



## Postharvesting population dynamics of the South American sea lion (*Otaria byronia*) in the southwestern Atlantic

VALENTINA FRANCO-TRECU,<sup>1</sup> Proyecto Pinnípedos, Sección Etología, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; MASSIMILIANO DRAGO, Departamento de Ecología & Evolución, Centro Universitario Regional Este (CURE), Universidad de la República, Maldonado, Uruguay; CLAUDIA BALADÁN, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; MATEO D. GARCÍA-OLAZÁBAL, Departamento de Ecología & Evolución, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; ENRIQUE A. CRESPO, Laboratorio de Mamíferos Marinos, Centro Nacional Patagónico (CONICET), Puerto Madryn, Chubut, Argentina and Universidad Nacional de la Patagonia, Puerto Madryn, Chubut, Argentina; LUIS CARDONA, Department of Animal Biology and Irbio, Faculty of Biology, University of Barcelona, Barcelona, Spain; and PABLO INCHAUSTI, Departamento de Ecología & Evolución, Centro Universitario Regional Este (CURE), Universidad de la República, Maldonado, Uruguay.

### ABSTRACT

Many pinniped populations precipitously declined during the 19th and 20th centuries due to overharvesting. In Uruguay, the South American sea lion (SASL) was harvested until 1986. Birth rates in two nearby breeding colonies have had opposite trends for at least 20 yr. We assessed different mechanisms that could explain opposite trends in birth rates in the two SASL colonies. We compared feeding habits ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) of breeding females, birth mass, individual growth rate and early survival of pups and the social structure between colonies. Breeding females from the two colonies did not differ in their feeding habits. However, male and female pups grew faster but had a lower survival in the second month in the smallest colony. We found differences in the social structures, with a higher proportion of males in the smallest colony. The latter is important because peripheral SASL males may abduct and kill pups, which may explain the lower survival of pups in smaller colonies. We believe that the cumulative effects of population extractions have lowered the local SASL population size and disrupted its social structure to the point where Allee-like effects could become important and hamper the recovery of the Uruguayan SASL population.

Key words: population dynamics, harvesting, behavior, population recovery, Allee effect.

Overfishing and commercial exploitation have caused the decline of many populations and even the extinction of tens of marine species (Dulvy *et al.* 2003, Davidson *et al.* 2012). Marine top predators have been strongly affected by several global

<sup>1</sup>Corresponding author (e-mail: pinnipedosuy@gmail.com).

anthropogenic drivers and approximately 25% of marine mammal species are currently classified as threatened (IUCN 2013). The relatively high level of threat of marine mammal species has been associated with their commercial exploitation in the past which, combined with their low population growth rates and relatively small population sizes, brought many marine mammal species to the brink of extinction (Costa *et al.* 2006). Once commercial exploitation finished or became regulated, populations were to recover to preharvesting levels or at least to levels of abundance consistent with available food resources and suitable breeding habitats. The recovery of a population released from harvesting pressure requires it to attain a high birth rate (which depends on both the breeding success and pup survival) and high adult survival rates. However, the capacity of impacted marine mammal populations to recover from low, postharvesting abundances has been jeopardized by the joint impact of habitat degradation and overfishing on the functioning of marine food webs and ecosystems in many coastal areas used by these species (Springer *et al.* 2003, Millenium-Ecosystem-Assessment 2005, Bulleri and Chapman 2010, Williamson *et al.* 2014)

Populations of many pinniped species declined precipitously during the 19th and 20th centuries due to overharvesting (Bonner 1982, Gerber and Hilborn 2001), including the South American sea lion (*Otaria byronia*) because many of its local populations suffered great reductions in their sizes (Crespo and Pedraza 1991, Sielfeld 1999). Since the end of commercial harvesting, South American sea lion populations in the South Atlantic Ocean have shown different responses. The population from northern Patagonia remained stable for almost 30 yr until it started to grow in 1990 (Dans *et al.* 2004). A similar trajectory was observed in the Falkland Islands (Islas Malvinas) population, where *ca.* 44,000 South American sea lions were killed between 1935 and 1962, and the local South American sea lion population has increased at a rate of  $\sim 3.8\%$  per year between 1995 and 2003 (Thompson *et al.* 2005). In contrast, despite the end of the commercial exploitation of the South American sea lion in 1986 at Isla de Lobos, the number of pups born each year has continued to decline, reaching approximately 1,200 pups born in 2000 (Ponce de León 2000), a figure that is roughly 25% of those born in 1956 before the start of the harvest (Vaz-Ferreira *et al.* 1984). More than 47,000 pups were harvested between 1963 and 1984 at Isla de Lobos (Ponce de León 2000), and even though harvesting prior to 1963 was unknown, 400 pups were harvested from this rookery between 1985 and 1986 (Ponce de León 2000). Regardless of the observed decline in the birth rate at Isla de Lobos between 1956 and 2000, 429 juveniles (285 females,  $\bar{x} = 20$ ,  $SD = 17$ /yr) were further captured and sold to zoos and aquariums between 1996 and 2008 (DINARA 2008, 2010). Nevertheless, it remains unclear why the Isla de Lobos South American sea lion population has failed to recover after the end of the intense harvesting in 1986.

South American sea lions breed in two colonies separated by *ca.* 70 km along the Uruguayan coast (Fig.1): Isla de Lobos (currently the smaller rockery), where birth rates have steadily declined between 1995 and 2004, and Cabo Polonio/Valizas, where birth rates have steadily increased since 1995 (Páez 2006). Despite these contrasting trends, the overall South American sea lion population in Uruguay supposedly has declined at an average annual rate of 1.73% in 1995–2007 (Páez 2006, DINARA 2012). Genetic analyses for the southwest Atlantic have showed that the South American sea lion functions as a single population with relatively high female philopatry (Feijoo *et al.* 2011). However, at a more local

level, further genetic analyses suggest that the two Uruguayan colonies are part of a single breeding population (Feijoo 2009). Assuming that South American sea lion females could potentially recruit indistinctly to either colony in Uruguay when first breeding, it is still unclear why the postharvesting birth rates have differed between Cabo Polonio and Isla de Lobos.

Here, we assess different mechanisms that could explain the contrasting trends in birth rates in two South American sea lion colonies in Uruguay. Given that females are highly dependent on local food resources (Riet-Saprizza *et al.* 2013), we hypothesize that differences in food availability to females of each colony lead to differences in mass at birth, early growth rates and early survival rates of pups. Our second hypothesis is that differences in the population structure between colonies could lead to a different early survival of pups between the two colonies. Although the South American sea lion does not have terrestrial predators, harassment by conspecifics peripheral males (adults and subadults) may lead to high pup mortality (Campagna *et al.* 1992, Drago *et al.* 2011). We tested these hypotheses using data on the feeding habits of females, birth mass, individual growth rate and first month survival of pups, and the social structures in the two sea lion breeding colonies in Uruguay. From these hypotheses, we predict (1) that differences in the female pre-partum feeding habits could lead to differences in the mass at birth and individual growth rates between colonies, (2) that higher mass at birth and individual growth rates should be associated with higher pup survival rates, and (3) that higher proportion of peripheral males (adults and subadults) in smaller colonies would be associated with higher pup mortality (McMahon *et al.* 2000, Baker and Fowler 2009).

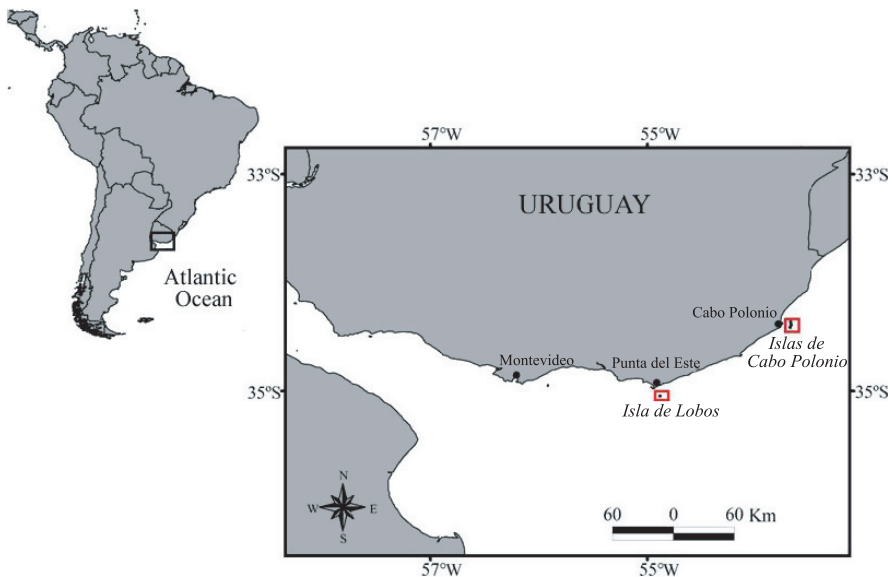


Figure 1. Breeding colonies of the South American sea lion (*Otaria byronia*) in Uruguay in Isla de Lobos and Cabo Polonio.

## MATERIALS AND METHODS

### *Study Area*

The South American sea lion rookeries on the Uruguayan continental shelf are the northernmost breeding sites of this species in the Atlantic Ocean. Isla de Lobos and Cabo Polonio (declared a Marine Protected Area by decree 337/2009), are located in the easternmost part of the Río de la Plata estuary and in the Atlantic Ocean, respectively (Fig. 1). These zones have a highly dynamic mixing regime resulting from the mixing of freshwater and the convergence of the Brazil and Falkland/Malvinas currents that generate a frontal regime of high primary productivity (Ortega and Martínez 2007). We worked in a breeding area located in the northwest part of Isla de Lobos, where *ca.* 90 pups are born each year (Trimble and Insley 2010) and in Isla Rasa, Cabo Polonio, where *ca.* 600 pups are born each summer (VF-T, unpublished data).

### *Data and Sample Collection*

At the beginning of the 2013 breeding season (January), we captured 88 and 151 randomly chosen newborn pups with a hoop net in Isla de Lobos and Cabo Polonio, respectively. All pups were identified with Allflex tags applied to both fore flippers, their standard length and weight ( $\pm 0.10$  kg) were measured, and their sex was registered. Whenever possible, we obtained 5 mL blood samples ( $n = 20$  in Isla de Lobos and  $n = 17$  in Cabo Polonio) from the caudal digital vein. Blood samples were preserved in sterile tubes and centrifuged in the field site and blood cells were stocked at  $-20^{\circ}\text{C}$  until further analyses. On the second week of January, we conducted four exhaustive counts in each colony, differentiating individuals by age class (adult males, subadult males, pups, juveniles and females). Breeding females were also counted, but their numbers were discarded because they could not be distinguished visually from juveniles of either sex. All terrestrial counts were conducted from short distances from reproductive areas using  $10 \times 50$  binoculars. Marked pups were recaptured, weighted and further blood samples were obtained in the third week of February using the method described above, except that only serum samples were retained for further analyses. During February and March, we carried out fortnightly scan samplings (Martin and Bateson 1991) in each colony to visually recapture the marked pups. Because during the first months of their lives South American sea lion pups exclusively feed on maternal milk, their isotope values can be used to investigate the adult females' foraging ecology (Drago *et al.* 2010b, Franco-Trecu *et al.* 2012). Furthermore, given that serum half-life in endotherms is 3–4 d and that of blood cells is 28–30 d (Hobson and Clark 1993, Hilderbrand *et al.* 1996), the isotopic value of blood cells collected just after birth and that of the serum collected 5–6 wk later can be used as proxies of the South American sea lion female diet in the prepartum and early lactation periods, respectively. All procedures of animal manipulation were submitted and approved by the Ethics Committee in Animal Experimentation of the Universidad de la República, Uruguay as valid according to the national laws in animal welfare.

### *Sample Treatment: Stable Isotope Analysis*

Feeding habits of the females with marked pups were studied using stable isotope ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) analyses based on the fact that prey-to-consumers isotopic

enrichment to change in a predictable manner according to the specific dietary fractionation of marine food chains (Hobson *et al.* 1994, Post 2002, Newsome *et al.* 2007).  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  denote the trophic position (Post 2002) and the feeding sources used by predators (DeNiro and Epstein 1978, Bearhop *et al.* 2004) at different temporal scales depending on the moment of production and the turnover rate of the tissue analyzed (Dalerum and Angerbjörn 2005).

Once thawed, blood cell and serum samples were dried at 60°C and grounded to a fine powder with mortar and pestle. Lipids were extracted with a chloroform/methanol (2:1) solution (Bligh and Dyer 1959) because they are depleted in  $^{13}\text{C}$  in comparison with other molecules, thus they could confound the results by decreasing the  $\delta^{13}\text{C}$  value (DeNiro and Epstein 1978). Nevertheless, since chemical extraction of lipids may lead to unpredictable changes in  $\delta^{15}\text{N}$  values due to the unintended removal of amino acids (Sotiropoulos *et al.* 2004, Ryan *et al.* 2012), we extracted them for carbon isotope analysis and used a nonextracted subsample for nitrogen determination.

Stable isotope analyses were carried out at the Scientific-Technical Services of the University of Barcelona, Spain. Stable isotope ratios are expressed in delta ( $\delta$ ) notation as parts per thousand (‰), and are reported and defined as:  $\delta^iX = [(^iX/^iX)_{\text{sample}} / (^iX/^iX)_{\text{standard}}] - 1$ , where  $^iX$  is the heavier isotope ( $^{13}\text{C}$  or  $^{15}\text{N}$ ), and  $^iX$  is the lighter isotope ( $^{12}\text{C}$  or  $^{14}\text{N}$ ) in the analytical sample and international measurement standard (Bond and Hobson 2012); reference standards were the Vienna Pee Dee Belemnite (VPDB) calcium carbonate for  $\delta^{13}\text{C}$  and atmospheric nitrogen (air) for  $\delta^{15}\text{N}$ . Secondary isotopic reference materials of known  $^{13}\text{C}/^{12}\text{C}$  ratios, as given by the International Atomic Energy Agency (IAEA, Vienna, Austria), namely polyethylene (IAEA CH<sub>7</sub>,  $\delta^{13}\text{C} = -31.8\text{‰}$ ), graphite (IAEA USGS<sub>24</sub>,  $\delta^{13}\text{C} = -16.1\text{‰}$ ) and sucrose (IAEA CH<sub>6</sub>,  $\delta^{13}\text{C} = -10.4\text{‰}$ ), were used for calibration to a precision of 0.2‰. For nitrogen, secondary isotopic reference materials of known  $^{15}\text{N}/^{14}\text{N}$  ratios, namely (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> (IAEA N<sub>1</sub>,  $\delta^{15}\text{N} = +0.4\text{‰}$  and IAEA N<sub>2</sub>,  $\delta^{15}\text{N} = +20.3\text{‰}$ ) and KNO<sub>3</sub> (IAEA NO<sub>3</sub>,  $\delta^{15}\text{N} = +4.7\text{‰}$ ) were used to a precision of 0.3‰.

### Data Analysis

The specific growth rate (*SGR*), expressed as percentage of body weight gained or lost per day (%/d), was calculated according to the following expression:  $SGR = [\ln(W_{t+d}/W_{t0}) * d^{-1}] \times 100$ , where  $W_{t0}$  is the initial body weight (kg) of the pup,  $W_{t+d}$  is the final body weight (kg) after  $d$  days. We compared differences in the  $W_{t0}$ , *SGR*, and blood cells and serum stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) between colonies using two way ANOVAs that included colony and sex (because the South American sea lion is a sexually dimorphic species) as categorical explanatory variables and their interaction. When possible, we simplified the initial statistical models by the stepwise removal of terms without any significant effects. We used the Akaike Information Criterion (AIC) to select the most parsimonious model from a priori set of plausible statistical models. Models with  $AIC > 2$  in relation to the AIC of the model with lowest AIC tend to have little empirical support (Bolker 2007). We used separate analyses of covariance to evaluate whether pups'  $W_{t0}$  was related with  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  female's blood cell isotopic values and whether these relations varied depending on pup sex and colony. These analyses allowed corroborating whether a female's diet during prepartum affected her newborn pup's mass. The same procedure was used to determine whether pup's *SGR* was related with serum  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (as early lactation diet) and the extent to which these relationships varied depending on the

pup sex and colony. Finally, we compared the population structure between colonies by comparing the proportions of adult and subadult males using the chi-squared test for multiple proportions. All statistical analyses were carried out in free software R 3.0.2 (R Development Core Team 2013).

We estimated the monthly pup survival rate for each sex and breeding colony using the standard Capture, Mark and Recapture method (Cormack-Jolly-Seber model; Williams *et al.* 2002) for the fortnightly scans that yielded a presence-absence matrix for 239 pups over three months. We performed the standard goodness of fit test of Cormack-Jolly-Seber model using the software UCARE 2.2 (Choquet *et al.* 2009) and assessed overdispersion using the bootstrap method according to Cook and White (2006). We formulated 19 *a priori* statistical models (Table 3) involving whether monthly survival and the recapture probability varied between colonies, time, and/or sexes and with none of them. Model selection based on the Akaike Information Criterion was performed as described before after correcting for overdispersion as needed. All models of monthly survival were fitted using the program MARK 6.0 (White and Burnham 1999).

## RESULTS

The average  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in blood cells from newborn pups (Fig. 2) did not significantly differ between either colonies or sexes (models 9 and 11, Table 1). The mean  $\pm$  SD values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in blood cells for Cabo Polonio were  $-16.3 \pm 0.3$  and  $19.9 \pm 0.3$ , while for Isla de Lobos were  $-16.1 \pm 0.3$  and  $19.9 \pm 0.5$ , respectively (Fig. 2). The same was true for the  $\delta^{13}\text{C}$  value in serum

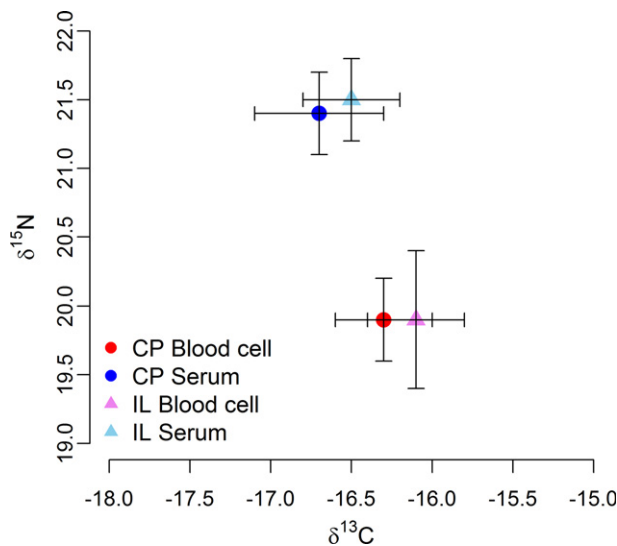


Figure 2. Biplot of the isotopic contents of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of blood cells (red and pink) and serum (blue and skyblue) of the South American sea lion pups (*Otaria byronia*), from Cabo Polonio (CP, circles) and Isla de Lobos (IL, triangles). Error bars correspond to standard deviations of each variable.

Table 1. Two way ANOVA for the initial mass ( $W_{t0}$ ), the specific growth rate ( $SGR$ ), and the isotopic value ( $\delta^{13}C$  and  $\delta^{15}N$ ) in serum (s) and red blood cells (rc) of South American sea lion (*Otaria byronita*) pups, with sex and breeding colony as explanatory variables. The table shows the set of models formulated for each analysis that were simplified on the basis of the  $\Delta AIC < 2$ . The selected models (lowest AIC) for each analysis is highlighted in gray. Reference levels are Isla de Lobos (IL) for colony and male for sex.

|    | Model   | Intercept           | Colony (IL)       | Sex (male)        | Colony*Sex    | AIC    |
|----|---|---------------------|-------------------|-------------------|---------------|--------|
| 1  | $W_{t0} \sim \text{Colony} * \text{Sex}$            | 14.30 ( $<<0.01$ )  | -0.97 (0.08)      | 1.68 (0.002)      | 0.92 (0.26)   | 403.86 |
| 2  | $W_{t0} \sim \text{Colony} + \text{Sex}$            | 14.20 ( $<<0.01$ )  | -0.56 (0.17)      | 2.05 ( $<<0.01$ ) | —             | 403.15 |
| 3  | $W_{t0} \sim \text{Sex}$                            | 13.90 ( $<<0.01$ )  | —                 | 2.10 ( $<<0.01$ ) | —             | 403.06 |
| 4  | $SGR \sim \text{Colony} * \text{Sex}$               | 0.75 ( $<<0.01$ )   | 0.44 (0.027)      | 0.28 (0.15)       | -0.08 (0.75)  | 39.67  |
| 5  | $SGR \sim \text{Colony} + \text{Sex}$               | 0.77 ( $<<0.01$ )   | 0.39 ( $<<0.01$ ) | 0.23 (0.08)       | —             | 37.78  |
| 6  | $SGR \sim \text{Colony}$                            | 0.91 ( $<<0.01$ )   | 0.37 ( $<<0.01$ ) | —                 | —             | 39.23  |
| 7  | $\delta^{13}C_{rc} \sim \text{Colony} * \text{Sex}$ | -16.40 ( $<<0.01$ ) | 0.21 (0.16)       | 0.14 (0.37)       | -0.07 (0.73)  | 20.03  |
| 8  | $\delta^{13}C_{rc} \sim \text{Colony} + \text{Sex}$ | -16.40 ( $<<0.01$ ) | 0.18 (0.08)       | 0.10 (0.32)       | —             | 18.16  |
| 9  | $\delta^{13}C_{rc} \sim \text{Colony}$              | -16.30 ( $<<0.01$ ) | 0.15 (0.12)       | —                 | —             | 17.23  |
| 10 | $\delta^{15}N_{rc} \sim \text{Colony} * \text{Sex}$ | 19.90 ( $<<0.01$ )  | 0.03 (0.90)       | -0.08 (0.71)      | -0.009 (0.98) | 48.84  |
| 11 | $\delta^{15}N_{rc} \sim \text{Colony} + \text{Sex}$ | 19.90 ( $<<0.01$ )  | 0.02 (0.88)       | -0.09 (0.55)      | —             | 46.84  |
| 12 | $\delta^{15}N_{rc} \sim \text{Colony} * \text{Sex}$ | -16.70 ( $<<0.01$ ) | 0.18 (0.33)       | 0.09 (0.60)       | -0.13 (0.58)  | 36.53  |
| 13 | $\delta^{13}C_s \sim \text{Colony} + \text{Sex}$    | -16.60 ( $<<0.01$ ) | 0.11 (0.39)       | 0.01 (0.89)       | —             | 34.87  |
| 14 | $\delta^{15}N_s \sim \text{Colony} * \text{Sex}$    | 21.54 ( $<<0.01$ )  | 0.05 (0.7)        | -0.22 (0.14)      | 0.02 (0.91)   | 20.64  |
| 15 | $\delta^{15}N_s \sim \text{Colony} + \text{Sex}$    | 21.53 ( $<<0.01$ )  | 0.07 (0.49)       | -0.21 (0.04)      | —             | 18.66  |
| 16 | $\delta^{15}N_s \sim \text{Sex}$                    | 21.57 ( $<<0.01$ )  | —                 | -0.22 (0.03)      | —             | 17.19  |

(early lactation) (model 13, Table 1), but the  $\delta^{15}\text{N}$  values were significantly higher in female pups (model 16, Table 1). The mean values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  serum in Cabo Polonio were  $-16.7 \pm 0.4$  and  $21.4 \pm 0.3$ , while in Isla de Lobos they were  $-16.5 \pm 0.3$  and  $21.5 \pm 0.3$ , respectively (Fig. 2). Although the birth mass of male pups ( $0 \pm \text{SD}$ :  $16.0 \pm 2.1$ ) was significantly higher than female pups ( $13.9 \pm 1.8$ ) in both colonies, there was no significant difference between colonies (Cabo Polonio =  $15.2 \pm 2.07$ , Isla de Lobos =  $14.5 \pm 2.4$ ) (model 3, Table 1). The mean  $\pm$  SD pup specific growth rate was significantly higher in Isla de Lobos ( $1.28 \pm 0.4$ ) than in Cabo Polonio ( $0.91 \pm 0.4$ ), being marginally higher for male pups (model 5, Table 1, Fig. 3). None of the statistical models selected (Table 1) had significant interactions between sex and colony. Pup's initial mass was marginally related to the red blood cell  $\delta^{13}\text{C}$  (prepartum), and it increased for higher values of red blood cell  $\delta^{15}\text{N}$  (Table 2, Fig. 4b). In turn, pup *SGR* was not related to the serum  $\delta^{13}\text{C}$  (postpartum period). However, *SGR* decreased for higher values of  $\delta^{15}\text{N}$ , being significantly higher in Isla de Lobos (Table 2, Fig. 4a).

The most parsimonious model of pup monthly survival included temporal variation (months) and colony (Table 3, Fig. 5) and received 68% of the empirical support from the data. Prior to comparing these models, we had assessed the goodness of fit of the data to the saturated model and found it acceptable ( $P = 0.748$ ), according

*Table 2.* Analyses of covariance of the initial mass ( $W_{i0}$ ) and specific growth rate (*SGR*) as a function of the isotopic value of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in serum and red blood cells of South American sea lion pups (*Otaria byronia*), with sex and breeding colony and their interaction as categorical variables. The *F*-values (and its associated *P*-value) for each explanatory variable and interaction (columns) are shown for the entire set of statistical models for each response variable (rows). The initial statistical models and the criteria for model simplification are explained in the main text.

|            | $\delta^{13}\text{C}$ red<br>blood | Colony        | Sex         | Colony*Sex  |
|------------|------------------------------------|---------------|-------------|-------------|
| $W_{i0}$   | 4.12 (0.05)                        | 1.4 (0.25)    | 2.95 (0.09) | 1.86 (0.18) |
|            | 4.00 (0.05)                        | 1.36 (0.25)   | 2.87 (0.10) | –           |
|            | 3.84 (0.06)                        | –             | 1.80 (0.19) | –           |
|            | 3.78 (0.06)                        | 1.28 (0.26)   | –           | –           |
|            | 3.76 (0.06)                        | –             | –           | –           |
|            | $\delta^{15}\text{N}$ red<br>blood | Colony        | Sex         | Colony*Sex  |
| $W_{i0}$   | 7.81 (0.01)                        | 4.75 (0.04)   | 4.34 (0.05) | 2.03 (0.16) |
|            | 7.56 (0.01)                        | 4.59 (0.04)   | 4.20 (0.05) | –           |
|            | $\delta^{13}\text{C}$ serum        | Colony        | Sex         | Colony*Sex  |
| <i>SGR</i> | 0.29 (0.59)                        | 10.1 (0.003)  | 2.14 (0.15) | 0.18 (0.68) |
|            | 0.31 (0.58)                        | 10.3 (0.003)  | 2.20 (0.15) | –           |
|            | 0.29 (0.60)                        | 8.50 (0.006)  | –           | –           |
|            | $\delta^{15}\text{N}$ serum        | Colony        | Sex         | Colony*Sex  |
| <i>SGR</i> | 11.8 (0.001)                       | 15.5 (0.0004) | 0.24 (0.63) | 0.09 (0.77) |
|            | 12.2 (0.001)                       | 15.9 (0.0003) | 0.24 (0.63) | –           |
|            | 12.3 (0.001)                       | 15.9 (0.0003) | –           | –           |



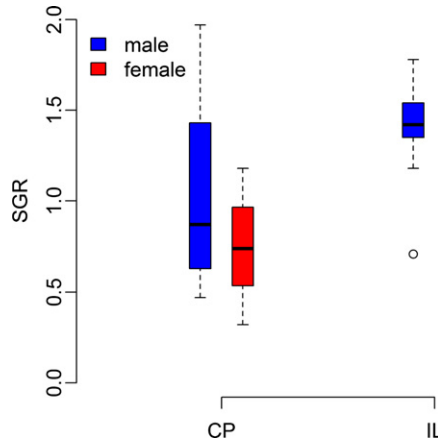


Figure 3. Boxplots for the specific growth rate (*SGR*) of pups of each sex of the South American sea lion in the breeding colonies of Cabo Polonio (CP) and Isla de Lobos (IL).

to the criteria of Choquet *et al.* (2009). In the selected model (Table 3, Fig. 5), while the first month survival rate of pups was practically the same in both colonies (Cabo Polonio: 0.82, CI = 0.58–0.99; Isla de Lobos: 0.86, CI = 0.62–0.99), there are important differences in the pup monthly survival between colonies during the second month (Cabo Polonio: 0.70, CI = 0.48–0.99; Isla de Lobos: 0.32, CI = 0.19–0.51).

Finally, the percentages of males (adults + subadults) obtained from the terrestrial counts in each colony differed significantly between colonies ( $\chi^2 = 26.045$ ,  $df = 4$ ,  $P = 3.0 \times 10^{-5}$ ), being  $17\% \pm 2.3\%$  and  $36\% \pm 5.5\%$  in Cabo Polonio and Isla de Lobos, respectively.

## DISCUSSION

We found that breeding females from the two South American sea lion colonies in Uruguay did not differ in their feeding habits and that pups grew faster and had a lower survival in March in the smallest colony that also had the highest proportion of males.

In otariids, the pup growth rate is strongly influenced by their mothers' feeding habits through the energetic quality of the resources consumed and the frequency and duration of maternal attendances on land (Trillmich and Weissing 2006, Drago *et al.* 2010a). Among the prey consumed by SASL, Franco-Trecu *et al.* (2012) found that pelagic species in the Uruguayan continental shelf had lower values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  than benthic ones. Although potential pelagic prey of South American sea lion often contain a higher energy input than benthic ones due to their higher lipid content (Drago *et al.* 2009), gathering pelagic prey typically requires longer foraging trips and higher search effort for lactating South American sea lion mothers. Therefore, the negative relation between the *SGR* and the  $\delta^{15}\text{N}$  suggests that higher pup *SGR* were attained whenever pelagic prey predominated female diet (Drago *et al.* 2010a). However, the feeding habits of breeding South American sea lion females did not differ between colonies, thus suggesting that they fed on prey at similar trophic levels in food webs sustained by the same primary producers (Fig. 2). The latter is expected

Table 3. Models of monthly (February, March) survival and recapture ( $p$ ) probabilities for the South American sea lion pups (*Otaria byronia*) in Uruguay, where both parameters could vary between sexes, breeding colonies (Cabo Polonio and Isla de Lobos), over time ( $t$ ; February, March) or being constant (.) (or combinations thereof). The Akaike Information Criterion (AIC), the difference between each model AIC and the smallest AIC of all models considered ( $\Delta$ AICc), the AICc weight, and the number of parameter estimated are shown for each model.

|    | Model   | AICc   | $\Delta$ AICc | AICc weights | Parameters |
|----|---|--------|---------------|--------------|------------|
| 1  | survival (colony, $t$ ), $p$ (.)                    | 455.99 | 0             | 0.68         | 5          |
| 2  | survival (colony, $t$ ), $p$ (sex,colony)           | 458.45 | 2.45          | 0.2          | 8          |
| 3  | survival (colony,sex, $t$ ), $p$ (.)                | 460.05 | 4.06          | 0.09         | 9          |
| 4  | survival (sex,colony, $t$ ), $p$ (sex,colony, $t$ ) | 465.67 | 9.68          | 0.01         | 12         |
| 5  | survival (sex,colony), $p$ (.)                      | 465.91 | 9.92          | 0            | 5          |
| 6  | survival (colony), $p$ (.)                          | 465.97 | 9.98          | 0            | 3          |
| 7  | survival (.), $p$ (.)                               | 466.81 | 10.82         | 0            | 2          |
| 8  | survival (sex,colony), $p$ (colony)                 | 466.96 | 10.97         | 0            | 6          |
| 9  | survival (colony), $p$ (colony)                     | 467.07 | 11.08         | 0            | 4          |
| 10 | survival (sex,colony), $p$ (sex)                    | 467.15 | 11.15         | 0            | 6          |
| 11 | survival (colony), $p$ (sex)                        | 467.48 | 11.49         | 0            | 4          |
| 12 | survival (.), $p$ (colony)                          | 467.92 | 11.93         | 0            | 3          |
| 13 | survival (colony), $p$ (sex,colony)                 | 468.1  | 12.11         | 0            | 6          |
| 14 | survival (.), $p$ (sex)                             | 468.3  | 12.31         | 0            | 3          |
| 15 | survival (.), $p$ (sex,colony)                      | 468.69 | 12.69         | 0            | 5          |
| 16 | survival (sex), $p$ (.)                             | 468.73 | 12.74         | 0            | 3          |
| 17 | survival (sex), $p$ (colony)                        | 469.86 | 13.86         | 0            | 4          |
| 18 | survival (sex), $p$ (sex)                           | 470.04 | 14.04         | 0            | 4          |
| 19 | survival (sex,colony), $p$ (sex,colony)             | 470.7  | 14.71         | 0            | 8          |

since the two South American sea lion breeding colonies are separated by only 70 km, a distance well within the range of female's foraging trips (39–136 Km, Riet-Sapriza *et al.* 2013). Had differences in South American sea lion females' feeding habits affected pup success, we would have expected to find significant relationships between the  $\delta^{15}\text{C}$  and  $\delta^{15}\text{N}$  values in blood cell and serum and the pup's body mass at birth and *SGR*, respectively. Thus, while differences in the foraging strategies of lactating females may explain differences in the pup growth rate, they could not account for differences between colonies in Uruguay. Thus, SASL females from Isla de Lobos may have lower costs to resources than those of Cabo Polonio, which may increase their efficiency of energy transfer and lead to higher pup growth rates (Trillmich and Weissing 2006). Even though the availability of trophic resources in areas surrounding each colony could differ, such differences might not necessarily be reflected in the isotopic values of pup serum and blood cells.

Drago *et al.* (2011) found that South American sea lion pups grew faster and had a lower survival in smaller colonies in northern Patagonia, even though the diet composition of females was unrelated to local population size. That is, pups both in Uruguay and northern Patagonia grew faster but had a lower survival where females had a higher per capita resource share due to lower local abundance. In both cases, the negative correlation between individual growth and pup early survival seems unrelated to the availability of trophic resources and changes in feeding habits and its causes must lie elsewhere. Drago *et al.* (2011) also found that the survival rate of pups increased with colony size and with the ratio pups to subadult males, and attributed

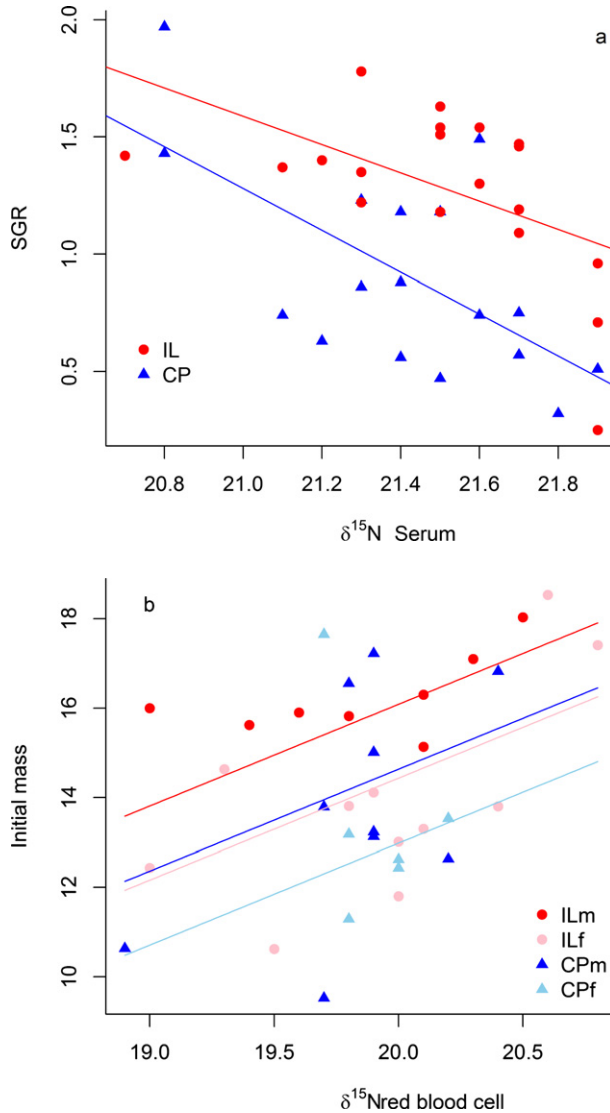


Figure 4. Relations between the (a) specific growth rate (SGR) and (b) the initial mass with the  $\delta^{15}\text{N}$  contents in serum and blood of the South American sea lion (*Otaria byronia*) pups (m: male; f: female) born in the two breeding colonies (CP: Cabo Polonio; IL: Isla de Lobos) in Uruguay. The straight lines correspond to the best fit lines of the selected models shown in Table 1.

the finding to Allee-like effects that could help explain the kinetics of recovery of local South American sea lion populations since the end of harvesting.

The differences in pup survival rates between the Uruguayan colonies can be explained by differences in neither female dietary habits nor the initial mass of the newborn pups. The higher pup survival and lower growth rates found in the largest

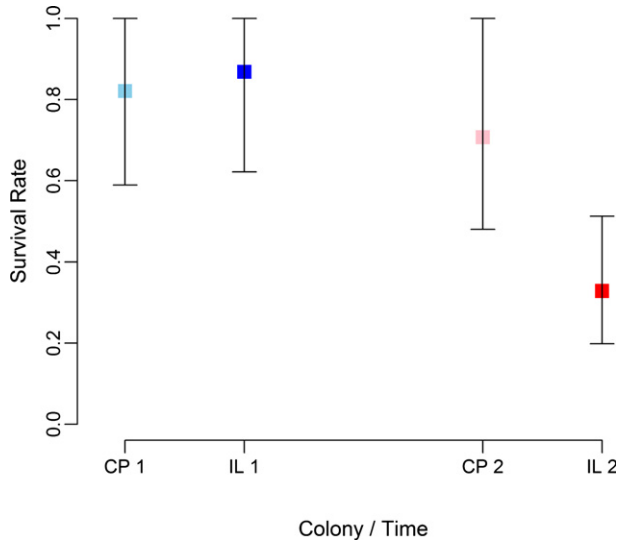


Figure 5. Monthly (February = 1 and March = 2) survival rates (and their 95% confidence interval) of South American sea lion (*Otaria byronia*) pups born in the two breeding colonies (CP: Cabo Polonio; IL: Isla de Lobos) in Uruguay.

Uruguayan colony could be explained if pups were born larger in Cabo Polonio, allowing them to withstand longer fasts between consecutive attendances of their mothers. Nevertheless, we did not find significant differences in the pup's masses at birth between colonies. Conversely, we did find differences in the social structure between the colonies, with a higher proportion of subadult and adult males in the smaller colony. An antisocial behavior (abduction and eventual killing of pups) of peripheral South American sea lion males has been reported (adults and subadults) in both Uruguayan (Vaz-Ferreira 1965, 1976) and Argentine colonies (Campagna *et al.* 1988). Given the differences in the social structures found between colonies, the antisocial behavior could point to infanticide as a likely cause for the higher pup mortality rates found in the smaller colony. Our results are then in agreement with those found in colonies of northern Patagonia and would imply that colony size is related to both SGR and early South American sea lion pup survival (Drago *et al.* 2011). Although SGR values were almost the same as in small and large colonies in Argentina (smaller colony:  $1.3\% \pm 0.7\%/d$  and larger colony:  $0.6\% \pm 0.6\%/d$ ) and Uruguay, pup survival rates reported by Drago *et al.* (2011) for Argentina were higher (0.91–0.97) than those estimated in Uruguay (lower and upper mean 0.32–0.86). However, these pup survival estimates cannot be directly compared because they were based on very different approaches (proportion of death animals in Argentina and capture-mark-recapture in Uruguay) and methods that do not jointly estimate survival and recapture probabilities generally yield biased survival rates (Williams *et al.* 2002).

The birth rate of the smallest South American sea lion colony (Isla de Lobos) in Uruguay has shown a historical decline since 1956 (Ponce de León 2000, Páez 2006). While the low birth rates until the 1980s probably resulted from the impact of pup harvesting, the recovery of the Isla de Lobos population would have been expected

30 yr after the end of harvesting. However, the Isla de Lobos colony had a lower early pup survival and a higher proportion of males than Cabo Polonio. We believe that the cumulative effects of population extractions (pup harvesting and zoo and aquaria sales) could have not only lowered the local population size, but also disrupted its social structure to the point where Allee-like effects could have become important and have hampered the postharvesting recovery of South American sea lion in the southwest Atlantic.

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