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ARTICLE

Breeding season of the South American fur seal (*Arctocephalus australis*, Otariidae: Carnivora): New data for establishing independent evolutionary histories?

Temporada reproductiva del lobo fino Sudamericano (*Arctocephalus australis*, Otariidae: Carnivora): ¿Nuevos antecedentes para establecer historias evolutivas independientes?

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Resumen.- El lobo fino Sudamericano (SAFS) se distribuye desde Perú hasta Uruguay. Sin embargo, existe un área de 2,300 km a lo largo de la costa de Chile donde no se registran ejemplares de SAFS. A partir de comparaciones morfológicas se ha identificado la presencia de 3 formas geográficas (Peruana, Chilena austral y Atlántica), a la vez que estudios moleculares preliminares sugieren la presencia de 3 tipos genéticos distintivos (Peruana, Chilena austral y Atlántico). Sin embargo, ambas aproximaciones apoyan la existencia de 2 historias evolutivas independientes para los SAFS (Peruana, Atlántica), en cuyo caso, se podría esperar encontrar similares diferencias también en aspectos de la historias de vida de la especie entre estas poblaciones locales (*e.g.*, en el tiempo de la estación reproductiva). En este estudio, se comparó la estación reproductiva de ejemplares del SAFS establecidas en Punta Pichalo (19°36'S-Chile), Isla Guafo (43°33'S-Chile), e Isla de Lobos (35°01'S-Uruguay) con otros datos publicados para Punta San Juan (15°21'S-Perú). El período de formación de los harenes, el período de pariciones y el de cópulas ocurrieron en fechas semejantes en Punta Pichalo y Punta San Juan y aproximadamente un mes más tarde en Isla Guafo e Isla de Lobos. El máximo de pariciones se registró en Isla Guafo el 15 de diciembre, en Isla de Lobos el 17 de diciembre, y en Punta Pichalo el 27 de noviembre. Estas diferencias no estuvieron relacionadas con las características demográficas, ni con las condiciones oceanográficas o con el fotoperiodo de las colonias bajo estudio, ni tampoco estaría relacionado con el efecto latitudinal sobre la fenología reproductiva. En base a los resultados, se sugiere que ciertas características de las historias de vidas pueden también ayudar a identificar especies con historias evolutivas independientes.

Palabras clave: Lobo fino, estación reproductiva, fenología reproductiva, unidades evolutivas independientes

Abstract.- The South American fur seal (SAFS) is distributed from Peru (Pacific Ocean) to Uruguay (Atlantic Ocean). However, there is a section of coastline of about 2,300 km along the Chilean coast where no SAFS are recorded. Based on morphological comparisons 3 geographic forms have been reported (Peruvian, South Chilean, Atlantic), whereas preliminary genetic studies suggest the presence of 3 distinct genetic types (Peruvian, South Chile, Atlantic). However, both of these approaches are support only the existence of 2 independent evolutionary histories for SAFS (Peruvian, Atlantic), in which case, we would also expect to find some differences in the species' life histories among these locals populations (*e.g.*, in the timing of the breeding season). In this study, we compare the breeding seasons of SAFS at Punta Pichalo (19°36'S-Chile), Isla Guafo (43°33'S-Chile), and Isla de Lobos (35°01'S-Uruguay) with data published for Punta San Juan (15°21'S-Peru). The periods for establishing territories, pupping, and mating took place on similar dates at Isla Guafo and Isla de Lobos, but occurred about a month earlier at Punta Pichalo and Punta San Juan. Pupping peaked at Isla Guafo on 15- December, at Isla de Lobos on 17- December, and at Punta Pichalo on 27- November. These differences in timing were not related to demographic, oceanographic or photoperiod conditions of the breeding sites under study, neither is related with the latitudinal effects on the breeding phenology. Based on results, we suggest that certain characteristics of life history can help identify species with independent evolutionary histories.

Key words: Fur seals, breeding season, breeding phenology, evolutionary independent units

INTRODUCTION

The South American fur seal (hereafter SAFS, *Arctocephalus australis* Zimmermann, 1783)¹ is an otariid species with a widespread distribution along the coasts of South America, ranging from Mazorca Island (11°23'S) in Peru (Pacific Ocean), even though some specimens may reach lower latitudes, through Tierra del Fuego (55°40'S) to Isla de Lobos (35°01'S) in Uruguay (Atlantic Ocean) (Sielfeld 1983, 1999; Torres & Contreras 1987², Jefferson *et al.* 1993, Bastidas & Rodriguez 2005). Recently was suggested that the northernmost occurrence of *Arctocephalus australis* in the Pacific coast is at Isla Foca (5°12'S, 81°12'W) 765 km north to Mazorca in the Peruvian coast (Dra. Oliveria, pers. comm. 2015³). However, this species is absent along 2,300 km of the Chilean coastline (Pacific population), from Antofagasta Region (23°S) to Chiloe Island (43°S) (Pavés 2008, Túnez *et al.* 2013) (Fig. 1). The reasons for this gap are unknown.

The widespread distribution of SAFS has motivated several morphological and genetic researches with the aim of clarify the taxonomic status of this species. Comparisons of morphometric measurements (traditional and geometric) of skull shape and size, have allowed the differentiation of 3 distinct geographic forms (Peru-North Chile, South Chile, Atlantic populations; Oliveira *et al.* 1999, 2008; Oliveira 2004). On the other hand, 3 well-defined clusters (Peru, South Chile-South Argentine, Uruguay populations) of this species had been identified using mitochondrial DNA analysis (Túnez *et al.* 2006, 2013). However, both morphological and genetic data support the existence of only 2 distinct evolutionarily significant units (ESUs) for these populations of SAFS (*i.e.*, Peruvian, Atlantic), as proposed by Oliveira *et al.* (2005, 2008). An ESU is defined as a lineage demonstrating highly restricted gene flow from other such lineages within the higher organizational level of the species,

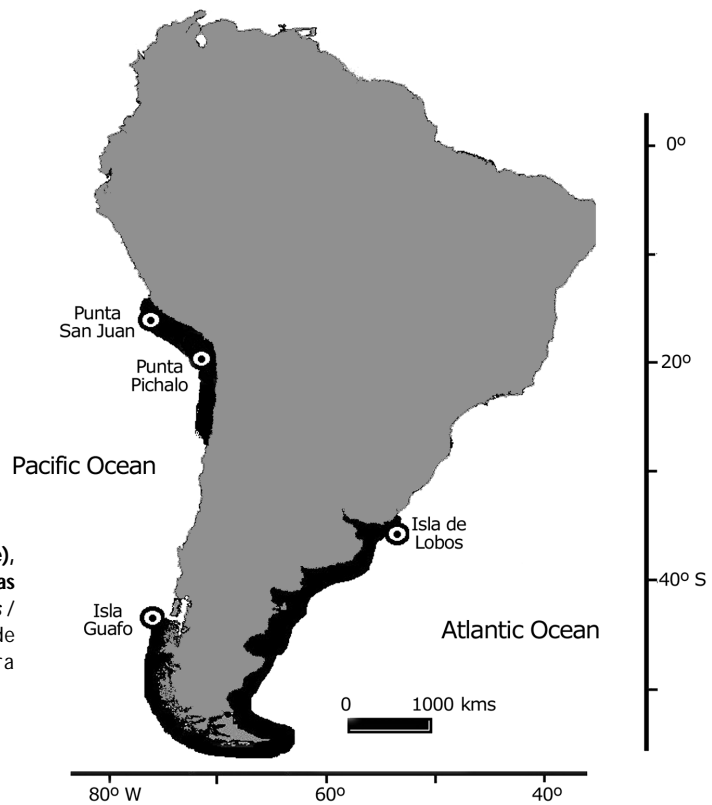


Figure 1. Geographic location of Punta Pichalo, and Isla Guafo (Chile), Isla de Lobos (Uruguay), and Punta San Juan (Peru). Dark gray areas represent the zones inhabited by *Arctocephalus australis gracilis* / Ubicación geográfica de Punta Pichalo e Isla Guafo (Chile), Isla de Lobos (Uruguay), y Punta San Juan (Perú). El área gris oscura representa la zona habitada por *Arctocephalus australis gracilis*

¹Taxonomy of this species according Committee on Taxonomy. 2014. List of marine mammal species and subspecies. Society for Marine Mammalogy, www.marinemammalscience.org, consulted on (Sept 26, 2015).

²Torres J & L Contreras. 1987. Presencia del lobo fino austral (*Arctocephalus australis*) en Isla Guafo, Chiloé. Informe Final, Proyecto Fondecyt 86/1461, 4 pp. <<http://w1.conicyt.cl/bases/bibfon/html/6/1/1861461.html>>

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and for to probe the complete isolation between local populations imply in the ESUs, is necessary use of different molecular markers and morphological traits (Túnez *et al.* 2013). Therefore, if the populations of this species do have distinct evolutionary histories and constituting different ESUs, we would also expect to find differences in their natural histories (*e.g.*, phenology or the timing of the breeding season). Following this rationale, biologically significant differences between peak reproductive dates could have produced reproductive isolation barriers between populations, facilitating speciation (*i.e.*, distinct breeding periods, Futuyma 1997).

Like most Otariidae, the reproductive activities of SAFS occur in spring-summer, within a short period of time known as the reproductive synchronization period (Majluf 1987, 1992; Pavés *et al.* 2005, Pavés & Schlatter 2008). This period coincides with greater marine productivity and higher temperatures in coastal environments, favoring the development and survival of the offspring and ensuring the reproductive success of otariids species from year to year (Bowen 1991, Trites & Antonelis 1994, Testa 2002, Gibbens & Arnould 2009). During the breeding season, adult males establish territories in specific areas of the breeding sites, defending those territories from other males that arrive later. When reproductive females arrive at the established territories, the birthing (pupping) and mating periods begin. Pupping and mating are generally observed over the course of one month, with a few weeks lag between them (*i.e.*, less than a week; Boness 1991, Bowen 1991). This phenology repeats year after year at the same time in each breeding colony (Campagna 1985, Boness 1991, Majluf 1992, Trites & Antonelis 1994).

The paper aim to compare the breeding patterns of 3 populations of SAFS at distinct latitudes within its distribution range: two Pacific Ocean populations (Punta Pichalo-19°36'S in North Chile; Isla Guafo-43°S in South Chile) and one Southwest Atlantic Ocean population (Isla de Lobos-35°01'S in Uruguay). These data were compared with results from a Peruvian population (Punta San Juan-15°21'S; Majluf 1987, 1992; Cárdenas 2007). If the populations of this species have distinct evolutionary histories, we would expect to find differences in their breeding seasons regardless of the oceanographic conditions and photoperiod duration at the breeding colonies.

MATERIALS AND METHODS

BREEDING COLONIES

Punta San Juan (Peru; 15°21'S; 75°11'W; Fig. 1): is a 0.22 km² peninsula located 500 km south of the city of Lima (Peru). This is a protected Guano Reserve administered by

PROABONOS, a Peruvian governmental company. The study carried out by Majluf (1987) took place in the beach site (called S3), the biggest and the most commonly used breeding site during each year for the fur seals at Punta San Juan. Two observation points were established on top of 30 m and on cliffs that overlook the study site which allowed observations without disturbing fur seals (Majluf 1987). Daily observations were carried out throughout the entire breeding season (1984, 1985, 1987, 1988), from early October to late December (Majluf 1992).

Punta Pichalo (North Chile; 19°36'S; 70°14'W; Fig. 1): has been considered to be one of the most important breeding site, with the highest number of births each year for the northern Chilean population of SAFS since 1986, when El Niño Southern Oscillation (ENSO) event made fur seals to migrate from Peru to North Chile (Guerra & Torres 1987). The Punta Pichalo breeding site is located 150 km north of Iquique (20°13'S; 70°09'W). Behavioral and census data were collected between September and March in 2001 and 2006, between 08:00 and 14:00 h, accumulating a total of 170 observation hours.

Isla de Lobos (Uruguay; 35°01'S; 54°52'W; Fig. 1): is located 6 nautical miles (nm) southeast of Punta del Este (34°53'S; 56°09'W). Periodic observations were carried out during 3 breeding seasons: 1991 (December), 2004-2005 (November to February), and 2005-2006 (November to late January). During the first breeding season, observations were made at Las Bovedas (1991), from 6 to 22 December, between 08:00 and 18:00 h, for a total of 170 observation hours. During the 2004-2005 (27 November to 23 February) seasons, observations were made at El Muelle from 07:00 to 10:00 and from 16:00 to 19:00 h, for a total of 270 observation hours. During the 2005-2006 (14 November to 17 January) seasons, only daily censuses of territorial males and direct pup counts were made. El Muelle and La Boveda are located less than 2 kms away.

Isla Guafo (South Chile, 43°33'S; 74°51'W; Fig. 1): this is the breeding colony of SAFS with the highest annual pup production between the 18°S and 48°S (Pavés & Schlatter 2008). Punta Weather is on Isla Guafo, 30 nm from the Port of Quellón (43°07'S; 73°36'W) on the southwest extreme of Chiloe Island. The two largest breeding sites on Isla Guafo, with an annual production of 1,200 pups (Pavés & Schlatter 2008), were chosen for this study. Direct observations of groups and their breeding behavior were conducted from 08:00 to 20:00 h using binoculars. Data collection took place during 2 breeding seasons: 2004-2005 (November to February) and 2005-2006 (December to early January), resulting in 450 h of observations.

DEMOGRAPHY, BREEDING SEASON AND ANALYSES

The numbers of juveniles, females, territorial males (= number of territories), pups, and mating events were registered at each site. Two or 3 detailed counts of all social age classes were carried out weekly by observers. Censuses were repeated when counts among observers differed by 10% or more (Pavés *et al.* 2005, Pavés & Schlatter 2008). A territory was determined as established when a territorial male was permanently rounded by at least 2 adult females in a specific place, and the male tried continuously to group them around him. Therefore, the fluctuation of the territories was obtained from census data. Mating were registered using scan observation methods. For each breeding site, one or 2 researcher performed continuous scan for a period of 6-12 h. The number of mating was standardized in each breeding colony by the effort unit (observation hours per day). Pupping and mating dates (periods and peak) at the distinct breeding colonies were estimated using the sigmoid method described by Trites (1992), and applied by García-Aguilar & Aurióles-Gamboa (2003), Soto *et al.* (2004), Pavés *et al.* (2005), and Pavés & Schlatter (2008) in sea lions and fur seals. As the numbers of pups or mates increases during the breeding season in a logistic way, they can be fitted to a sigmoidal equation (Gompertz model), enabling the breeding periods (frequency curves) and peak (maximum) of each breeding season to be estimated from the daily incremental difference of each fitted Gompertz model for births and mates. The increasing number of pups and the rate of mate per hour throughout the breeding season were used to characterize the season of birth and mating by using the following equation (1): $P_t = A / 1 + c e^{-kt}$; (1), where, P_t is the accumulated number of pups per day or mating per hour of the day 't'; A is the asymptote; c is the integration constant; k is the fixed increase rate.

This equation was adjusted using the sum of the minimum squares to determine the distinct parameters support in the Curve Expert v1.0 program. From the adjusted logistical equation (eq. 1) we determined the relative daily increase/decrease rate of mating and births building frequency curve for each parameter (=number pups, =number mating) (Trites 1992). By using these curves, we determined the periods in which synchronization of birth or synchronized pupping period and mating or synchronized mating period, as the period during which 90% of all births or mating occurs (Boness 1991). Moreover, the median point of the accumulated frequency curves allowed us to estimate the median birth date (*i.e.*, births peak, pups peak or pupping peak) or median mating dates (Boness 1991). Nevertheless, these peaks were confirmed with the mathematical

estimation of the average date of maximum births (M_b) and mating (M_m) obtained from the following equation (2): $M_p = [-\ln(1/c)]/k$; (2), where, the parameters used in equations (2) were those obtained in equation (1) (Trites 1992).

When the logistic curves were fitted for pupping or mating data for each year and location considered, an average was calculated between the sampled years to obtain the breeding phenology for each colony. Pupping patterns were successfully determined for all colonies during 2004-2005 and 2005-2006 breeding seasons. The mating periods were not fully determined for the Lobos population in the 1991 and 2004-2005 breeding seasons, but we present qualitative data to describe the general trend. This situation is related with the methods applied at Lobos site, where no observations were done between 10:00 to 16:00 h. In the others colonies we do not have problem to estimate the mating periods. Then, pupping and mating periods were obtained from data modeling.

LOCAL CLIMATOLOGY AND ANALYSIS (CLIMATE FORCING)

Data for monthly local climatology of sea surface temperature (SST), chlorophyll (Chl-*a*), and photoperiod duration were collected for the period 2002-2012 for each SAFS colony. It is necessary to mention that these local climatologically data does not apply to the breeding site Las Bovedas studied in 1991. Photoperiod durations for the 10-year period were obtained from the National Oceanic and Atmospheric Administration (NOAA)⁴ web site, whereas the SST and Chl-*a* data were obtained from satellite images (4-km resolution; MODIS AQUA) between July 2002 and February 2012. Values of Chl-*a* and SST were averaged over an area with a radius of ~200 km around the colony; this represents the foraging area limits of reproductive females, which is less than 200 km for several otariids (Thompson *et al.* 1998, Campagna *et al.* 2001, Thompson *et al.* 2003, Page *et al.* 2006). For SST and Chl-*a* data, we obtained monthly averages of 4-micron night products from the Giovanni Website⁵ (Acker & Leptoukh 2007). These data were later re-analyzed to perform climatology analyses for all the study areas. In this research, the data for describe the breeding phenology in SAFS was not collected during strong ENSO periods (<www.shoa.cl>).

STATISTICAL ANALYSIS

Statistical analyzes were performed using STATISTICA 7.0 (Statsoft, Inc)⁶. Normality assumptions were evaluated with the Shapiro-Wilk (W) test and the homogeneity of variance of the

⁴<www.srrb.noaa.gov/highlights/sunrise/NOAA_Solar_Calculations_year.xls>

⁵<http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month>

⁶Statsoft. 2001. Statistica. Data analysis software system, Version 8. <www.statsoft.com>

data with Levene's test. When these conditions were not met or their transformation was not achieved, non-parametric tests were used. The ANOVA and Kruskal-Wallis (H) tests were used to determine differences in the type of distribution of the reproductive patterns between breeding colonies (*i.e.*, ANOVA for the number of territorial male or territories, and Kruskal-Wallis for the birth, and mating data). The results of the Kruskal-Wallis test were analyzed using a multiple comparison test (z) for non-parametric data in order to identify the variables that best explained the difference, or to determine the breeding colony that explained the difference (Zar 1999; Statsoft Inc. 2001⁶). Median tests were applied to determine differences in the dates of reproductive phenology among breeding colonies. The Median test is a 'crude' version of the Kruskal-Wallis ANOVA in that it frames the computation in terms of a contingency table. Specifically, STATISTICA will simply count the number of cases in each sample that fall above or below the common median, and compute the *Chi*-square value for the resulting 2 x k contingency table. Under the null hypothesis (all samples come from populations with identical medians), we expect approximately 50% of all cases in each sample to fall above (or below) the common median. The mean \pm standard deviation of each demographic value was calculated. Pearson correlations (r) of monthly means were performed using annual SST and Chl-*a* for the study sites (breeding colonies).

RESULTS

DEMOGRAPHIC DATA

Punta Pichalo (northern Chile): During 2001-2006, the maximum number of fur seals counted was of 747.2 ± 194.5 animals (mean \pm standard deviation, SD) ranging between 570 and 974. Of the 747 animals counted, 7.3% were adults males (range= 35-81), 71.7% were females and juveniles (range= 416-701), and 21.0% were pups (range= 108-206).

Isla de Lobos (Uruguay): During 1990-1991, the maximum number of fur seal was 511.6 ± 79.8 individuals (range= 479-615). Of 511 animals counted, 5.1% were adults males (range= 23-29), 45.6% were females and juveniles (range= 188-265), and 49.4% were pups (range= 135-361). During 2004-2006 breeding seasons, maximum average number of SAFS was 691.0 ± 48.1 animals (range= 657-725). The 5.6% of these fur seals were adults males (range= 36-41), 47.6% were females and juveniles (range= 308-350), and 46.8% were pups (range= 308-339).

Isla Guafo-Punta Weather (southern Chile): The maximum number of fur seals counted at Guafo during the two breeding seasons (2004-2006) was $2,969.3 \pm 257.7$ (range= 2,787-

3,152). The 8.0% of these fur seals were adults males (range= 221-256), 53.0% were females and juveniles (range= 1568-1577), and 39.0% were pups (range= 998-1319).

BREEDING SEASON

At Punta Pichalo, territorial males were observed from the third week of September until the second week of March. Most territories (~40 territories) were established between the fourth week of November and third week of December (Table 1). The maximum number of territorial males was recorded in the second week of December. In the Peruvian population (Punta San Juan), during the 1984-1985 breeding season, 85% of the territories were identified between 25 November and 14 December, with a maximum registered on 7 December (Table 1). The territorial males at Punta San Juan were recorded over 3 months (October-December) (Majluf 1987, Cárdenas 2007) (Table 1).

At Lobos, during the beginning of the 2004-2005 sampling season (third week of November), around 50% of the maximum number of territories had been occupied, leading to the conclusion that the adults males had begun to occupy the breeding areas some weeks earlier. Most territories were abandoned in late January, although some adult males continued to defending territories until the first week of February. Most territories were held between early and mid-December, with a daily average of 5.8 ± 0.5 to 32.3 ± 2.0 territorial males from November 2004 to February 2005 (Table 1). The maximum number of territories within the study area ($n= 36$ for 2004-2005) occurred during the fourth week of December, and 90% of territorial males protected their territories between the third and fourth weeks of that month (Table 1). During the 1991 season, the number of territorial males was relatively constant, with 28 to 36 territorial males (average 33.7 ± 0.9) between the first and third weeks of December (Table 1).

At Isla Guafo, the first territories were established during the first week of November and the last territory was established during the first week of February. Most territories were established between late November and early December, with a daily average for the 2 seasons of 183.2 ± 35.8 territorial males. The maximum number of territories ($n= 220$, 2004-2005; $n= 121$, 2005-2006) was recorded during the third week of December, and 90% of these were observed in the second week of December (Table 1).

Variation in the date of establishment of the territories differed significantly between breeding colonies (Kruskal-Wallis test: $H_{2,289} = 34.41$, $P < 0.05$; Table 1, Fig. 2a). Punta Pichalo differed significantly from the rest of the colonies (Pichalo vs. Lobos: $z = 5.45$, $P < 0.05$; Pichalo vs. Guafo: $z =$

Table 1. Dates for reproductive patterns of South American fur seals at Punta San Juan, Peru; Punta Pichalo and Isla Guafo, Chile; and Isla de Lobos, Uruguay, during the breeding seasons: 2001-2006 (Pichalo), 2004-2005 and 2005-2006 (Lobos, Guafo). EM= El Muelle; LB= Las Bovedas / Fechas de los patrones reproductivos del lobo fino sudamericano en Punta San Juan, Perú; Punta Pichalo e Isla Guafo, Chile; e Isla de Lobos, Uruguay, durante las temporadas reproductivas: 2001-2006 (Pichalo), 2004-2005 y 2005-2006 (Lobos, Guafo). EM= El Muelle; LB= Las Bovedas

	Punta San Juan ¹ (Peru) 15°21'S;75°11'W	Punta Pichalo (Pichalo, Northern Chile) 19°36'S;70°14'W	Isla de Lobos (Lobos, Uruguay) 35°01'S; 54°52'W	Isla Guafo (Guafo, Southern Chile) 43°33'S; 74°51'W
Last Territorial Male	4 th week Dec.	2 nd week March	1 st week Feb.	1 st week Feb.
Maximum number of territories	1 st week Dec.	2 nd week Dec.	4 th week Dec.	3 rd week Dec.
90% Territorial Males	25 Nov. - 14 Dec. ²	27 Nov.- 15 Dec.	3 rd and 4 th of Dec,	2 nd week Dec.
First birth	5 Oct. (1984) 9 Sept. (1985), 9 Oct. (2005)	20 Sept. 2001	16 Nov.(EM)	11 Nov.
Last birth	29 Nov. (1984), 12 Dec. (1985), 15 Dec. (2004), 9 Dec. (2005)	18 Dec.	7 Jan. (EM)	3 Jan.
Pupping peak	11 Nov. (1984), 19 Nov. (1985), 3 rd week of Nov. (2005)	27 Nov. 2001	17 Dec.(EM) 10 Dec. (LB)	15 Dec.
Birth synchronization (90%)	1-3 Nov. - 1-4 Dec. (1984, 40 days), 4 th week of Nov. - 1 st week of Dec. (2005)	Nov.-Dec.	27 Nov. - 5 Jan. (40 days)(EM)	1-30 Dec. (30 days)
First mating	20 Oct. (2004)	20 Oct. 2001	25 Nov.	12 Nov.
Last mating	15 Dec. (2005)	13 Dec. 2001	13 Jan.	24 Jan.
Mating peak	3 rd week Nov.	Not observed	20 Dec. ³	20 Dec.
Mating synchronization (90%)	1 st week Dec. - 2 nd week Dec. (2005)	Not observed	4 Dec.- 3 Jan (31 days) ³	5 Dec.-3 Jan. (30 days)

¹Majluf (1987, 1992); Cárdenas (2007). ²85% Territorial Males. ³Franco-Trecu *et al.* (2014)

3.69 $P < 0.05$) while Isla Guafo and Isla de Lobos did not show any statistical differences ($z = 1.81$, $P = 0.21$). In other words, territories were established on similar dates at the Guafo and Lobos breeding colonies, but at Punta Pichalo and Punta San Juan, they were established one month earlier (see overlap of the median, and 25-75% percentiles; Fig. 2a).

THE PUPPING SEASON

The pupping season at Punta Pichalo lasted from September to December, with the pupping peak on 27 November (Table 1). For the Peruvian population (San Juan), the synchronized pupping period for the 1984-1989 seasons lasted 40 days and took place between 11 and 19 November (Majluf 1987, 1992) (Table 1).

The birth synchronization period at Isla de Lobos (El Muelle study area), was estimated between the fourth week of November and the first week of January, lasting ~40 days during 2004-2006 breeding seasons (Table 1), with maximum pupping on 17 December. In this same island but at Las Bovedas breeding site, the pupping peak was estimated to be 10 December, and the birth synchronization period occurred throughout December 1991 (Table 1). At Isla Guafo occurred between the first and the fourth weeks of December, lasting 30 days; pupping peaked on 15 December.

A comparison of our results (Isla Guafo, Isla de Lobos) with Majluf's data (1992) revealed significant differences in the birth synchronization periods between these populations (Kruskal-Wallis test: $H_{2, 286} = 184.23$, $P < 0.05$; Fig. 2). No such difference occurred between Isla de Lobos and Isla Guafo (multiple comparison, $z = 0.904$, $P > 0.05$; Fig. 2b, c), suggesting that these breeding colonies had similar pupping periods, but both colonies differed from those at Punta Pichalo and Punta San Juan (see overlap of the median, and 25-75% percentiles; Fig. 2b; Table 1).

THE MATING PERIOD

At Punta Pichalo, the mating period occurred between November and December. Mating activity was first recorded on 20 October and continued until 13 December. At Punta San Juan, the mating period was between October and December, with peak mating activity in November (Cárdenas 2007).

The synchronized mating period for the population at Isla de Lobos was not possible to determine during our study, but mating was observed from the last week of November to the second week of January (Table 1). In a recent research, Franco-Trecu *et al.* (2014) found that the mating's synchronization period at Isla Lobos ('El Muelle') lasted 31 days (*i.e.*, 4 December 2010 to 3 January 2011) with the peak mating date

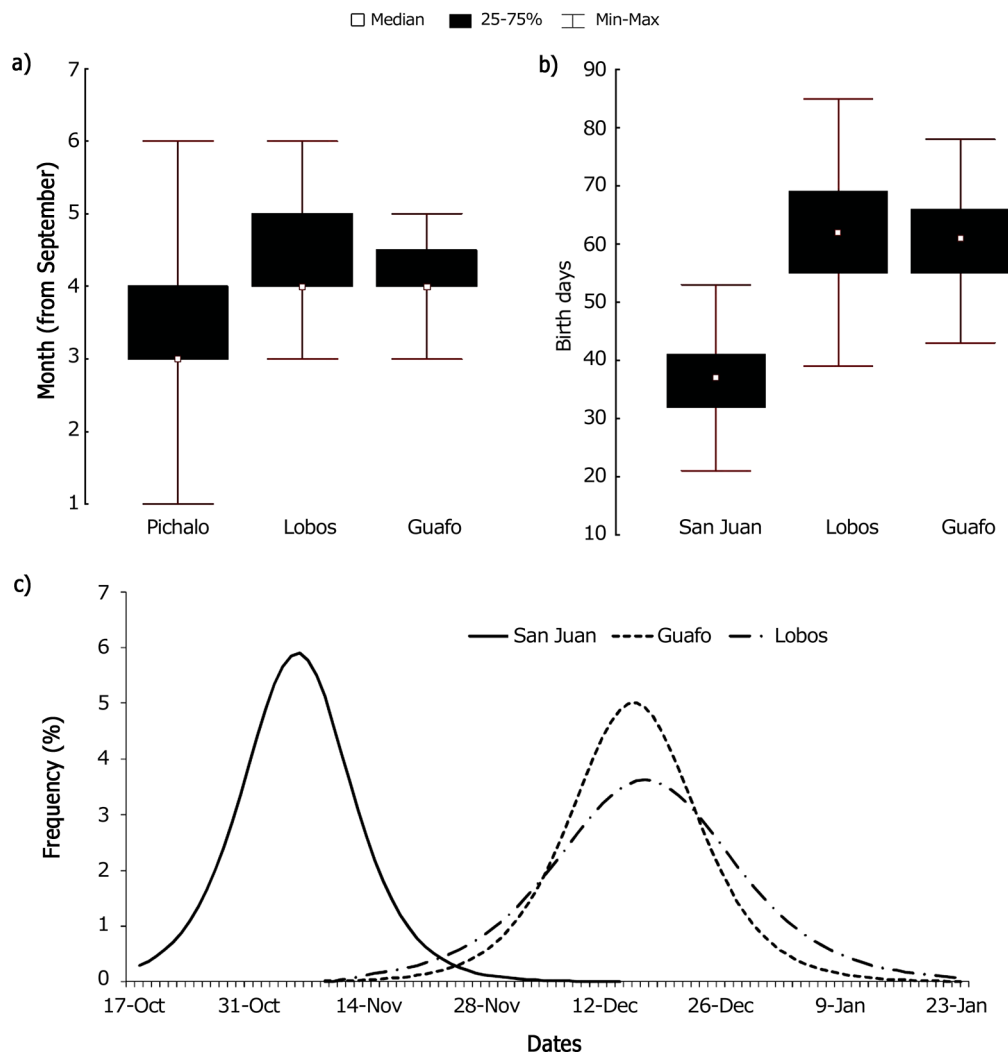


Figure 2. Variations in territorial male establishment and birth dates at 4 South American fur seal breeding colonies. In: a) Dates of male territory establishment during the breeding season obtained from census data; b) Timing of births throughout the breeding season obtained from data modeling (day 10= 10 Oct); and c) Pupping season at the 3 colonies obtained from data modeling. Data for San Juan were obtained from Majluf (1992); whereas for Pichalo, Guafo, and Lobos data come from this study / Fluctuación en el período de establecimiento de los territorios y fechas de pariciones de 4 agrupaciones reproductivas del lobo fino Sudamericano. En: a) Período de establecimiento de los machos territoriales durante la estación reproductiva obtenida desde los datos censales; b) Período de partos obtenida de los datos modelados (día 10= 10 de oct); y c) Variaciones de las fechas de pariciones a los largo de la estación reproductiva en 3 colonias, obtenida desde los datos modelados. Los datos de San Juan fueron obtenidos de Majluf (1992); mientras que para Pichalo, Guafo, y Lobos, los datos fueron obtenidos del presente estudio

on 20 December 2010. Thus, the mating period showed a similar trend to the pupping period (Table 1). At Isla Guafo lasted 30 days and took place between the first week of December and the first week of January, with the peak mating date on 20 December.

Even though it was not possible to determine the exact mating peaks or its synchronization period at Isla de Lobos and Punta

Pichalo, we assumed that these would follow the trends in the pupping peak, but with a lag of 6 to 8 days as observed in at least 12 Otariidae species, included the SAFS (Riedman 1990, Boness 1991). Thus, the mating period (maximum date) at Isla de Lobos occur within the same month as at Isla Guafo (December) but one month later than at Punta Pichalo and Punta San Juan.

Territorial establishment, pupping, and mating periods were observed on similar dates at Isla Guafo and Isla de Lobos breeding colonies, but occurred earlier and lasted longer at Punta Pichalo and Punta San Juan (Table 1). This lag was not related to changes in latitudinal differences of photoperiod duration since the sunlight duration decreased to 12 h per day in the same month for all sites considered (March, Fig. 3). Nor was the observed lag in breeding season among sites related to changes in latitudinal differences in SST since all sites displayed the same temperature pattern (Pearson $P < 0.001$, $r > 0.98$; Fig. 4). The trend in surface chlorophyll, used here as an index of local productivity, differed from that of SST. The only two sites where similar and significant Chl-*a* climatology was observed was between Punta San Juan and Isla Guafo ($r = 0.64$, $P = 0.02$, $n = 12$), which coincided with the sites with the greatest distance between them. These 2 sites showed strong differences in breeding phenology (see results). In contrast, the two study sites nearest each other (Punta Pichalo and Isla San Juan) showed distinct Chl-*a* climatologies ($r = 0.41$, $P = 0.18$, $n = 12$). Trends in Chl-*a* concentrations were similar at both sites from January to July, with the highest Chl-*a* concentrations occurring in austral spring and summer (Nov-Mar), then gradually decreasing through autumn (Mar-Jun). Minimal values were recorded in winter (Jun-Aug), coinciding with the lowest temperatures. However, unlike San Juan, Chl-*a* at Punta Pichalo did not increase from winter to spring but remained relatively stable and even decreased until austral summer. We must remember that Punta Pichalo and Isla San Juan had similar trends in their breeding phenology (this study). On the other hand, seasonality at Isla de Lobos was slight, with relatively low Chl-*a* values

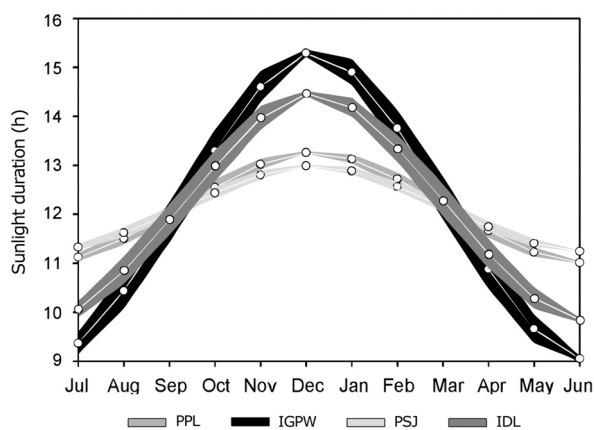


Figure 3. Annual variation of photoperiod duration at the 4 sampling sites included in this study. Mean values and standard errors of ~10 years of monthly data (2002-2012) were obtained from NOAA (<www.srrb.noaa.gov>) / Variación anual de la duración del fotoperiodo de las 4 colonias relevadas en este estudio. Los valores promedio y sus errores estándar fueron obtenidos de datos mensuales de ~10 años (2002-2012) de la NOAA (<www.srrb.noaa.gov>)

throughout the year ($< 3 \text{ mg Chl-}a \text{ L}^{-1}$) that increased in austral spring. The latter trend was the opposite to that recorded at Punta Pichalo, the closest latitudinal sampling site ($r = -0.64$, $P = 0.02$, $n = 12$). Thus, neither latitudinal temperature trends nor local productivity (herein, Chl-*a*) seem to explain the changes in the breeding season at Punta San Juan, Punta Pichalo, Isla de Lobos, and Isla Guafo.

DISCUSSION

Despite of the lag of about one month between reproductive synchronization of Guafo-Punta Lobos Island and Punta Pichalo-Punta San Juan, the reproductive phenology at each of these sites, is highly consistent year after year. This condition is common in other Otariidae and Phocidae demonstrating that there is stability within breeding traits of different population of a species when the environmental conditions are stable. Therefore, the phenology observed in the present time could help us to understand or estimate the phenology for the past 5 or 10 years ago (Campagna 1985, Duck 1990, Boness 1991, Majluf 1992, Trites 1992, Trites & Antonelis 1994, Boyd 1996, Pitcher *et al.* 2001, García-Aguilar & Aurióles-Gamboa 2003).

Interannual variability in the breeding phenology between populations could be due to demography (age structure), physiology (embryonic implantation period), nutritional state (female nutritional condition), and climate forcing (photoperiod, air and water temperature, marine productivity) (see for more details Ims 1990, Vila 1991, Trites 1992, Campagna *et al.* 1993, Temte 1993, 1994; Boyd 1996, Costa & Gales 2003, Soto *et al.* 2004). Nevertheless, the populations studied herein had similar demographic characteristics, age structures, as well as sea surface temperature, and Chl-*a* climatology (see Results). Therefore, none of these factors could explain the asynchronous breeding season of the SAFS recorded in our research between the Peruvian - North Chile, and South Chile - Uruguayan populations (with ~one-month lag in the maxima).

As other southern Otariidae, the reproductive activities of SAFS occur in spring-summer (*i.e.*, late November to early January; Campagna 1985, Majluf 1992, Pavés *et al.* 2005), coinciding with increased productivity and higher temperatures in the coastal environments, which favor the development and survival of the offspring and presumably enhances the reproductive success (Majluf 1987, Bowen 1991, Trites & Antonelis 1994, Testa 2002, Pavés *et al.* 2005, Gibbens & Arnould 2009). Riedman (1990) and Boness (1991) analyzed the seasonality and reproductive synchrony of Otariidae by using latitude to describe the relationship between climatic seasonality, food availability, and the reproductive periods of these otariids species. Species with non-seasonal, non-annual reproductive

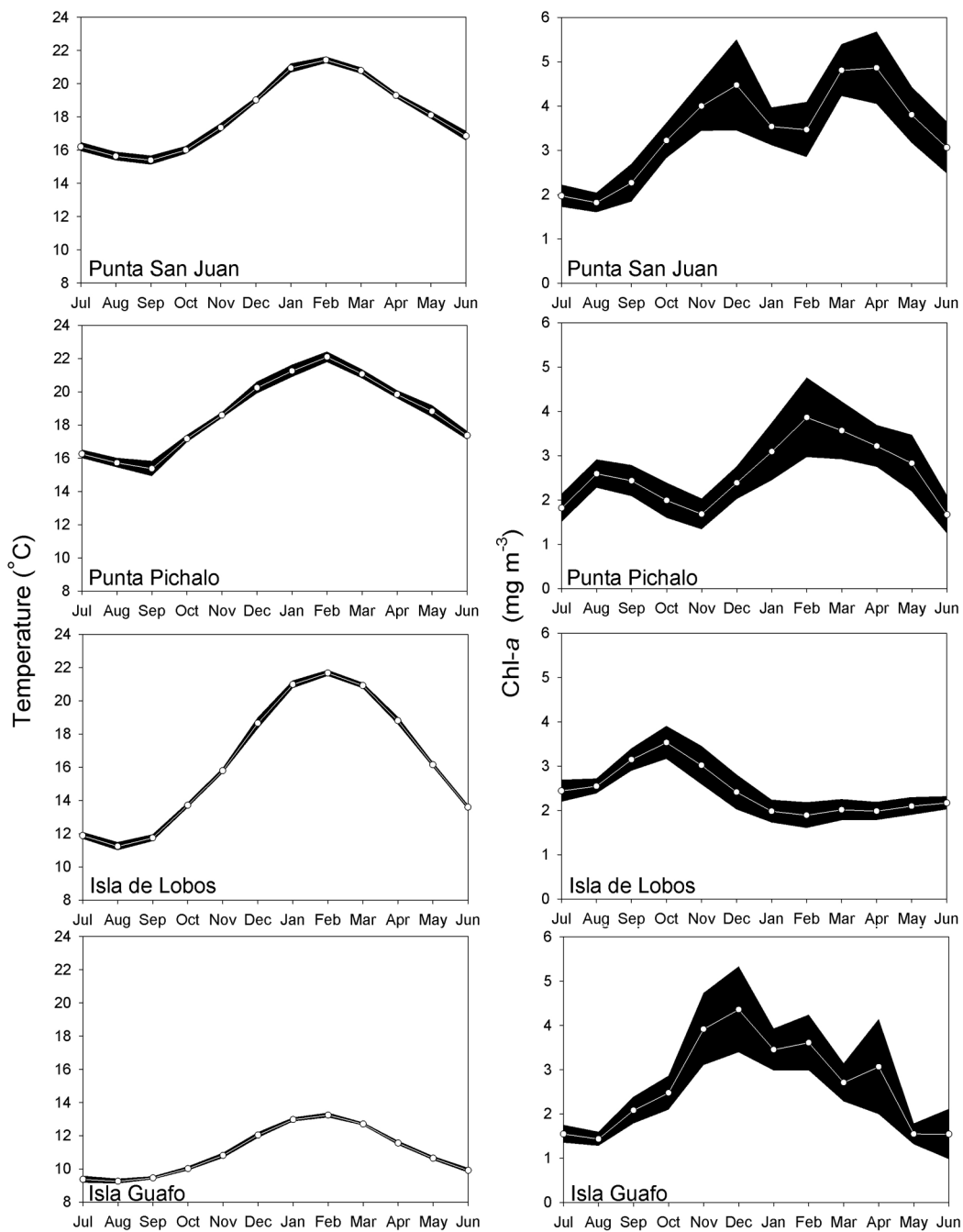


Figure 4. Annual climatology of sea surface temperature (SST; °C) and Chl-a (mg m⁻³) at the 4 sampling sites included in this study. Mean values (white dots) and standard errors (black fill) of ~10 years of monthly data (Jul. 2002-Feb. 2012) were obtained from MODIS AQUA satellite. Punta San Juan= San Juan; Punta Pichalo= Pichalo; Isla de Lobos= Lobos; Isla Guafo= Guafo / Climatología anual de la temperatura superficial del mar (SST; °C) y la Chl-a (mg m⁻³) de los 4 sitios muestreados e incluidos en este estudio. Los valores promedios (puntos blancos) y su error estándar (barras negras) de ~10 años de datos mensuales (Jul. 2002-Feb. 2012) fueron obtenidos del satélite MODIS AQUA. Punta San Juan= San Juan; Punta Pichalo= Pichalo; Isla de Lobos= Lobos; Isla Guafo= Guafo

cycles and non-synchronized reproductive events were expected to inhabit environments with lower or no climatic seasonality, low productivity, and/or food resources of low energetic quality. For example, Australian sea lions [*Neophoca cinerea* (Péron 1816)] have a reproductive cycle of approximately 18 months (Higgins 1993, Costa & Gales 2003), and the Mediterranean monk seal (*Monachus monachus*, Hermann, 1779) has births throughout the year (Pastor & Aguilar 2003), conditions thought to be related with the specialized diet on low density prey, low productivity and seasonality observed between their distribution area (Higgins 1993, Costa & Gales 2003, Pastor & Aguilar 2003, Goldsworthy *et al.* 2009).

The relationship between latitude and breeding synchrony had been observed in both Otariidae and Phocidae, including: *Mirounga leonina* (Linnaeus, 1758) by Campagna *et al.* (1993), *Pagophilus groenlandicus* (Erleben, 1777) by Stenson *et al.* (1993), *Zalophus californianus* (Lesson, 1828), and *Phoca vitulina* (Linnaeus, 1758) by Temte (1993), *Phoca vitulina vitulina* (Linnaeus, 1758), and *Phoca vitulina richardsi* (Gray, 1864) by Temte (1994), *Arctocephalus forsteri* (Lesson, 1828) by Goldsworthy & Shaughnessy (1994), *Eumetopias jubatus* (Schreber, 1776) by Pitcher *et al.* (2001), and *Z. californianus* by García-Aguilar & Aurióles-Gamboa (2003). The SAFS should constitute an example of the relationship between latitude and breeding season described by Boness (1991) due to the species' wide geographical range, which, though fragmented, clearly establishes populations within temperate climates, where other fur seals species are also found (Duck 1990). Despite differences in the breeding seasons of the populations studied here, the overall results do not agree with the trend reported by Boness (1991). The differences of about one month between breeding seasons at Punta Pichalo-Punta San Juan and Isla Guafo-Isla de Lobos are not related to a latitudinal effect, but this effect described by Boness (1991) is observed between the breeding seasons at Isla Guafo and Isla de Lobos. Birth synchronization lasts longer at Isla de Lobos than Isla Guafo, and pupping peaks earlier at Isla Guafo than Isla de Lobos, as expected given the latitudinal effect reported by Boness (1991) (Table 1, Fig. 2) and observations for other species (Campagna 1985, García-Aguilar & Aurióles-Gamboa 2003).

It is still unknown if differences in breeding phenology recorded at Punta Pichalo, Punta San Juan, Isla Guafo, and Isla de Lobos have implications to generate reproductive isolation barriers and the establishment of a new species (Futuyma 1997). An extended lag in the breeding season between populations could prevent genetic flow and, consequently, produce a phylogenetic separation of the

populations. A three-day lag between peak of mating within the same population during different years or between distinct and distant populations (*e.g.*, Lobos vs. Guafo) may not generate reproductive barriers, however, a lag of approximately one month may have much greater reproductive significance.

The breeding patterns of the populations from Punta Pichalo (northern Chile) and Punta San Juan (Peru) differed from those Isla Guafo (southern Chile) and Isla de Lobos (Uruguay) similar pattern to the situation reported with morphological and genetic data (Oliveira 2004, Túnez *et al.* 2006, Oliveira *et al.* 2008). Guerra & Torres (1987) noted that the Northern Chilean population (Pichalo) was derived from the Peruvian population, which was only observed after the 1982 ENSO, when SAFS migrations were observed from the southern Peruvian coast to the northern Chilean coast.

By comparing morphological characteristics, Oliveira *et al.* (1999, 2008), and Oliveira (2004) were able to clearly differentiate 3 geographic forms of SAFS in South America: Peru-North Chile (form 1), South Chile (Magellan channels) (form 2), and Atlantic (Lobos) (form 3). Genetic studies, revealed 3 clusters for this species (Peruvian, South Chile, and Atlantic populations). With both studies was possible to determine the existence of two ESUs, where the morphological and genetic data could support the isolation between Peruvian and Atlantic population. Unfortunately, this later study did not include any genetic information from the southern Chile population (Túnez *et al.* 2006, Oliveira *et al.* 2008). Nevertheless, Túnez *et al.* (2013) using only one type of molecular marker identified 2 conservation unit (South Chile-South Argentina and Uruguay population), recommending the use others molecular markers to establish the existence of others ESUs. Thus both, genetic and morphological scenario supports the existence of two distinct evolutionary histories in SAFS, one for Peruvian population, and other for the Atlantic population. This coupled with the existence of premating isolation mechanism - both spatial (~2,300 km long gap off the Chilean coast) and temporal (difference in breeding phenology; this study) - could lead to the differentiation of at least 2 evolutionarily independent units of SAFS (Peru-Northern Chile, Southern Chile-Atlantic) as proposed by Oliveira *et al.* (2005, 2008) and Oliveira & Brownell (2014). Recently, others authors have postulated the idea that both units could be consistent with the existence of 2 subspecies, one for Peruvian and north Chilean population, and other South Chile and Atlantic population (Berta & Churchill, 2012). Then, the results of breeding phenology found here agree with the previous morphological and genetic evidence for the species (Oliveira *et al.* 1999, 2008; Oliveira 2004; Túnez *et al.* 2006, Oliveira *et al.* 2008). Thus, our approach, with its faults and successes, could be help to shed

some light into the existence of independent evolutionarily histories reported for SAFS populations (Túnez *et al.* 2006, Oliveira *et al.* 2008, Oliveira & Brownell 2014), constituting new information with which to evaluate the taxonomic status of this species in South America. However, more conclusive results could be obtained by including the breeding colonies located in the southernmost part of South America, together with a simultaneous sampling effort of different breeding colonies along South America during non-ENSO conditions; situation which would indeed imply a huge international logistical and financial effort.

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