés elephant seal colony leveling off in population size in the past decade, we are left with the question about the process responsible. We have not detected any increase in the number of dead pups in the colony, so we do not believe that pup mortality has increased (Campagna and Lewis, unpublished data). On the other hand, we have observed female groups without males in the northern part of Península Valdés. We have wondered whether females fail to become pregnant there now, perhaps reducing recruitment, although females could move to other beaches after weaning to mate or adopt alternative mating strategies (*e.g.*, de Bruyn *et al.* 2011).

Other explanations would be based on food supplies. This mechanism has been discussed for other populations, see for example McMahon *et al.* (2003) and Pistorius *et al.* (2008). Elephant seals from the Peninsula feed along ocean fronts associated with the Malvinas and Brazil currents (Campagna *et al.* 2007, Rivas and Pisoni 2010). These productive conditions were probably in place prior to the 20th century, and we have found no reference to recent changes. In the absence of oceanographic changes, we are left with the possibility that seals exerted sufficient predation pressure to reduce their own food supply over the past 40 yr. This would be population regulation in the most classic sense.

²Contact Claudio Campagna and Mirtha Lewis for details about the interview.

Our census effort at Península Valdés spanned about two and a half decades, but partial previous counts from other authors allow coverage of a significant proportion of the history of the colony in the area. The relative isolation of the southern elephant seal colonies, compared to that of the northern species, and the extreme northern latitude of the Península Valdés colony for a subantarctic seal, provides an opportunity to study populations that may depend entirely on their ability to replace themselves through time. This makes them vulnerable to threats and physical changes operating at the regional basis, allowing the partitioning of threats for the temperate and cold oceans of the southern hemisphere, for which each circumpolar colony may act as an indicator. Each southern elephant seal colony forages in frontal areas of regional relevance, with the Patagonian shelf break and the Argentine Basin the most relevant for the Patagonian seals of Península Valdés (Falabella *et al.* 2009). The shelf break front of Patagonia is unique in its dependence on the bathymetry of the shelf and the circulation of the Malvinas Current, making its productivity seasonally predictable. It is thus unlikely that the density-dependence growth of this colony is explained on changes in regional productivity.

In summary, we argue that the colony of elephant seals at Península Valdés is recent, consolidated in the past century, and largely self-sustaining. No other southern elephant seal colony has behaved like the Patagonian one: all were well-established when discovered and have mostly been declining. Our censuses and modeling conclusions suggest that the size of the colony is regulated independently of the large colony at South Georgia. We suggest that stabilizing density-dependence is operating and predict that the population will produce close to 15,000–16,000 pups until other large changes in the environment intervene. This puts us in a position to detect future human impacts on the population, such as competition from deep sea fisheries or climate change altering marine productivity. The elephant seal is relatively easy to count, and thus functions as a sentinel about changes in the pelagic marine environment, otherwise distant and difficult to study. Since this is the most accessible breeding colony of southern elephant seals in the world, for both tourists and scientists, we have a long-term interest in monitoring its status and predicting its future growth.

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