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Original investigation

Is recolonization pattern related to female philopatry? An insight into a colonially breeding mammal

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ABSTRACT

Colony formation is related to dispersal, philopatry, conspecific attraction, available suitable habitat, proximity and availability of food resources, and reproductive success. In this study we analyzed if female South American sea lions, (SASL, *Otaria flavescens*), exhibit natal fidelity at a small geographic scale (between colonies of the same breeding area) in a context of a recovering population with population expansion and recolonization. We examined the mitochondrial genetic diversity and investigated spatial genetic structure, considering new and traditional colonies. We recovered 36 haplotypes (23 novel), with the contemporary presence of common and private haplotypes in each colony. AMOVA analysis indicated no population genetic structure, however F_{st}, SAMOVA and AIS analyses suggested some level of genetic structure between northern and southern colonies. Therefore female SASL display different strategies when they choose where to breed: some are residents of -or return to- one particular colony whereas others disperse within the study area. In conclusion the recolonization of SASL may be the effect of weak female philopatry attenuated and/or interacting with other processes like site fidelity to near-by feeding grounds, breeding success, terrestrial habitat selection for breed and dispersal.

Introduction

Colonial breeding is a form of social reproduction in which individuals breed within densely distributed mating territories (Danchin and Wagner, 1997). Colonialism is an evolutionary trait resulting from multiple interacting factors that balance fitness cost (increased transmission of parasites and diseases, inbreeding, increased intraspecific competition, cannibalism and infanticide) and benefits (enhanced food-finding abilities, reduced predation and male harassment, increased ability to find favorable habitats, increased reproductive success) of breeding at high densities (Cassini, 1999, 2000; Danchin and Wagner, 1997). Colonialism has been intensively studied from an evolutionary perspective in birds and mammals (e.g., Packer et al., 1990; Rolland et al., 1998; Siegel-Causey and Kharitonov, 1990; Wittenberger and Hunt, 1985), however the temporal and spatial dynamics of colonial breeding species are poorly known (Barbraud et al., 2003; Gaggiotti et al., 2004; Oro and Ruxton, 2001). Some of the processes involved in the formation and growth of a colony are likely to be dispersal, philopatry (i.e., natal site fidelity), conspecific attraction, available suitable habitat, availability of coastal food resources, and reproductive success in different social contexts (Bradshaw et al., 2002; Grandi et al., 2008; Serrano and Tella, 2003).

Among mammals, several species of pinnipeds are seasonal colonial breeders (Riedman, 1990). Due to their gregarious nature and predictability on land, most species were heavily exploited by humans during the 19th and 20th centuries (Bonner, 1982). Several populations have been reduced to such small sizes that they were locally extirpated or came close to extinction (Gentry and Kooyman, 1986; Kovacs et al., 2012). Some stocks have recovered throughout the 20th century to different degrees, although mainly after long periods of time (Gentry, 2009; Gerber and Hilborn, 2001; Wickens and York, 1997). This has led to the recolonization of much of their former range (Bonin et al., 2013; Campbell et al., 2008; Dussex et al., 2016; Huisamen et al., 2011; Lancaster et al., 2006; Wynen et al., 2000).

Philopatry, or natal site fidelity, is a widespread evolutionary strategy for pinnipeds that forage widely at sea but aggregate sea-

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sonally at terrestrial sites to locate a mate, give birth, and raise a pup (Stirling, 1983). Due to this reproductive behavior, females tend to be more philopatric while males tend to disperse more (Boness 1991; Gentry and Kooyman, 1986). Moreover, this breeding behavior has the potential to influence the genetic diversity within and between populations (Higgins and Gass, 1993; Pomeroy et al., 2000). Species that display a high degree of philopatry might be expected to exhibit strong genetic differentiation between breeding colonies (Dickerson et al., 2010). Among otariids, Australian sea lions (*Neophoca cinerea*) showed an extreme female philopatry that led to strong population structure at a fine spatial scale (Campbell et al., 2008), while other species showed moderate to high genetic differentiation between colonies e.g., New Zealand sea lion (*Phocarctos hookeri*; Chilvers and Wilkinson, 2008; Collins et al., 2017); Steller sea lion (*Eumetopias jubatus*; Hoffman et al., 2006a; Koyama et al., 2008; Trujillo et al., 2004); Juan Fernandez fur seals (*Arctocephalus philippii*; Goldsworthy et al., 2000); Antarctic and Subantarctic fur seals (*A. gazella*, *A. tropicalis*; Hoffman et al., 2006b; Hoffman and Forcada, 2012; Wynen et al., 2000); California sea lions (*Zalophus californianus*; González-Suárez et al., 2009); and Galapagos sea lion (*Z. wollebaeki*; Wolf and Trillmich, 2007).

The South American sea lion (SASL, *Otaria flavescens*) is 1 of 7 sea lion species in the world. Over recent decades there has been growing concern over the conservation status of sea lion species. Moreover, among sea lions, SASL and California sea lions are the only species currently listed as recovering (IUCN, 2017). Consequently, understanding the species capacity to recover after severe population declines, and the factors involved in population expansion, recolonization or colonization of new habitat are essentials for the effective management and conservation of many species in recovery.

The population of SASL from northern Patagonia (Argentina) provides an ideal case study to explore the impact of historical exploitation on contemporary patterns of genetic diversity and population structure. This population declined from an estimated 137,500 individuals in 1938 (Godoy, 1963) to 18,396 individuals in 1947 (Carrara, 1952) passing through its lowest numbers (~5,000 individuals) in the 1960s (Koen-Alonso and Yodzis, 2005; Romero et al., 2017). After hunting ban in 1962, the population started recovering in 1990 (Crespo and Pedraza, 1991) with an annual rate of 5.7% (Dans et al., 2004). This growth was characterized by a recolonization process where new breeding sites arose next to established high density rookeries (i.e., traditional or focal colonies) (see Grandi et al., 2008 for details). Focal colonies likely represent refugia from where the species could have recolonized its former range at the end of commercial sealing. Even though Patagonia has hundreds of kilometers of suitable coastal habitat, there is a geographic pattern in which SASL colonies were not randomly established, but instead appeared to grow and persisted only near-by focal colonies (Grandi et al., 2008, 2015). This particular recolonization process suggests that the process of formation of new colonies and population expansion would be the consequence of complex dynamics involving dispersal, philopatry, available suitable habitat, and reproductive success in different social-structure contexts (Grandi et al., 2008).

Recent genetic studies on the population structure of SASL support the hypothesis that the Pacific and Atlantic populations should be considered distinct Evolutionarily Significant Units, with low inter-oceanic female gene flow (Oliveira et al., 2017). Additionally, within large Atlantic breeding areas (Uruguay, Patagonia and Malvinas/Falkland Islands) several studies suggest strong female fidelity while gene flow is mediated by males (Feijoo et al., 2011; Hoffman et al., 2016; Oliveira et al., 2017; nez et al., 2007, 2010; Túnez et al., 2010). At a smaller geographical scale (within Patagonia) distinct population units were distinguished between groups of colonies in northern and central Patagonia, Santa Cruz and the Malvinas/Falkland Islands (Feijoo et al., 2011; Hoffman et al., 2016; nez et al., 2007, 2010; Túnez et al., 2010). However, on a smaller scale (within a colony) the level of female philopatry has never been explored.

The aim of this study is to analyze whether female SASL shows natal fidelity at a small geographic scale (between colonies of the same breeding area) in the context of a recovering population with population expansion and recolonization. Using a genetic approach we will try to understand the effect of philopatry in the formation of new colonies. Given the existence of philopatry in SASL females, this study expect to find that: a) maternal lineages within a colony will be more similar to each other than lineages in other colonies, and b) geographically closer colonies will be more genetically related than distant ones.

Material and methods

Study area and sample design

Since the objective of the present study is to test whether SASL females are philopatric at a small geographic scale, it is imperative to know birth location. Therefore, skin samples of a maximum of 20 newborn pups from 10 different breeding colonies were used instead of samples collected opportunistically (as done by Feijoo et al., 2011; nez et al., 2007, 2010; Túnez et al., 2010). Different colonies from northern Patagonia (Fig. 1a) were studied considering 3 focal colonies [Punta Buenos Aires San José Gulf 1 (PB1, N = 19), Faro Punta Norte (FN, N = 19) and Punta León (PL, N = 20)] and 7 new breeding colonies [Barrancas Blancas (BB, N = 20), Punta Quiroga San José Gulf (PQ, N = 12), Larralde (LR, N = 19), Punta Buenos Aires San José Gulf 2 (PB2, N = 19), Ensenada Medina (EM, N = 20), La Ernestina (ER, N = 19) and La Pastosa Cría (PC, N = 19)] (Fig. 1b and Table 1) (Grandi et al., 2008). Colony boundaries were defined as the beginning of a complete discontinuity between aggregations of animals or denoted by the presence of a terrestrially impassable barrier, typically a cliff or sandy beach, between adjacent groups of sea lions (Grandi et al., 2008). Therefore, to minimize sampling bias, newborn pups were sampled randomly from several areas of each colony. Skin samples were taken from the trailing edge of the hind flippers of 186 SASL during the breeding seasons of 2011 and 2013. Pups were captured using a noose pole (Gentry and Holt, 1982) and skin samples were stored in 20% dimethyl sulfoxide saturated with salt and kept at −20 °C (Amos and Hoelzel, 1991).

The SASL mating system is defined as female–defense polygyny, where males defend territories containing multiple females in a harem (Campagna and Le Boeuf, 1988). The breeding cycle starts early December with the arrival of adult males at the rookeries. Adult females arrive and establish territories between mid-December and the beginning of January. Mating occurs from mid-December to mid-February and the maximum number of births occurs in mid-January (Campagna, 1985; Campagna and Le Boeuf, 1988). In February, at the end of the breeding season the breeding structure dissolves slowly: males abandon the colony, and later adult females leave with their pups (up to May) (Campagna, 1985).

Mitochondrial DNA analysis

Total genomic DNA was extracted using a modified salting out procedure (Miller et al., 1988). Due to females being the focus of the study, a ~550 bp fragment of the maternally inherited mtDNA control region (D-loop) was amplified using the primers L16274 (5′-TACACTGGTCTTGTAAACC-3′; Lamont et al., 1996) and H34 (5′-CCAAATGCATGACACCACAG-3′; Stanley et al., 1996) with the following PCR profile: 2 min at 92 °C; then 35 cycles at 94 °C,

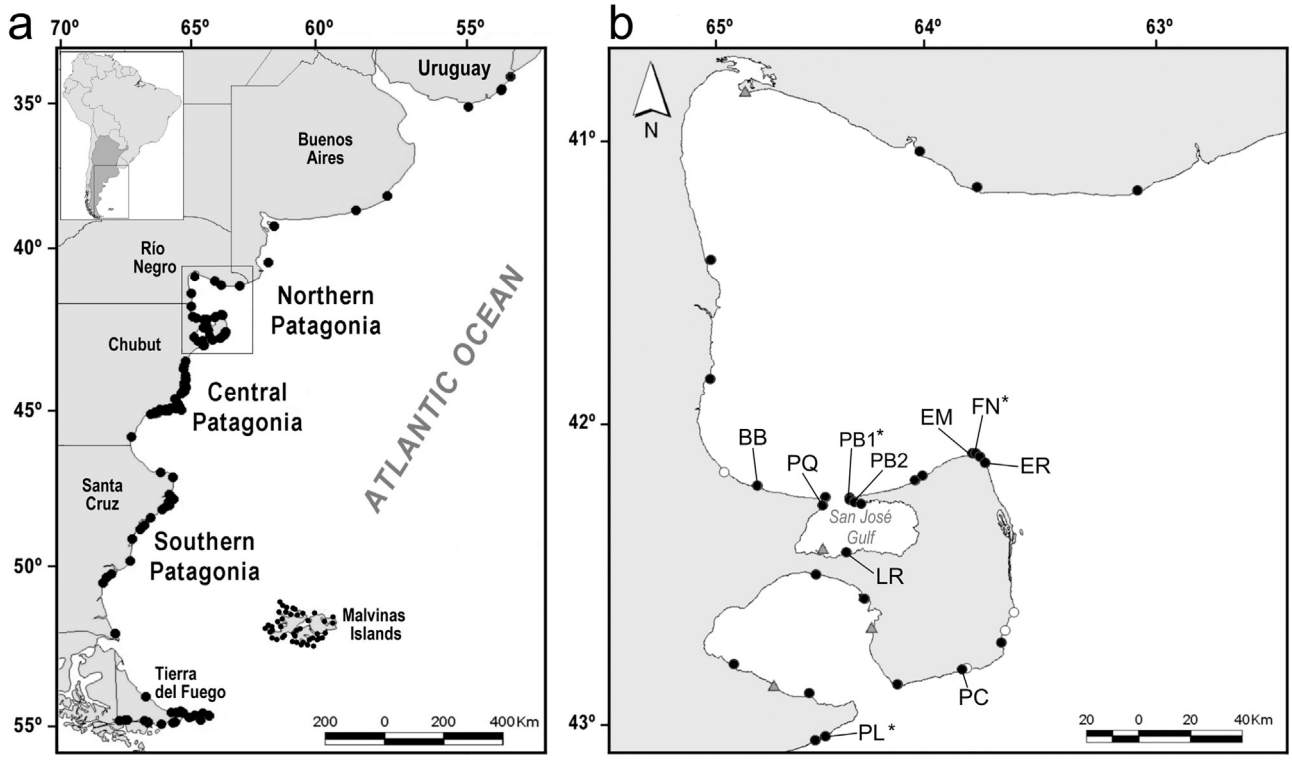

Fig. 1. a) Current distribution of *Otaria flavescens* colonies along the coast of Southwestern Atlantic. The box denotes the study area in northern Patagonia. b) Details of the distribution and type of colonies in the study area in northern Patagonia, with the sampled sites indicated. Black circles: breeding colonies, white circles: haul-out colonies, and grey triangles: occasional colonies. Asterisks indicate traditional colonies. Names of colonies (ID) are in Table 1.

50 °C, 72 °C of 1 min each step and a final extension phase of 10 min at 72 °C. All PCRs (50 μl, final volume) contained: 5 μl of DNA template (approximately 50 ng), 5 μl of Buffer (10×), 1.5 μl of $MgCl_2$ [50 mM], 3.75 μl of dNTPs [20 mM], 1 μl of each primer [0.25 pM], 0.2 unit Taq polymerase (Invitrogen). Purification and sequencing reactions were conducted by Macrogen Inc. (Seoul, Korea). Sequences were aligned manually using BioEdit (Hall, 1999).

Data analysis

Number of haplotypes (H), nucleotide diversity (π) (Nei, 1987), haplotypic diversity (h) and Fu's Fs (Fu, 1997) were estimated for each colony and the overall population using Arlequin V3.1 (Excoffier et al., 2005). The same software was used to estimate pairwise F-statistics (F_{st} based on matrix distances) between colonies and hierarchical Analysis of Molecular Variance (AMOVA) using 10,000 permutations. For the population structure analysis 10 sampled colonies were considered as subpopulations (Fig. 1b and Table 1). Given the population expansion and recolonization process observed (Grandi et al., 2008) we tested different scenarios (Table 2): (i) focal colonies as distinct subpopulation from new colonies; (ii and iii) each focal colony[1] as distinct subpopulation from new colonies around it (iv) nearest colonies as distinct subpopulation from distant ones; and (v) use of the major geographic partition identified by Feijoo et al. (2011) to define the two main groups as population units.

Haplotype network was constructed using the median-joining approach (Bandelt et al., 1999) implemented in the NETWORK 4.5.

Sequences obtained were compared with available D-loop sequences (see Appendix A, Supplementary data) to identify possible novel haplotypes.

[1] Except PL that only have one new colony (PC) close around.

Spatial genetic analysis

Isolation-by-distance (IBD) was tested using a Mantel test implemented in Arlequin V3.1. Geographical distance was calculated as the shortest swimming distance (km) that a sea lion would have to travel from the midpoint of each colony to the midpoint of all other colonies (Grandi et al., 2008).

Spatial analysis of molecular variance (SAMOVA, Dupanloup et al., 2002) was used to identify partitions of sampling sites that were maximally differentiated from each other. Analyses were based on 100 simulated annealing steps, we examined maximum indicators of differentiation (FCT values) varying $K = 2$ to $K = 9$, and tested each hypothesis using AMOVA.

Finally, we employed genetic landscape surfaces (GLS) implemented in Alleles In Space (AIS, Miller, 2005) to visually check if geographical regions in which genetic differentiation was maximized were congruent with the optimal clustering identified by SAMOVA. GLS interpolation was parameterized at multiple scales with surfaces based on the midpoints of edges derived from Delaunay triangulation and raw genetic distances. Following the interpolation procedure, a 3D surface plot was generated to interpolate genetic distances where X and Y coordinates corresponded to geographical locations and surface plot heights (Z) reflected genetic distances. Analyses were performed using a variety of grid sizes (20×20, 50×50, 100×100) and with a range of distance weighting parameters ($a = 0.5$–2) to ensure that interpolation parameters chosen for the analysis were correct.

Results

Mitochondrial DNA control region diversity

After quality screening the dataset consisted of 504pb D-loop sequences from 170 individuals. These sequences contained 32

Table 1
Colony names and the year of establishment (as the first year that was found on surveys). Pairwise comparisons of SASL colonies indicated by genetic F_{st} (bottom diagonal) and geographical Km (top diagonal) distances. Percentage of samples amplified (%*N*), haplotypes recovered and private haplotypes (H/H_p), and measures of genetic diversity (haplotype diversity, $h \pm SD$, nucleotide diversity, $\pi \pm SD$) and population expansion (Fu's *Fs*) by colony.

ID	Colony	BB	PQ	LR	PB2	PB1	EM	FN	ER	PC	PL	%*N*	H/H_p	π	*h*	*Fs*
BB	Barrancas Blancas (1995)		32.49	53.13	40.02	37.70	82.69	84.07	89.90	186.41	250.17	55.0	7/3	0.007504 ± 0.004616	1.00 ± 0.0388	−8.45231**
PQ	Pta. Quiroga G. San José (1996)	−0.008		20.64	12.77	10.74	62.04	63.28	69.11	165.62	229.38	91.67	8/2	0.010967 ± 0.006442	1.00 ± 0.0388	−6.54349**
LR	Larralde (1990)	−0.028	0.002		20.07	20.31	73.08	74.32	80.15	176.66	240.42	100	9/2	0.006939 ± 0.004133	1.00 ± 0.0171	−21.91317**
PB2	Pta. Bs. As. G. San José 2 (2005)	−0.035	−0.035	−0.001		2.32	56.55	57.79	63.62	160.13	223.89	94.74	9/4	0.00922 ± 0.005302	1.00 ± 0.0185	−17.06204**
PB1	Pta. Bs. As. G. San José 1 (1938)	−0.006	−0.034	0.007	−0.024		54.23	55.47	61.30	157.81	224.05	100	11/4	0.011301 ± 0.006332	1.00 ± 0.0171	−16.48137**
EM	Ensenada Medina (1983)	−0.039	−0.028	−0.029	−0.041	−0.017		1.24	7.07	103.58	167.34	90.0	9/3	0.007911 ± 0.00464	1.00 ± 0.0185	−18.66969**
FN	Faro Pta. Norte (1938)	−0.015	0.08925*	0.013	0.047	0.030	0.029		5.83	102.34	168.58	100	7/1	0.005906 ± 0.00361	1.00 ± 0.0171	−23.86149**
ER	La Ernestina (1995)	0.004	0.021	0.012	0.014	−0.014	0.004	0.003		96.51	160.27	94.74	10/2	0.006743 ± 0.004047	1.00 ± 0.0185	−20.429**
PC	La Pastosa cría (2005)	−0.013	0.005	−0.018	0.022	0.049	−0.011	0.07821*	0.07157*		61.07	94.74	9/2	0.005559 ± 0.003445	1.00 ± 0.0185	−22.70189**
PL	Pta. León Norte (1938)	−0.008	0.004	0.002	0.031	0.058	0.000	0.09608*	0.07228*	−0.040		95.0	8/0	0.004846 ± 0.003069	1.00 ± 0.0171	−25.96694**

* Significance at the 0.05 level after 10,000 permutations.
** Significance at the 0.001 level after 10,000 permutations.

Table 2
Support for population groupings based on AMOVA results using F_{st} values calculated on distance matrix. Colonies names defined in Table 1.

	Hypothesis	Groups	F_{st}	*P*	% variation among		
					Groups	Populations within groups	Within populations
i	focal vs new colonies	(PB1-FN-PL) vs (BB-PQ-LR-PB2-EM-ER-PC)	0.00473	0.2291	−0.85	1.32	99.53
ii	PB1 focal vs closer colonies	(PB1) vs (BB-PQ-LR-PB2)	−0.00847	0.72366	1.15	−2.00	100.85
iii	FN focal vs closer colonies	(FN) vs (EM-ER)	0.01436	0.2415	0.64	0.80	98.56
iv	close vs distant colonies	(BB-PQ-LR-PB1-PB2) vs (EM-FN-ER) vs (PC-PL)	0.01523	0.2203	2.19	−0.66	98.48
v	northern vs southern colonies	(BB-PQ-LR-PB1-PB2-EM-FN-ER) vs (PC-PL)	0.0281	0.2221	3.11	−0.3	97.19

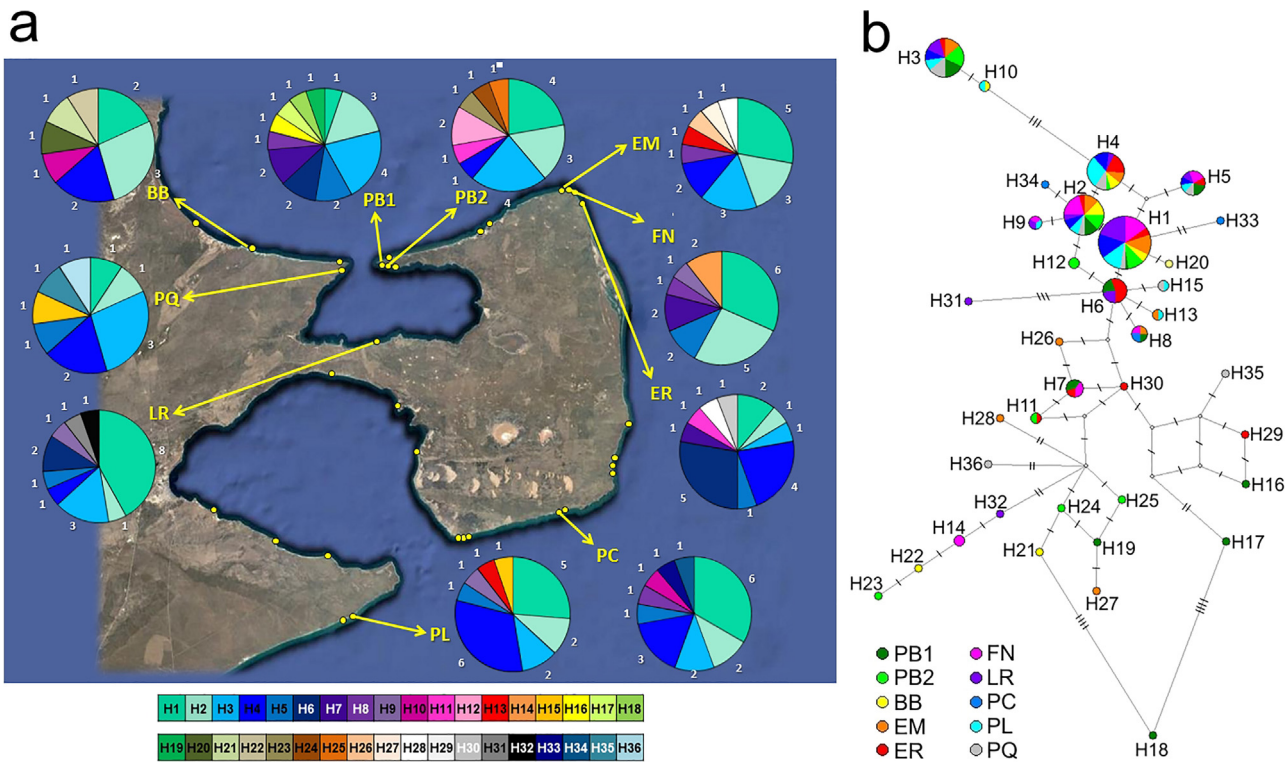

Fig. 2. a) Haplotype composition in each sampled colony. Names of colonies (ID) are in Table 1. b) Haplotype network for the mtDNA control region, each color circle represents a unique haplotype, with size being proportional to its frequency. Colors represent the SASL colony at which the haplotype was found and number of mutations is represented by vertical bars.

polymorphic sites identifying 36 haplotypes, 21 of which were represented by a single individual (Fig. 2a). Overall h was high (0.889), but π was low (0.0070). Each colony h was 1.00 while π ranged from 0.0048 to 0.0113 (Table 1). Fu's *Fs* statistic was significantly negative at all colonies (Table 1) suggesting a demographic expansion, concordantly with the median-joining network (Fig. 2b). The network showed two common haplotypes H1 and H2, it seems that H1 is the ancestral haplotype from which the maternal lineages diverged (Fig. 2b). The singularity of the network is the presence of several private haplotypes (H12, H14, H16-H36) mostly deriving from H6 (Fig. 2b). Haplotypes H1 and H2 were observed in 23.53% and 14.12% of 170 individuals respectively and found in all colonies sampled. H3 and H4 were present in 8 sampling sites, whereas H5 was only found in 7 colonies. The 31 remaining haplotypes (H6-H36) were present in 1–4 sampling sites. Moreover all colonies showed between 1 and 4 private haplotypes, for a total of 23 private haplotypes (H12, H14, H16-H36) (Table 1 and Fig. 2a and b). The exception was PL, where all the haplotypes in the colony were shared with the rest of the rookeries.

Comparing the 36 haplotypes recovered with available sequences from Patagonia Argentina (N = 37, see Appendix A, Supplementary data), using a 305 bp D-loop segment, we found that 28 are novel haplotypes for the Patagonian population under study. Comparing our sequences with the haplotypes reported for the distribution range of the species (N = 136, see Appendix A, Supplementary data), for a 236 bp segment we also found 23 novel haplotypes for the species as a whole (GenBank accession numbers: MG386937-MG386959).

Genetic and geographic structure

The AMOVA analyses showed no population genetic structure, with low F_{st} value for the scenarios proposed (Table 2). More than 97% of the variance was within population in all comparisons. This was further supported by the network, which showed no geographic substructuring (Fig. 2b). Moreover, F_{st} showed overall low genetic structure among colonies (range −0.0407 – 0.096; Table 1) with few significant comparisons (FN ≠ PQ, FN ≠ PC, FN ≠ PL, ER ≠ PC and ER ≠ PL; Table 1), suggesting some level of genetic structure between northern (FN and ER) and southern (PC and PL) colonies. Nonetheless, we found no evidence of IBD (Mantel test: $r = 0.259$, $P = 0.126$). The SAMOVA analyses indicated weak genetic structure among northern Patagonian colonies (Table 3). The largest mean *FCT* index was found for nine populations units (FN, ER, PB1, PQ, LR, BB, PB2, EM, and PC-PL; Table 3), suggesting the southern colonies differed from northern ones. Genetic landscape surface (AIS analysis) showed higher similarity among southern colonies than between northern colonies (Fig. 3), concordantly with SAMOVA analysis (Table 3).

Discussion

In this study we investigated the genetic structure of *O. flavescens* at a small geographic scale in a context of population recovery and recolonization following historical overexploitation. Despite extensive harvesting and extirpation of multiple breeding colonies during the first half of the 20th century, SASL retains high haplotypic diversity and low nucleotide diversity based on 504 bp of the D-loop. A matrilineal panmixia was observed among SASL colonies distributed over approximately 250 km in northern Patagonia.

Female philopatry and consequently strong genetic structure among colonies, has been inferred in other species of sea lions (see Introduction section for more detail), but SASL from northern Patagonia rookeries seems to be the exception suggesting a combination of ecological or life-history traits unique to this species in the Southwestern Atlantic ocean. Unperturbed populations may currently show panmixia across their range (Lowther et al., 2012), but

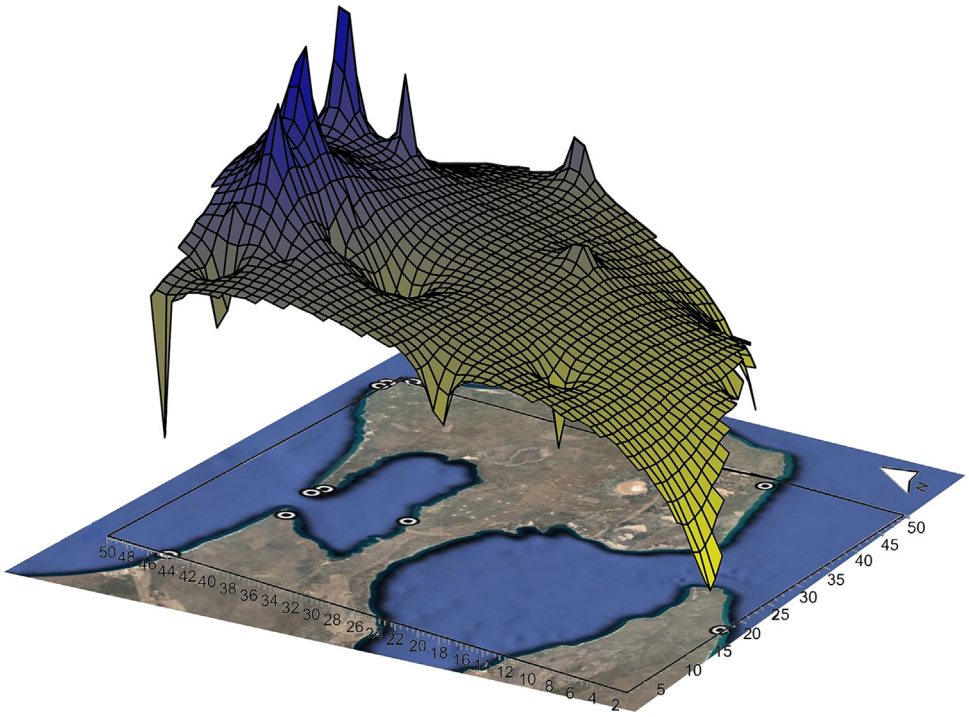

Fig. 3. Genetic landscape surface (Alleles in space interpolation plot) showing patterns of genetic distance for *Otaria flavescens* from northern Patagonia. *Y*- and *X*- axis corresponds to UTM north and east geographic coordinates, and the *Z*- axis (height) corresponds to genetic distance. Positive peaks represent areas with high genetic discontinuities (high pairwise genetic distance) and negative peaks or valleys are indicative of areas with high genetic similarities (low pairwise genetic distance).

Table 3
Spatial analysis of molecular variance, SAMOVA; *FCT* values obtained from mtDNA control region of *Otaria flavescens* from northern Patagonia.

Groups	*K*	*FCT*	*P*
(FN-ER) vs (PB1-PQ-LR-BB-PB2-EM-PC-PL)	2	0.03205	0.02053
(FN-ER) vs (PB1-PQ-PB2) vs (BB-LR-EM-PC-PL)	3	0.03877	0.0000
(FN) vs (ER) vs (PB1-PQ-PB2) vs (BB-LR-EM-PC-PL)	4	0.04042	0.0000
(FN) vs (ER) vs (PB1-PQ) vs (LR-BB-PB2-EM) vs (PC-PL)	5	0.04247	0.00098
(FN) vs ER) vs (PB1) vs (LR-BB) vs (PQ-PB2-EM) vs (PC-PL)	6	0.04541	0.00098
(FN) vs (ER) vs (PB1) vs (PQ) vs (LR) vs (BB-PB2-EM) vs (PC-PL)	7	0.05013	0.00196
(FN) vs (ER) vs (PB1) vs (PQ) vs (LR) vs (BB) vs (PB2-EM) vs (PC-PL)	8	0.05118	0.00293
(FN) vs (ER) vs (PB1) vs (PQ) vs (LR) vs (BB) vs (PB2) vs (EM) vs (PC-PL)	9	0.05309	0.02151

SASL population is recovering and recolonizing its historical distribution along the Patagonian coast, thus this maternal unstructured genetic population may possibly be the result of this process.

High mitochondrial h (0.889), low π (0.007), a significantly negative Fu's statistic, which is considered a powerful test to detect population expansion (Ramos-Onsins and Rozas, 2002) and the shape of the haplotype network all indicates that SASL have experienced a rapid population expansion (Avise, 2000), with accumulation of mutations (Grant and Bowen, 1998), represented by the high percentage of unique haplotypes. The population expansion detected here in SASL is similar to that in other otariid species (Lopes et al., 2015) and appears to arise from pre-sealing rather than post-sealing demography (Berry et al., 2012; Matthee et al., 2006; Weber et al., 2004). Several studies of marine animals, including SASL, suggest that the actual genetic structure of Atlantic populations was shaped by Late Pleistocene glaciations, that generated demographic contraction during the glacial period followed by population expansion when the glaciers retreated (Crespo et al., 2015; Feijoo et al., 2011; Hoelzel et al., 1993; Loizaga de Castro 2013; Matthee et al., 2006; Oliveira et al., 2017; Pimper et al., 2010; Siegel-Causey 1997; Túnez et al., 2007, 2010, 2013). Even though historical harvesting may have contributed in shaping the population genetic structure currently found in SASL, by means of local extirpation and subsequent recolonization from refugial populations, no bottleneck occurred (Feijoo et al., 2011; Hoffman et al., 2016; Túnez et al., 2007, 2010; Túnez et al., 2010). Moreover, low levels of genetic structure could also be the consequence of the homogenizing effect of gene flow at small scale (Wolf et al., 2008) or homoplasy at hotspots for substitutions in the mitochondrial control region (Túnez et al., 2013), a process already described in other mammal species (e.g., Fernando et al., 2000; Galtier et al., 2006; Herrnstadt et al., 2002).

The high mitochondrial h is reflected by the high percentage of novel haplotypes (75%) found in the present study. On one hand the new haplotypes described for the species suggest that mitochondrial diversity is not fully described yet. This could be solved with the inclusion of samples from other colonies within the study area and examining ancient DNA from SASL bones collected from remains at the time of intense human exploitation. On the other hand the high percentage of unique haplotypes (63.8%) found in the present study is representative of unique maternal lineages in almost all colonies (new and traditional). This result indicates that female SASL probably display two different strategies when they choose where to breed: some females are resident of -or return to- one particular colony and others disperse within the study area. Within a species site fidelity may vary with sex, age, and reproductive success (e.g., Cameron et al., 2007; Greenwood and Harvey, 1982; Meise et al., 2013; Switzer, 1997). Several studies have shown

that individuals have a higher probability of returning to breeding locations where they have bred successfully (e.g., Greenwood, 1980; Pyle et al., 2001; Weatherhead and Boak, 1986). It has been demonstrated that SASL pup survival is higher in large dense rookeries (i.e., traditional ones) than in isolated or marginal breeding areas (Campagna et al., 1992; Drago et al., 2011; Franco-Trecu et al., 2015). So if females choose to return to breeding locations where they have successfully raised offspring, and if this behavior lasts long enough, this will be reflected by the fixation of certain haplotypes. However male-mediated gene flow through sex-biased dispersal patterns or alternative mating tactics could also reduce the degree of population differentiation seen in microsatellites relative to maternally inherited mtDNA (Feijoo et al., 2011; Hoffman et al., 2016; Oliveira et al., 2017). The use of additional nuclear markers could help to elucidate patterns of genetic structure not identified in this study, as well as determine male role in the recolonization process. Nonetheless, other studies show that for adult females that are constrained by the energetic requirements of dependent offspring as well as by maintaining their own energetic needs, foraging success and thus the optimal choice of their foraging habitat is particularly important, which might explain why the correlation between genetic pattern and habitat is stronger for mitochondrial DNA (Jeglinski et al., 2015; Wolf et al., 2008).

Our results support the proposed hypothesis of female philopatry in SASL at small geographic scale. In central-place foraging otariids, breeding colonies tend to be located in proximity to suitable foraging grounds to facilitate offspring survival with normal delivery of nutrition to lactating offspring (Boyd, 1998). Therefore, adult females should be free to move between colonies that are located within range of a common suitable habitat (Lowther et al., 2012). Given that the mean maximum distance between northern Patagonian colonies is 267.32 ± 40.2 km (mean $\pm$ SD), females can move easily between colonies and find a suitable habitat to nurse and forage to maintain the survival of their calves. During the austral summer different oceanographic features (defined as: coastal upwelling events (Pisoni et al., 2014), thermohaline front (Piola and Scasso, 1988), the Península Valdés tidal front (Tonini et al., 2013) and insight gulf fronts (Pisoni, 2012)) develop generating high productive areas in northern Patagonia. This may be the force acting on SASL populations and resulting in a matrilineal panmixia among colonies sharing the same foraging habitat. At scales where alternative foraging locations become more costly to access, adult females should be more restricted in their dispersive abilities and genetic structure should then become more evident (Lowther et al., 2012).

All in all the present study shows a female panmixia, i.e., weak genetic population structure. However, SAMOVA and AIS analyses show some level of differentiation between northern and southern SASL colonies. Such differences should be taken into account when implementing management strategies. During the last decade tourism activities based on wildlife have grown massively. These activities use coastal fauna as a main attraction (Tagliorette and Losano, 1996) and since SASL group in colonies in predictable places every year, exhibiting striking behaviors during breeding season, they are very attractive to the public and profitable for the local industry (Kirkwood et al., 2006). Therefore, many cattle farms of the region with a coast line have developed private excursions focusing on coastal fauna, such as SASL. These activities could become conflictive, since only 16 of the 36 registered SASL colonies in the region are established within a system of national, provincial or private reserves, and only 9 have some degree of protection of individuals with the presence of gamekeepers (Dans et al., 2004). On the other hand, the social composition of most of the new colonies have a high percentage of juveniles (Dans et al., 2004; Grandi et al., 2008), which are more susceptible to the disturbance generated by the presence of visitors. As colonies are interrelated and therefore not independent (Grandi et al., 2008) a disturbance of the social structure of one colony may affect the dynamics of others. Such complex population dynamic should be taken into account when implementing management or conservation measures tending to the recovering of the population.

In conclusion, our result shows that the recolonization pattern of SASL from northern Patagonia was weakly related to female philopatry. Perhaps the effect of this behavior is attenuated and/or interacting with other processes like site fidelity to feeding grounds close to colonies (e.g., Lowther et al., 2012; Jeglinski et al., 2015), breeding success, terrestrial habitat selection for breeding and dispersal. The next step will be to analyze the relative importance and interaction of these other factors and processes to fully understand the formation of a new colony in the context of a recovering population with population expansion and recolonization.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.mambio.2017.12.002.

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