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Inferring the impact of past climate changes and hunting on the South American sea lion

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Abstract

Aim: Many pinniped species have experienced drastic demographic changes due to their interaction with humans. Most studies, however, have failed to detect recent bottlenecks in otariids from genetic data. The South American Sea Lion *Otaria flavescens* have a long history of population changes associated with interglacial expansion and hunting to almost extinction. This study aimed at investigating these different demographic fluctuations integrating population genetics and phylogeographic approaches.

Location: Pacific coast of South America.

Methods: Eighty-five samples from the Chilean coast were collected. Eight microsatellite loci were genotyped, and D-Loop mitochondrial DNA (mtDNA) sequenced. Genetic diversity was assessed, and tests of recent genetic bottlenecks were performed. Past demographic changes were inferred based on neutrality tests, adjustment of a sudden expansion model and Bayesian skyline plots. The magnitude and timing of the different population size changes were further investigated through approximate Bayesian computation (ABC) of coalescent inferences.

Results: The mtDNA shows relatively high diversity (h = 0.98 and π = 0.01) compared to most otariids, corroborates the divergence between Pacific and Atlantic populations, around 80,000 years ago (ya), and revealed a secondary contact zone in the Magellan strait. Microsatellite data support a second genetic discontinuity at 40°S, associated with post-glacial colonization of Patagonia. ABC analyses confirmed that glaciation affected the effective population size (N_e) all along the Pacific Coast, between ~50,000 and 15,000 ya. A strong reduction of N_e was also inferred for the hunting period (73–66 ya from sampling).

Main conclusions: *O. flavescens* shows clear signatures of susceptibility to climatic and anthropogenic disturbances and a spatial genetic structure that should be taken into account in the context of management and conservation policies. Yet, despite a recent history of demographic bottlenecks, the genetic diversity remains high, likely

a consequence of the demographic dynamics in otariids, characterized by large and connected metapopulations.

KEYWORDS

Bayesian Inference, genetic bottleneck, historical demography, hunting, *Otaria flavescens*, South America

1 | INTRODUCTION

Populations of large-size mammals have been affected by the conjunction of anthropogenic and climatic factors since the advent of *Homo sapiens*, driving many species to extinction (Koch & Barnosky, 2006; Mondanaro et al., 2019; Sandom et al., 2014). For Pinnipeds (seal and sea lions), as for many wild animals, the situation has not been different. Particularly, Pinnipeds are known to have suffered drastic population reductions associated with indiscriminate hunting and oceanographic fluctuations (Alastair et al., 2015; Crespo et al., 2012; Hoffman et al., 2016; Sielfeld, 1999; Sielfeld & Guzmán, 2002; Southward et al., 2005; Soto et al., 2006; Páez-Rosas et al., 2021), with anthropogenic effects being the principal driver of drastic demographic declines (Baylis et al., 2015; Crespo et al., 2012; Hoffman et al., 2016; Páez-Rosas et al., 2021; Sielfeld, 1999; Sielfeld & Guzmán, 2002; Soto et al., 2006; Southward et al., 2005). Recent demographic change due to hunting and climatic events may be difficult to reconstruct through genetic markers, because past drastic demographic change due to geological events may confuse those effects. Because of that, in order to investigate the genetic effects of recent events, the joint effects of ancient and recent demographic changes must be taken into account in order to better understand the demographic history of species.

Populations of seals (family Phocidae) and sea lions (family Otariidae) were substantially reduced by commercial sealers globally in the 18th and 19th centuries (Bonner & Laws, 1964; Lotze & Worm, 2009). Two species were hunted to extinction (Caribbean monk seal and the Japanese sea lion) and others reached a reduction over 90% (South American sea lion between 1937–1975; Gerber & Hilborn, 2001). Although most otariids have been managed to increase their population size after the reduction of hunting pressure (Lotze & Worm, 2009; Wickens & York, 1997), direct (i.e., intentional shooting by fishermen) or indirect fisheries interactions (i.e., competition for fish resources and fisheries-induced changes to ecosystems that eventually cause nutritional stress among pinnipeds) continue to be considered as the dominant threat along with climate fluctuation (Kovacs et al., 2012).

In the southeastern Pacific, pinnipeds have suffered at least two additional drastic reductions in numbers during the last 30 years due to El Niño Southern Oscillation (ENSO) effects (Bradshaw et al., 2000; Guinet et al., 1994; Le Boeuf and Crocker, 2005; Oliveira et al., 2006; Sielfeld et al., 1997; Soto et al., 2004, 2006; Trillmich et al., 1991). ENSO events reduce primary productivity directly influencing the distribution and abundance of fish prey (Thiel et al., 2007; Trillmich et al., 1991). These impacts are further increased by

competition with coastal fishermen as fisheries collapse. However, the demographic consequences of these perturbations are poorly understood. A literature survey of studies investigating historical population size changes in otariids (Table 1) reveals that most studies failed to detect genetic signatures of recent demographic bottlenecks. The large and fragmented distribution of most species of otariids may help to buffer short-term disturbances by allowing local populations to recover through repeated migration from resilient or non-affected populations (Lancaster et al., 2010; Pinsky et al., 2010; Raum-Suryan et al., 2002). Highly connected metapopulations promote the retention of large amounts of genetic diversity despite reported demographic perturbations at the local scale (Paijmans et al., 2020). Indeed, most pinnipeds are capable of long-distance movements either for foraging or for reproduction (Giardino et al., 2016).

However, genetic discontinuities have been observed in most species (O'Corry-Crowe, 2008 and Hoffman et al., 2009 for the Steller sea lion, *Eumetopias jubatus*; Corrigan et al., 2016 for the Elephant seal, *Mirounga leonine*). In South America, both the common sea lion, *Otaria flavescens*, and the South American fur seal, *Arctocephalus australis*, are subdivided into two highly differentiated and spatially segregated genetic lineages between the Pacific and the Atlantic coasts (Artico et al., 2010; Feijoo et al., 2011; Oliveira et al., 2008, 2017; Túnez et al., 2007, 2010). *O. flavescens* is also strongly subdivided between the Falkland Islands and South America (Hoffman et al., 2016) and between Argentina and Uruguay in the Atlantic Coast (Oliveira et al., 2017). In the Pacific Coast, the genetic structure of the species is still unclear, with different patterns between genetic markers (Oliveira et al., 2017) and not in agreement with its demographic dynamic that, based on abundance, distribution and distance connectivity network analyses, suggests the existence of a discontinuity distribution of the species at ~40°S (Weinberger, 2013). Interestingly, most discontinuities in these pinnipeds species are not correlated to geographic distance but rather to biogeographic discontinuities or to past climate and demographic processes. To understand the implication of these patterns in terms of connectivity restrictions, we must consider that spatial genetic structure can emerge because of the effect of strong genetic drift, such as expected during strong demographic bottlenecks or founder events. In this context, the actual magnitude of connectivity and its effect on the persistence of genetic diversity, even under well-known demographic bottlenecks, is far from being understood.

The lack of evidence for a recent bottleneck in most otariid species (Table 1) can also be attributed to methodological drawbacks of the genetic approach, which is based on a disequilibrium

TABLE 1 Spatial structure and demographic inferences from genetic data available for the species in the family Otariidae and some other pinnipeds

Scientific name	Common name	Distribution	Genetic marker (Sample size; Marker length or no. loci)	Historical demographic inferences	Recent genetic bottleneck	Bottleneck detection method	References
Arctocephalus tropicalis	Subantarctic fur seal	Islands at the south of Antarctic Polar Front	D-loop (103;316)	–	–	–	1
Arctocephalus gazella	Antarctic fur seal	Islands along the Antarctic Polar Front	D-loop (145–246;316–263); microsatellite (183–2000; 5–39)	Long-term stationary; recent bottleneck due to hunting	Yes (>90% reduction)	Rare alleles loss; ABC; He/Heq	1,2,29
Arctocephalus pusilus	Cape fur seal and Australian fur seal	South-West Africa	D-loop (118–106;344–361); cytB (42); microsatellite (183;5)	Expansion: ~18.000–37.000 ybp($\mu = 5.8E^{-7}$); Expansion: ~26.000 ybp(μ: $2.745E^{-7}$)	–	–	3,4
		South-East Australia		Expansion	–	–	5
Arctocephalus australis	South American fur seal	South East Atlantic (Argentina-Uruguay, Falkland Is.) South West Pacific (South Chile and North Chile-Perú)	CytB (15;445); microsatellite (266;7)	Expansion	Yes (mild)	Rare allele loss; He/Heq	6,7,8
Arctocephalus phillippii	Juan Fernandez fur seal	Juan Fernandez Island, Chile (South-East Pacific)	D-loop (28;315)	Stationary	No	Neutrality tests; Mismatch distribution	9
Arctocephalus fosteri	New Zealand fur seal	South Island of New Zealand South-West Australia	CytB (56;261); microsatellites (383; 11)	Expansion in the pre-bottleneck time, followed by bottleneck due to hunting	Yes (99% reduction)	ABC	4,10
Arctocephalus townsendi	Guadalupe fur seal	Guadalupe Islands, Mexico (East Pacific)	D-loop (33;181)	Expansion in the pre-bottleneck time, followed by bottleneck due to hunting	Unclear	Pre-post sealing haplotype count	11
Arctocephalus galapagoensis	Galápagos fur seal	West coast of the Galápagos	d-Loop (90;220); microsatellites (90;18)	Stationary	No	He/Heq; Garza's M	12
Zalophus wollebaeki	Galápagos sea lion	Galápagos	D-loop+cytB (336; 1,123); microsatellite (1,323; 25); SNP (24; 13)	–	No	He/Heq; Skyline plot	13
Zalophus californianus	California sea lion	North-East Pacific Ocean	D-loop (299–355; 355–550); microsatellite (335; 10)	Stationary	No	Rare alleles loss; He/Heq; Garza's M	13,14,15
Callorhinus ursinus	Northern fur seal	Sea of Okhotsk, Bering Sea, North Pacific Ocean (north of 34°N)	D-loop (414–619; 157–375); microsatellite (619;7)	Expansion:~11,000 ybp followed by Bottleneck ~2,000 ybp to present ($\mu = 5.8^{8}$); Expansion: ~23,000 ybp ($\mu = 2.745^{-7}$)	Yes (85% reduction)	Skyline plot; ABC	16,17

(Continues)

TABLE 1 (Continued)

Scientific name	Common name	Distribution	Genetic marker (Sample size; Marker length or no. loci)	Historical demographic inferences	Recent genetic bottleneck	Bottleneck detection method	References
Otaria flavescens	South American sea lion	South East Atlantic (Argentina-Uruguay, Falkland Is.)	D-loop (49-115;266-750); cytB (49;445); microsatellite (60-63;8-13)	Expansion in Argentina: ~27.000ybp and the Falkland Is.: ~12,000 (μ = 2.745E^{-7})	Likely	He/Heq; Garza's M; ABC	8,18,19,20,21
		South West Pacific (Chile-Perú)		Expansion ~11,500 ybp (μ = 2.745E^{-7})	-	-	16,22
Neophoca cinerea	Australian sea lion	South-West Australia	D-loop (149-464;360-478); microsatellites (149;16)	Stationary; South - West divergence ~130,000 – 190,000 ybp (μ = 7.5E^{-8})	-	-	23
Eumetopias jubatus	Steller sea lion	Sea of Okhotsk, Kuril Islands Mixed zone: Bering Sea, Aleutian Island, Alaska North-East Pacific Ocean (North of 30°N)	AFLP (285;238); D-Loop (336-1,654; 238-1,378); microsatellite (588-700;16-13); CytB (1,131;1,140)	Several retraction and expansion cycles: ~60,000 – 180,000 ybp (μ = 1.7E^{-7})	-	-	2,24,25,26
Mirounga leonina	Southern elephant seal	Antarctic polar front	D-loop (318;325); microsatellites (318;17)	Post-glacial divergence, and expansion in South Georgia	No	Garza's M	27
Phocarctos hookeri	Hooker's sea lion	New Zealand	microsatellite (17)	Bottleneck due to hunting	Yes (72% reduction)	ABC	28

Note: 1. Wynen et al. (2000, 2001), 2. Hoffman et al. (2006), Hoffman et al. (2009), Hoffman et al. (2011), 3. Matthee et al. (2006), 4. Lento et al. (1997), 5. Lancaster et al. (2010), 6. Oliveira et al. (2008), 7. Oliveira et al. (2009), 8. Túnez et al. (2007), Túnez et al. (2010), Túnez et al. (2013), 9. Goldsworthy et al. (2000), 10. Dussex et al. (2016), 11. Weber et al. (2004), 12. Lopes et al. (2015), 13. Wolf et al. (2007), 14. González-Suárez et al. (2009), González-Suárez et al. (2010), 15. Schramm et al. (2009), 16. Dickerson et al. (2010), 17. Pinsky et al. (2010), 18. Feijoo et al. (2011), 19. Freilich (2004), 20. Artico et al. (2010), 21. Túnez et al. (2010), 22. Hoffman et al. (2016), 23. Campbell (2006), Campbell et al. (2008), 24. Harlin-Cognato et al. (2006), 25. O'Corry-Crowe et al. (2006, 2014), 26. Phillips et al. (2009, 2011), 27. Corrigan et al. (2016), 28. Osborne et al. (2016), 29. Paijmans et al. (2020). Garza's M test is available in Garza and Williamson (2001). Rare alleles loss and He/Heq are available in the software BOTTLENECK (Cornuet & Luikart, 1996). ABC methods of these studies used DIYABC (Cornuet et al., 2010), except 29. who used *fast-simcoal2* (Excoffier et al., 2013).

between allelic diversity and heterozygote frequencies created by the loss of rare allele. First, this is one of the most commonly implemented methods to detect genetic signature, but it is based on a transient pattern expected to last no longer than a dozen generations (Luikart et al., 1998). Second, the detection of such signatures requires strong statistical power (Cornuet & Luikart, 1996). Two studies illustrate the effort required to successfully detect recent bottlenecks: 1,205 individuals and 17 microsatellite markers for the New Zealand Sea Lion (Osborne et al., 2016) and >2,000 individuals and 39 microsatellite loci for the Antarctic Fur Seal (Paijmans et al., 2020). Finally, the capacity to detect a recent bottleneck also relies on the magnitude of allele loss during the population size change (Cornuet & Luikart, 1996). Therefore, populations that have accumulated little allelic diversity prior to a bottleneck may fail to evidence any demographic change because the genetic differences are too smooth (see Paijmans et al., 2020 for a detailed assessment of pre-bottleneck scenarios). This may be the case in certain regions that have experienced relatively recent colonization, such as post-glacial demographic expansions. Signatures of ancient demographic changes, associated with the last glacial maximum (LGM) and subsequent expansion during the Holocene, are detected in most species (Table 1). The effect of such historical processes might leave long-lasting signatures on the spatial pattern of genetic diversity and seems to be associated with several genetic discontinuities reported so far in pinniped species (Freilich, 2004; Hoffman et al., 2016; Oliveira et al., 2017; Túnez et al., 2010). Therefore, any inference on recent demographic fluctuations should be made in the context of a long-term demographic history.

The present study investigates the joint effects of ancient and recent demographic changes in the highly mobile South American sea lion *Otaria flavescens* (Shaw 1800). *O. flavescens* is the most common otariid species on the Chilean coast and, along with the South American fur seal *Arctocephalus australis*, is the otariid with the widest geographic distribution in South America (Oliveira et al., 2012). As for many species of pinnipeds, *O. flavescens* is usually in conflict with fisheries, because it competes for the same resources Hückstadt and Antezana, 2003,Hückstadt and Krautz, 2004,Hückstadt et al., 2007; Sepúlveda, Pérez, et al., 2007; Vilata et al., 2010; Kovacs et al., 2012; Riet-Saprizaa et al., 2013). Consequently, the species was catalogued as a "damager" in Chile and was indiscriminately hunted to almost extinction between 1929 and 1953. After this period, it became protected, but hunting resumed between 1976 and 1993 because of the conflict with fisheries (Sielfeld, 1999). Although the species is now under protection, recent initiatives such as current estimates of population size and distribution to define culling quotas (Aguayo et al., 1998; Bartheld et al., 2006; Oliva et al., 2007; Oporto et al., 1999; Sielfeld et al., 1997; Sepúlveda et al., 2007b; Venegas et al., 2001) suggest that commercial hunting may start over again in the near future. In this context, understanding the demographic history associated with major perturbations is highly relevant for the design of sound conservation policies. The major spatial discontinuities of the genetic diversity identified so far (Artico et al., 2010; Feijoo et al., 2011; Hoffman et al., 2016; Oliveira

et al., 2017; Weinberger, 2013) seem tightly associated to glacial–interglacial population dynamics, following detection of post-glacial demographic expansion (Freilich, 2004; Oliveira et al., 2017; Túnez et al., 2010). This study aims at testing the role of glacial–interglacial dynamics and recent perturbations associated with hunting and/or oceanic oscillations on the demographic history of *O. flavescens* populations along the Pacific coast.

2 | METHODS

2.1 | Study area and samples collection

Tissue and hair root samples from South American sea lions were collected from 21 colonies distributed along the entire Chilean coast. Sampling was performed by a remote biopsy system modified after Hoberecht (2006) and Cuadron et al. (2007), between January and February 2008 and December and February 2009 (breeding season). The dart has a removable stainless steel tip that extracts rooted hair and skin tissue (5 mm diameter and 1 cm deep) from adult males and females. We also collected tissue samples from dead individuals found on shore or floating on water. The samples were preserved in 96% alcohol for subsequent genetic analysis.

2.2 | DNA extraction, PCR analysis and sequencing/ genotyping

DNA from tissue samples was extracted using the DNeasy Blood and Tissue Kit (QIAGEN) according to the manufacturer's protocol. DNA from hair was extracted following Caudron et al. (2007). A ~ 550-bp fragment of the mtDNA control region (D-loop) was amplified for the 72 sampled individuals using primers L15926 (Kocher et al., 1989) and CCR-DR1 (Tchaicka et al., 2007) (Appendix S1 for PCR conditions and reactions). PCR products were purified and Sanger sequenced bi-directionally. The D-loop sequences were aligned and edited according to the chromatogram using Proseq v3.0 (Filatov, 2002). All sequences were realigned using ClustalX v2.012 (Thompson et al., 1997). For 63 individuals, eight microsatellite loci were used for genotyping following Gemmell et al. (1997; Appendix S1). Microsatellite profiles were analysed using PeakScanner (Applied Biosystems), and data were binned using Flexibin (Amos et al., 2006). Sample metadata of the mtDNA haplotype and microsatellite results are available in Appendix S2. No DNA ambiguities were found for the mitochondrial data. Assessment of microsatellite null alleles, test for departure from HWE and linkage equilibrium were estimated in Arlequin v3.1 (Excoffier et al., 2005) and are presented in Appendix S3. Genetic diversity indices were calculated for mtDNA (number of haplotypes, haplotype and nucleotide diversity) and microsatellite loci (allele richness, private allele richness, observed and expected heterozygosity) in Arlequin v3.1 (Excoffier et al., 2005) and the correlation between the diversity index and sample size in R software (R Core Team, 2013). A rarefaction analysis was conducted in ADZE v1.0

(Szpiech et al., 2008), for a standardized estimation of allelic richness and private allelic richness.

2.3 | Phylogeographic analysis

The Chilean mtDNA haplotypes were aligned with additional 10 D-loop haplotypes of 453 bp available in GenBank, for genealogy and divergence analysis. The relationships between Pacific and Atlantic haplotypes were examined by constructing a median-joining network (MJN) using Network v4 (Bandelt et al., 1999). Bayesian estimation of divergence time between Atlantic and Pacific populations was performed with BEAST v1.5.4 (Drummond & Rambaut, 2007) using (GTR + G + I) evolution model proposed by MODELTEST v3.06 (Posada & Crandall, 1998). Following Ho et al. (2005) and Ho et al. (2007), we used a mutation rate of 0.2745×10^{-6} substitutions per site per year, estimated for the mtDNA control region of the Steller sea lion, *Eumetopias jubatus* (Phillips et al., 2009), to calibrate the phylogeny. A strict molecular clock model was applied with a Yule speciation process prior for branching rates. Markov chains were run for 10,000,000 generations and sampled every 1,000 generations with the first 1,000,000 generations discarded as burn-in. The three independent runs were combined using LOGCOMBINER v.1.8.3. The parameter analyses for convergence and effective sample size (ESS) were assessed using TRACER v. 1.4 (Rambaut & Drummond, 2007). Finally, Tree annotator v. 1.8.3 was used to create a consensus tree, and FIGTREE v1.4.2 (Rambaut, 2009) was used to visualize the tree.

The demographic history of *Otaria flavescens* in the Chilean Pacific coast was evaluated. Deviations from a neutral model of mutation–drift equilibrium were detected with Tajima's *D* (Tajima, 1989) and Fu's *Fs* (Fu, 1997) tests conducted in ARLEQUIN V3.1. To examine historical population dynamics, the pairwise mismatch frequency distribution was adjusted to models of sudden demographic expansion (Rogers & Harpending, 1992) in ARLEQUIN V3.1. and bayesian skyline plots were reconstructed in BEAST v1.5.4 (Drummond & Rambaut, 2007). A generation time of 10 years was considered based on average reproductive age, lifetime and evidence of senescence in otariids (Beauplet et al., 2006; Boyd et al., 1999; Grau & Acuña, 1998; Wickens & York, 1997) and the same mutation rate described for the phylogeny was used. Three independent runs of 10,000,000 generations Markov chains were performed and combined, each sampled every 1,000 generations, with the first 1,000,000 generations discarded as burn-in. This model was compared by nested sampling with the coalescent constant population size model using NS v1.0.4 (Russel et al., 2018), with 20 Particle Count and 5,000 Sub Chain Length. For both models, default priors were used and convergence was assessed in TRACER v. 1.4 (Rambaut & Drummond, 2007).

2.4 | Genetic structure and migration inferences

Microsatellite markers were used to infer the population genetic structure of the South American sea lion in Chile by performing a discriminant analysis of principal components (DAPC) implemented in ADEGENET (Appendix S4, Jombart et al., 2010). We used the 18 sampling locations of microsatellite samples as a priori groups (see Figure 1), retained 5PCs as the optimal number by cross-validation. Spatial structure was further inferred by microsatellite markers and mtDNA sequences separately using GENELAND package for R (Appendix S5, Guillot et al., 2004). For both analyses, spatial coordinates were used as prior and the correlated model of allele frequency was used, taking explicitly into account the presence of null alleles for diploid data (Falush et al., 2003; Guillot et al., 2008); 200,000 iterations were run, saving one of every 100 iterations and eliminating the first 300 as burn-in. To check for convergence, we performed ten independent runs and explored the MCMC outputs. We estimated the contemporary migration rate between genetic clusters by BayesASS 3.0 (Wilson & Rannala, 2003; Rannala, 2007); 5 runs with different seeds were performed with 1,000,000 iterations and 100,000 as burn-in for different delta values (0.1, 0.2 and 0.3), with an acceptance migration rate change of 37%.
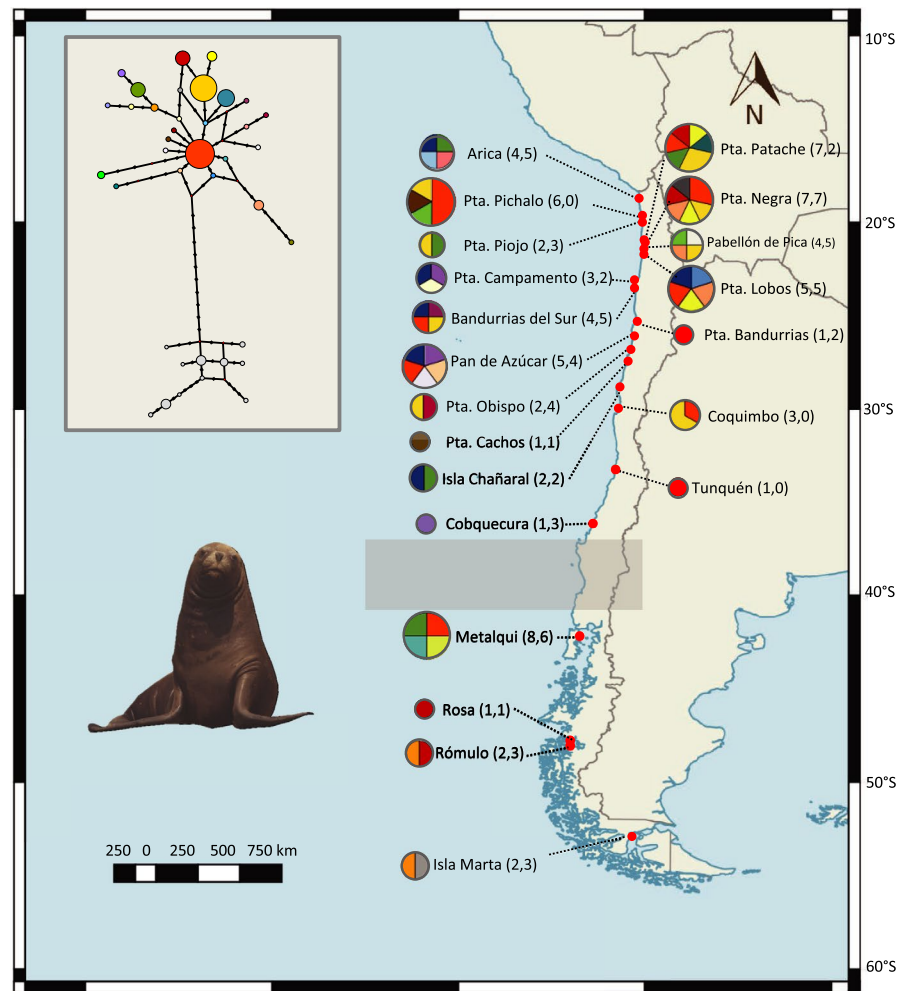
Genetic distances for the mtDNA sequence data were estimated using the JC69 mutation model (Jukes & Cantor, 1969) with g = 0.137 estimated by MODELTEST v3.06 (Posada & Crandall, 1998). For the microsatellite markers, the number of loci with allelic difference between pairs of individuals was used as the genetic distance.

The effective population size (N_e) was estimated using a maximum likelihood approach using the microsatellite data and integrating over the space of possible genealogies that could explain the observed data using a Markov chain Monte Carlo (MCMC) sampling. It was done in LAMARC 2.1 (Kuhner, 2006), which estimates the parameter Theta (θ) for each population (θ = $4N_e\mu$ with μ as the mutation rate per site per generation; Hartl & Clark, 2007; Kuhner, 2006) and the immigration rate (*M*) of each cluster. The number of effective immigrants per year (g) was also estimated, where g = $4N_e$m = θ*M*, m being the chance for a cluster to receive an immigrant per generation and *M* = m/μ (Beerli & Felsenstein, 1999).

2.5 | Recent demographic bottlenecks

The existence of a recent genetic bottleneck was tested for northern and southern genetic clusters with the program BOTTLENECK version 1.2.02 (Piry et al., 1999). First, the distribution of allele frequencies was examined to detect the loss of rare alleles, which is expected when a population passes through a recent bottleneck (Luikart et al., 1998). In addition, the sample heterozygosity ($H_e = 1 - \Sigma p_i^2$; p_i: frequency of allele *i*) at each locus was compared to the expected values under the assumption of allele mutation–drift equilibrium (H_{eq}). Populations that have experienced a recent reduction of their effective population size exhibit a faster reduction in allele numbers than He, creating a higher than expected heterozygosity under the assumption of mutation–drift equilibrium (Luikart et al., 2008). Wilcoxon signed-rank test (Cornuet & Luikart, 1996) was used for these comparisons.

FIGURE 1 Map of Chile showing the location of sampled haplotypes of the South American sea lion, *Otaria flavescens*. Numbers in brackets indicate the sample size for mtDNA and microsatellite markers, respectively. On the left, we show the median-joining network (MJN) of Chilean and Atlantic haplotypes (coloured and grey, respectively). The size of the circle in the MJN is proportional to sample size, the length of the branches is proportional to the polymorphic sites, and the colours represent the proportion of each haplotype in a location. The biogeographic discontinuity at ~40–42°S is indicated with grey squared area

Finally, the demographic disequilibrium of the population was assessed by calculating the ratio N_e/N, where N represents the census adult population size. Recently, reduced populations generally display a $N_e/N \ll 1$. For the estimation of N, we used the 2007 census values (Bartheld et al., 2006; Oliva et al., 2007; Sepúlveda et al., 2007b).

To explore the relative roles of post-glacial dynamics and hunting on present-day genetic diversity, we used an approximate Bayesian computation approach using the microsatellite data set in DIYABC (Cornuet et al., 2010) in 2 steps. The priors of population sizes and timing of the demographic changes are detailed in Table 2. We first compared five different scenarios (Run 1: S1 to S5) of demographic bottlenecks and/or founder effects associated with the last glacial period and the post-glacial colonization of Patagonia. Scenarios S2 to S5 assumed the effect of the hunting period during the 20th century to define the shape of the genealogy with different levels of complexity for the older events. Then, the best scenario was examined with or without the effects of hunting (S5 and S6). A total of 1,000,000 simulations per scenario were performed (see Appendix S6 for further details on summary statistics, model choice, model checking and posterior estimation of parameters).

3 | RESULTS

3.1 | Genetic diversity and population structure

A total of 28 haplotypes were identified for 555 bp of the mtDNA sequences from 21 colonies along the Chilean coast (Figure 1). Haplotype diversity of sea lion colonies did not show any significant correlation with sample size ($r = −0.20$, $p = .53$), and the rarefaction curves (Figure 2) indicated that sample size was acceptable. The genetic diversity for the Chilean population was high (h = 0.98 ± 0.01) compared to the post-sealing genetic diversity of other sea lion species (Wynen et al., 2000), but nucleotide diversity was low ($\pi = 0.01 ± 0.01$).

The median-joining network of the complete data set recovered two genetic clusters separated by 10 mutational steps (Figure 1): the Pacific cluster, which includes all our Pacific populations, and the Atlantic cluster. Haplotypes from both clusters were only found in the Isla Marta colony, which is located in the Magellan Strait, connecting the Pacific and Atlantic Oceans (Figure 1). The divergence time between the Pacific and the Atlantic clades was 79,828 years ago (ya) (CI$_{95\%}$: 48,437–116,110) when estimated using the constant population size coalescent model. It was very similar (i.e., 77,441 ya;

CI$_{95\%}$: 46,456–111,930) when estimated with the expansion population model.

The population structure evaluated using GENELAND for the Pacific Ocean shows different patterns for the mtDNA control region and microsatellites. For both markers, the analysis evidenced two genetic clusters, but separated at different latitude (Figure 2a, Appendix S5). For the mtDNA marker, the Pacific coast is conformed by one large cluster ($n = 70$) and a small one conformed by the southernmost colony, in the Magellan Strait ($n = 2$). Microsatellites, on the other hand, identify two genetic clusters separated approximately at 40°S (southern and northern clusters, named hereafter; with $n = 13$ and $n = 50$, respectively), with a significant F_{ST} value between clusters ($F_{ST} = 0.045$, $p < .001$). Results from the DAPC were in accordance with GENELAND results. DAPC revealed two slightly differentiated groups discriminated by the first component (horizontal axis), distinguishing the four locations from the Magellanic region but with some overlap with the remaining locations (Figure 2b, Appendix S4). The posterior probability of migration rate between clusters inferred by BayesASS is asymmetric: $m = 0.156 \pm 0.118$ from north to south and $m = 0.033 \pm 0.036$ from south to north. The microsatellite average H_e over loci for the northern cluster was 0.766 ± 0.408, while this was 0.791 ± 0.437 for the southern one. The rarefaction analysis showed that for both clusters, the allelic richness does not reach a plateau, but a constant and moderate increase with sample size (Figure 3), indicating that the sampling effort was sufficient to capture most of the allelic richness. The private allelic richness, on the other hand, stabilized at approximately 10 samples for each cluster indicating an acceptable assessment of the genetic diversity and private allelic richness. When the northern and southern clusters were combined, it increased constantly with sample size, not reaching a plateau.

3.2 | Demographic history

Neutrality tests for mtDNA indicated an excess of low-frequency alleles: Tajima's $D = -1.6$ ($p = .07$) and $Fs = -14.4$ ($p < .001$). The mismatch distribution of the Chilean haplotypes followed a unimodal distribution well-adjusted to the model of sudden expansion (SSD = 0.00137; $p = .73$), with $\tau = 3.28$ (Appendix S7), suggesting that the demographic change occurred approximately 13,300 ya. This historic expansion was further confirmed by the Bayesian skyline plot for the Chilean population that showed a smooth expansion process with more recent population stability (Figure 4) and with an overwhelming support over the constant population size model: log marginal likelihood equal to -947.7 (SD = 1.8) and -1038.4 (SD = 2.2), for the expansion and constant size model, respectively (BF = 90.7). The present-day female effective population size (N$_{ef}$) for the Chilean population was estimated at 63,400 (CI$_{95\%}$: 10,000–550,000) females.

For the northern and southern clusters identified by Geneland, LAMARC's coalescent-based estimates were θN = 24.64 and θS = 14.97, MN = 0.68 and MS = 1.49, respectively. With these population parameters, we inferred an effective population size (N$_e$) of 12,320 and 7,475 individuals for the northern and southern cluster, respectively. The resulting estimates of effective migration were 2.24 and 1.67 individuals per year from north to south and from south to north, respectively. For N$_e$/N estimation, population sizes of N = 41,571 adult individuals for the northern cluster and N = 32,571 for the southern cluster were considered, based on the 2007 census data (Sepúlveda et al., 2007b; Bartheld et al., 2006; Oliva et al., 2007). The ratio N$_e$/N was 0.296 in the north and 0.229 in the south.

Wilcoxon signed-rank and sign tests, under both mutation models of microsatellite evolution (SMM and TPM), indicated that the null hypothesis of mutation–drift equilibrium could not be rejected for both genetic clusters (Appendix S8). Additionally, the allele frequency distribution as revealed by the mode-shift indicator test indicated a typical L-shaped distribution for both genetic clusters, due to a large proportion of low-frequency alleles in each area (Appendix S8).

Approximate Bayesian computations revealed that scenario S5 was by far the best scenario to explain the observed data when comparing different possible effects of glacial–interglacial demographic dynamics, with a posterior probability of 0.9997 (run1; Figure 5,
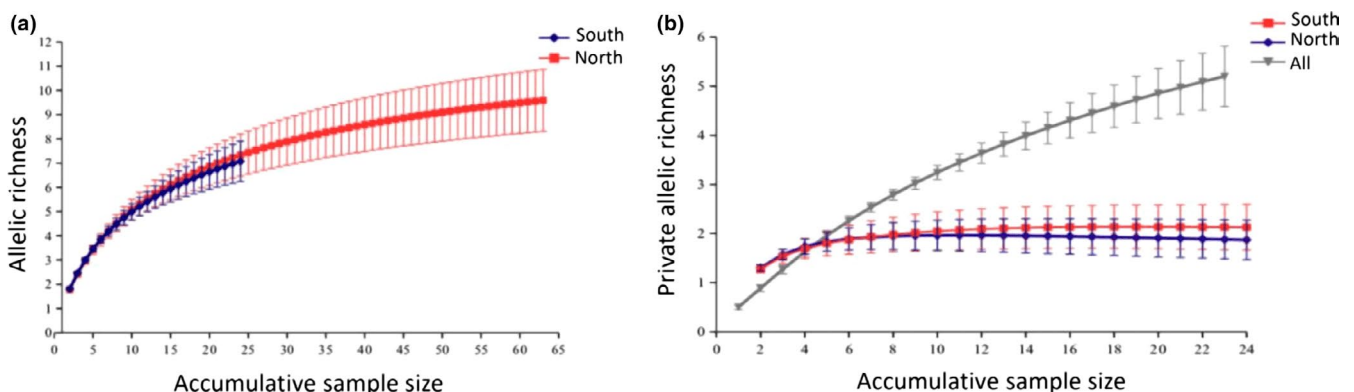

FIGURE 2 Rarefaction curve of allelic richness (a) and private allelic richness (b), for the cluster north of 40°S (North), for the cluster south of 40°S (South) and for both clusters together (All) of the South American sea lion (*Otaria flavescens*) from Chile. Microsatellite lines represent mean values for eight loci and associated standard error

Appendix S6). When comparing the different scenarios by new simulations with priors drawn from posterior distributions of S5 (shown in Table 2), S5 again had the highest posterior probability in 83.2% of the simulations, which is equivalent to a Type I error of 0.168. Posterior evaluation of scenario-prior combination revealed that the range of within-population diversity parameters obtained by

simulations most often included the observed values, but not the inter-population differentiation parameters (Appendix S6). Finally, run 2 confirmed that S5 performed best at explaining the observed data, with a posterior probability of 0.9677, suggesting there was a significant bottleneck effect due to hunting. The comparison of posterior estimates for N_e and N_b (using mode values in Table 2) suggest
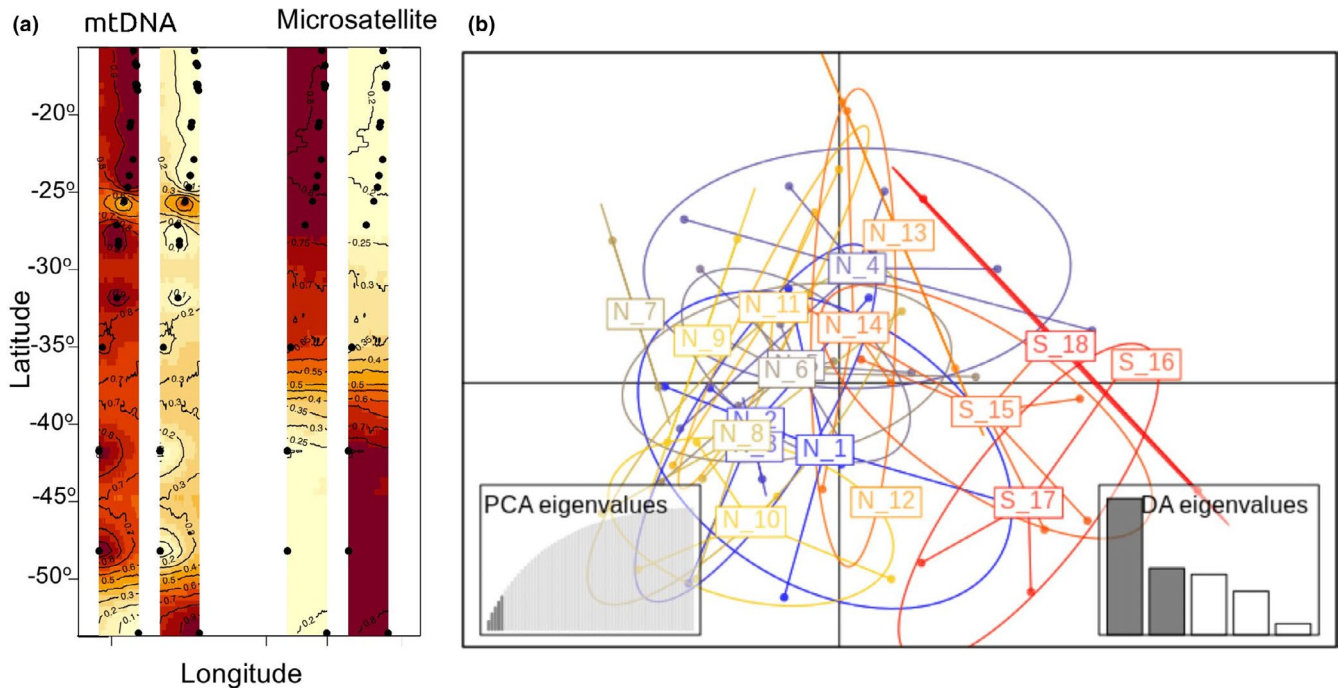

FIGURE 3 (a) GENELAND maps of posterior probability to belong to cluster 1 for K= 2 clusters (the highest probability of observing any K clusters), calculated for all pixels along the Chilean coast: derived from the analysis of the control region mtDNA sequence (555bp) of 72 South American sea lion (*Otaria flavescens*) individual from 21 locations (left; $n = 2$ and $n = 70$ for clusters 1 and 2, respectively) and for 8 microsatellite markers of 63 individuals from 18 locations (right; $n = 13$ and $n = 50$ for clusters 1 and 2, respectively). The highest probabilities of population membership to belong to cluster 1 are in light yellow and the lowest in red. (b) DAPC results using microsatellite markers; the name of the colonies is numbered from north to south, and the letter N indicates colonies from the northern cluster, and S from the southern cluster

FIGURE 4 Bayesian skyline plot showing the variation of N_e through time, as inferred from mtDNA D-Loop of the South American sea lion (*Otaria flavescens*) from Chile. Black line indicates average N_e, and thin grey lines indicate the limits of 95% posterior density. Grey area represents the last glacial period, and the blue area represents the last glacial maximum period
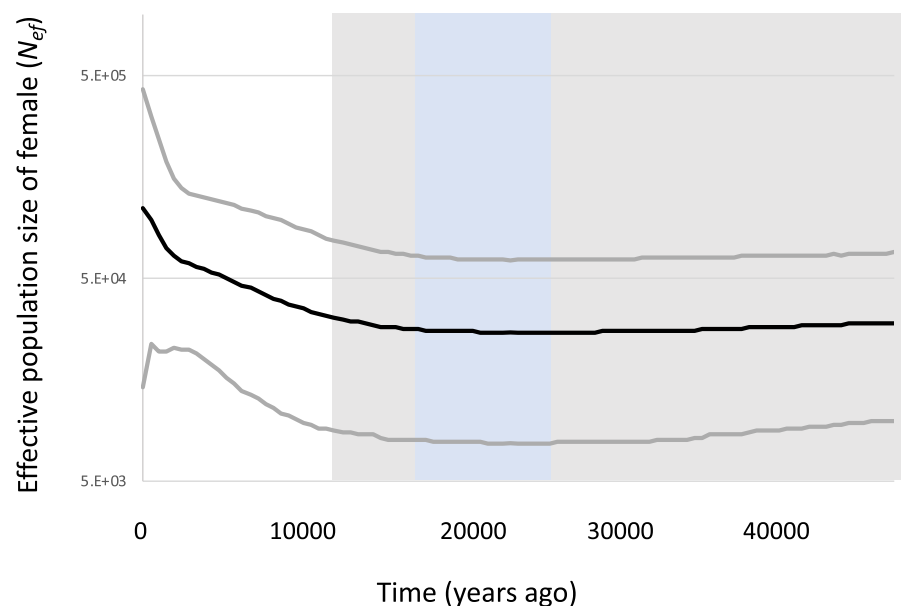
TABLE 2 Prior distribution and posterior estimation of demographic parameters of *O. flavescens* using the best fit scenario S5

Priors				Posterior estimates of scenario 5		
Parameters	Min	Max	Mean	Mode	q0.05	Q0.95
NN	100	100,000	67,500	66,400	36,700	96,200
NS	100	100,000	66,600	96,400	32,100	96,900
NNb	100	10,000	4,060	1,560	664	8,900
NSb	1	10,000	5,980	9,860	1,430	9,670
t1	10	100	61	73	20	97
db	1	100	28	7	3	70
t2	1,000	20,000	14,400	16,900	6,950	19,300
t3	15,000	25,000	17,900	15,100	15,200	23,100
t4	20,000	100,000	63,000	49,400	29,300	96,100
Mutation Rate	$1.00E^{-04}$	$1.00E^{-03}$	$1.58E^{-04}$	$1.00E^{-04}$	$1.00E^{-04}$	$2.67E^{-04}$

Notes: NN and NS are the present-day effective population sizes of the Northern and Southern clusters, respectively; NNb and NSb are the effective population sizes during bottleneck periods. t_x corresponds to time priors, expressed in years: t_1, end of the hunting bottleneck; t_2, end of the colonization of Patagonia; t_3, end of last glaciation; t_4, beginning of last glaciation. db: duration of the hunting bottleneck. q0.05 and q0.95 are estimates of the respective confidence limits.
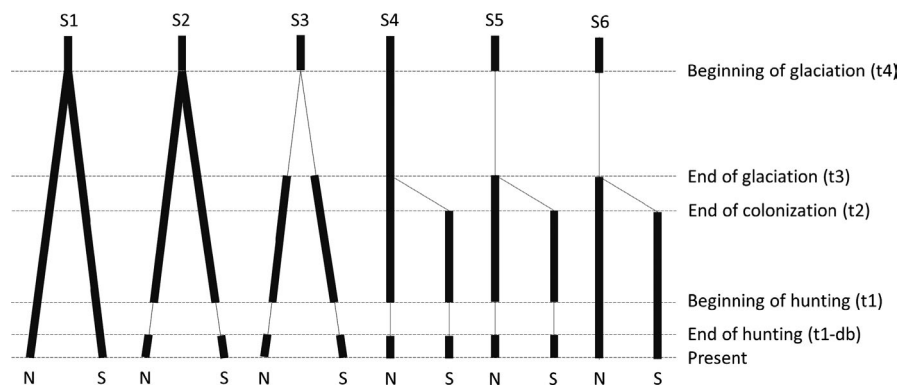

FIGURE 5 DIYABC scenarios representing the demographic history of the South American sea lion (*Otaria flavescens*) from the past (upper part) to present (lower part). Thick lines represent full population size (NN and NS in Table 2), while thin lines represent population bottlenecks (NNb and NSb n Table 2) in the six scenarios: S1: No bottleneck; S2: bottleneck caused by hunting; S3: bottleneck during glaciation and hunting; S4: founder effect in the southern populations after glaciation and bottleneck during hunting; S5: bottleneck during glaciation followed by founder effect in the southern populations after glaciation and bottleneck during hunting; S6: bottleneck during glaciation followed by founder effect in the southern populations after glaciation. Time scale indicated as in Table 2

a reduction to 2.6% of full effective size in the northern cluster and to 10.2% in the southern cluster.

From the mode of posterior distributions, it can be inferred that the effects of glaciation may have started about 49,400 ya (t4 in Table 2) lasting until about 15,100 ya (t3 in Table 2), when the northern population recovered its full size. The end of demographic expansion after the split of the Patagonian lineage (t2 in Table 2) was around 16,900 ya, suggesting that soon after the end of post-glacial melting, the southern population reached its full population size. The beginning of the recent bottleneck (t1 in Table 2) was estimated at 73 and 66 ya from sampling (for runs 1 and 2, respectively), fitting the first hunting period, before the first legal restriction to hunting. The recovery from this bottleneck is estimated in 7 years before sampling. These two estimates, however, had large and overlapping confidence intervals, suggesting the effect either lasted after the hunting period or was also caused by the strong ENSO events that occurred in 1982–1983 and 1997–1998 (Changnon, 2000; Quiroz, 1983), but lack of statistical power due to sample size cannot be rejected.

4 | DISCUSSION

4.1 | Divergence between Pacific and Atlantic coasts and the role of glacial cycles

A strong genetic divergence was observed between Atlantic and Pacific populations of *O. flavescens*. No mitochondrial haplotype was shared between the two coasts of South America, except in the Magellan Strait where both haplogroups are present. Interestingly,

the dating of the most recent common ancestor around 80,000 ya (confidence interval: 46,456–111,930 ya) suggests the genetic divergence started either during the previous interglacial period or during the early stages of the last glacial era. This result contrasts with previous estimation of divergence timing (1.0×10^6–3.3×10^6 ya; Oliveira et al., 2017), based on cytochrome b gene for which the authors calibrated the mutation rate based on the phylogenetic divergence between *Otaria* and other genus of otariids (Yonezawa et al., 2009). Such approach might suffer from some bias due to the combination of branching events occurring at very different time scales (i.e., among genera versus between populations within species; Ho et al., 2005). Our approach aimed to avoid such bias, although it may still retain other biases (i.e., single marker estimate, among others).

The differentiation between Atlantic and Pacific populations of *O. flavescens* seems best explained by allopatric and isolation events driven during the last glacial period. Indeed, the coastal ice sheet extended from 41°S to Cape Horn on the Pacific coast, over 1,800 km, whereas the Atlantic coast was completely ice free (Rostami et al., 2000). The coastal ice likely extirpated the colonies of *O. flavescens*, which strongly rely on the availability of rocky platforms for resting and nursing (Thompson et al., 1998, Riet-Saprizaa et al., 2013). Genetic divergence and eventually speciation associated with coastal ice formation in the Patagonia has been inferred in different aquatic organisms, including limpets (González-Wevar et al., 2011; Nuñez et al., 2015), mussels (Trovant et al., 2013) and shrimps (Bracken-Grissom and Felder, 2014). In all these cases, coastal ice was considered as a major driver of divergence either as an allopatric process or as a reinforcement of initially peripatric divergence (Trovant et al., 2013). Divergence times, when estimated for different organisms between Atlantic and Pacific coasts, varied between 100,000 ya (Nuñez et al., 2015) and the Plio-Pleistocene transition at 2.6×10^6–3.3×10^6 ya (Trovant et al., 2013), confirming that the evolutionary processes were tightly linked to the glacial cycles. Even if the estimated dates are hardly comparable between studies, because they rely on different mutation and demographic models, it is interesting to see that at least one example (Nuñez et al., 2015) is concordant with *O. flavescens* (80,000–100,000 ya). This further supports the influence of Patagonian habitat discontinuity during the last glacial period on the phylogeography of coastal marine species.

However, to fully understand whether the detection of individuals belonging to the Pacific and the Atlantic clades is indicative of ongoing admixture in the Magellan Strait for South American sea lion would require further sampling to characterize the shape and size of the secondary contact zone.

4.2 | Spatial genetic structure along the Chilean coast: biogeographic discontinuity at 40°S

The South American sea lion shows little genetic differentiation along the Chilean Coast, as previously described by other authors (Oliveira et al., 2017; Túnez et al., 2010). Besides that, the existence of a genetic discontinuity at ~40°S with asymmetric migration rate between zones (0.156 ± 0.118 from north to south and 0.033 ± 0.036 from south to north) coincides with changes in species demographic trends at this latitude and with more spaced and smaller breeding colonies at 32–40°S (Weinberger, 2013). Our findings of this genetic differentiation at this latitude can be affected by the small sample size for each cluster ($n = 50$ and $n = 13$ for the northern and southern cluster, respectively); despite that, this spatial subdivision is also consistent with the existence of a major geophysical, oceanographic and biogeographic discontinuity (Camus, 2001). Indeed, the West Wind Drift (WWD) divides at 40–42°S into the Humboldt Current flowing towards the north and the Cape Horn Current to the south (Escribano et al., 2003). The Humboldt Current is characterized by strong upwelling of cold, nutrient-rich water that promotes one of the highest primary productivity of the world (Thiel et al., 2007), whereas upwelling is absent in the Cape Horn current. There is also a sharp discontinuity in the shape of the coastline, being straight and open to the north, whereas it is a complex array of islands, fjords, channels and sounds to the south. Several other species, including mammals, show the same genetic discontinuity, (Pérez-Alvarez et al., 2015; Vianna et al., 2011). The case of the Chilean dolphin *Cephalorhynchus eutropia* (Pérez-Alvarez et al., 2015) shares several features with *O. flavescens* that would suggest a relatively high gene flow across the 40–42°S boundary: (i) both are capable of long-distance movement along the coast during their life-span; (ii) both are generalist in their diet, essentially based on pelagic fishes; (iii) both are capable of living in cold and temperate waters. However, both species show genetic discontinuity in the very same region despite the existence of no physical barrier to movement of individuals.

Therefore, one tentative explanation is that the genetic subdivision is maintained by ecological constraints to dispersal across the biogeographic boundary. Changes in sea lion prey may affect the foraging and feeding behaviour of these animals (Muñoz et al., 2013; Naya et al., 2002; Sielfeld, 1999; Soto et al., 2006; Thompson et al., 1998). Muñoz et al. (2013) identified a spatial variation in diet for South American sea lions that is concordant with the spatial genetic structure of ~40°S, suggesting ecological constraints may contribute to the persistence of this genetic discontinuity in spite of being a highly mobile species. However, it is not completely clear whether the spatial diet shift is a result of ecological divergence or an opportunistic behaviour.

Our findings support a break at ~40°S latitude using microsatellite data but not when using mtDNA, which show a different group in the southernmost location biased by the sample with the Atlantic haplotype, and unlike a previous study on the species, that grouped individuals a priori assuming a possible discontinuity at ~30°S (Oliveira et al. 2017) but did not evaluate the presence of a southern break. Differences between microsatellite and mtDNA markers may be a result of different demographic structures between males and females, or may reflect different temporal genetic patterns due to differences in mutation rates (Balloux and Lugon Moulin, 2002; Wan et al., 2004), together with a low differentiation between mtDNA haplotypes found for the species along the Pacific coast. Also, the use of a single organelle marker (mtDNA control region) with

smaller sample size by locality is expected to provide a less precise representation of the genetic structure of the species compared to 8 nuclear markers (Larsson et al., 2009). Notwithstanding this, for both males and females, high genetic connectivity along the coast is present, with discontinuities linked to marine biogeographic patterns and/or demographic history, instead of geographic distance and philopatry behaviour. Absence of genetic structure over large geographic scales seems to be a common pattern observed for pinnipeds species (Túnez et al., 2010 and Feijoo et al., 2011 for *O. flavescens*; Dickerson et al., 2010 for *Callorhinus ursinus* and Hoffman et al., 2006; Hoffman et al., 2009 for *E. jubatus*), despite their philopatric behaviour (Cassini, 2000; Hoffman et al., 2006; Pomeroy et al., 1994, 2000; Twiss et al., 1994; Wolf et al., 2007). This general pattern suggests that philopatry is not dominating the spatial distribution in these species, neither for females nor for males. Instead of that, high rate of exchanges among colonies seems to be a common process, supporting the metapopulation structure for these species. Moreover, evidence of patch colonization and patch extinction for *O. flavescens* reasserts these dynamics (Rodriguez & Bastida, 1998; Thompson et al., 2005).

The DIYABC analyses further suggest the existence of two independent glacial–interglacial dynamics: a long-term demographic decline during the last glacial period (Zech et al., 2008) in the northern cluster, and a founder effect associated with the re-colonization of the Patagonian fjords from the northern cluster after the onset of deglaciation (Mohtadi & Hebbeln, 2004). Population extirpation and post-glacial recolonization were inferred from phylogeographic studies on marine species including algae (see review by Guillemin et al., 2016), birds (Younger et al., 2016), mammals (Pérez-Alvarez et al., 2015) and invertebrates (González-Wevar et al., 2012, Nuñez et al., 2015; Trovant et al., 2015) and seems particularly common for marine predators (Younger et al., 2016). However, several species actually showed opposite patterns of genetic diversity, suggesting persistence in the glaciated region (Acosta et al., 2021; Unmack et al., 2009; Vianna et al., 2011; Xu et al., 2009; Zemlak et al., 2008, 2010). Because the sea lion is strongly dependent on the availability of rocky shores for the establishment of colonies, coastal ice was indeed a likely cause of extirpation all along Patagonia.

Another remarkable result is the detection of a glacial–interglacial demographic dynamics north of the ~40°S. In this region, no evidence of coastal ice has been reported, and so the population size changes must be explained by other factors. Most marine mammals seem to have reduced population sizes during the last glacial period (Younger et al., 2016). Specifically, changes in habitat quality were reported for the coast north of ~40°S: during glacial periods, the influence of the Antarctic Circumpolar Current (ACC) shifted towards the north leading to a northward shift of the Humboldt Current. This apparently caused a strong reduction of the upwelling condition between 41°S and 33°S, as evidenced by a reduction of plankton deposits in the region associated to LGM (Mohtadi & Hebbeln, 2004). On the contrary, long-term persistence of upwelling condition predominated along the coast north of 30–33°S. Evidence from biogenic compounds and foraminifera records suggest that upwelling

have even strengthened in this area at the beginning of post-glacial warming (11,000–17,500 ya; Mohtadi & Hebbeln, 2004). Upwelling is a major source of primary productivity, allowing the persistence of large fish populations, which are the principal feeding source of the sea lions. Therefore, changes in upwelling regimes during LGM post-glacial transition likely explain the genetic signature of demographic growth all along the coast.

4.3 | Hunting effects and conservation

The coalescent approach (i.e., DIYABC) was able to detect a recent bottleneck for this species associated with hunting, while N_e/N ratio and methods based on equilibrium genotypic diversity estimates were not. Several recent studies support the differences between statistical approaches for pinnipeds, while most studies failed to detect such bottleneck signatures (Table 1).

The N_e/N ratio was high and relatively similar in both the northern (0.296) and the southern (0.220) clusters and fell within what is considered as a typical range of values for marine species with large geographic range and moderate-to-high gene flow (Hare et al., 2011). Estimations of N_e/N from ecological data are generally close to 0.5 for populations with overlapping generations (Nunney, 1995; Nunney & Elam, 1994). These authors also found that it takes rather special circumstances for N_e/N to be outside the range of about 0.25–0.75, and populations in risk of extinction due to genetic depletion should have $N_e/N \ll 0.1$ (Nunney, 1995). The polygynous mating system is likely already reducing N_e compared to N, therefore restricting the detection of demographic drop-off. In addition, effective population sizes of 12,320 and 7,475 individuals, for the northern and southern cluster, respectively, are well above the minimum viable levels of N_e (~1,800 individuals) considered for vertebrates (Reed et al., 2003) and also above the critical values (~1,000 to 5,000) generally considered for securely persistent populations (Lynch & Lande, 1997). The coalescent approach used here (i.e., LAMARC) to estimate N_e integrates the many generations since the common ancestor. In this case, the long-term N_e estimate is a harmonic mean over generations, which makes it particularly sensitive to periods of small population size (Vucetich et al., 1997). Moreover, the DIYABC approach does not integrate gene flow within or among genetic clusters. Our model considered northern and southern clusters as single isolated populations, even though the DAPC and F_{st} results suggest the existence of a subtle genetic structure. This can introduce a bias that affects divergence and colonization time estimations (Zhivotovsky, 2001) and overestimates N_e (Wang & Whitlock, 2003). Despite this, our results indicate that contemporary migration rate is relatively low (<0.25) and that the effective dispersion of two individuals per year represents enough gene flow to account for the relatively low genetic differentiation observed. Also, although time estimations of past events can be affected by not integrating gene flow in the model, the estimated times of the start of the glaciation effects (~49,400 ya) and recolonization of Patagonia (~15,100 ya) and hunting period (between years ~1935–1942) are consistent with glacial advances at

~41°S of Chile, that reached its maximum at the pre-LGM (35,000–40,000 ya; Zech et al., 2008), post-glacial warming (11,000–17,500 ya; Mohtadi & Hebbeln, 2004) and the well-known dates of demographic decline by hunting (1929–1953; Sielfeld, 1999), respectively. Also, time estimation of recolonization of Patagonia is also consistent with results obtained by the mismatch distribution and skyline plot analysis and with results of Oliveira et al. (2017) of an expansion process (~10,000–13,000 ya).

The effective size during the hunting period was estimated to be lower than during the glacial period, with an average of nearly 4,000 individuals, with a mode at 1,600 individuals. Similar estimates have been reported for different pinniped populations in recent population declines (Table 1). Several studies on other otariids reported $N_e > 100,000$ (Curtis, 2009, Curtis et al., 2011), and up to 744,000 for the Antarctic fur seal, *Arctocephalus gazella* (Hoffman et al., 2011), despite was being devastated by hunting during the first decades of the past century. It seems therefore that the effective population size for *O. flavescens* in Chile is currently higher than any endangered species, but relatively modest compared to other pinnipeds affected by past sealing. Besides this, our results also show that the species is characterized by a relatively high genetic diversity, with an haplotype diversity of 0.98 for the Chilean clade, that was among the highest values described for otariids (see Oliveira et al., 2012).

The only two species (Guadalupe fur seal, *Arctocephalus townsendi* and northern fur seal, *Callorhinus ursinus*), for which the pre- and post-sealing molecular diversity were determined, show different patterns. The Guadalupe fur seal shows a decrease in haplotype and nucleotide diversities (Weber et al., 2004), while the northern fur seal did not lose molecular diversity, despite the evidence of a demographic bottleneck during intensive sealing (Pinsky et al., 2010). The low detection of genetic bottlenecks in otariids, despite the known demographic bottlenecks, can be attributed to different causes yet to be investigated: (i) the magnitude of population size changes might have been sufficiently moderate to maintain constant genetic diversity; (ii) the demographic perturbations were short enough (they lasted too few generations) to avoid the effects of genetic drift during periods of low population size; (iii) the migration among colonies is high enough to counteract the effects of local loss of genetic diversity due to population size changes; and (iv) the methods applied may have low statistical power.

In summary, evidence of demographic changes associated with major climatic transitions suggest that *O. flavescens*, as most of the otariids, is susceptible to environmental perturbations. Moreover, inferences of pre- and post-sealing dynamics of the southern sea lion in Chile suggest that species with high gene flow experienced moderate effects of indiscriminate sealing at the global scale. Some colonies of difficult access could have received less hunting pressure and likely acted as possible refuges for recolonization. However, these inferences did not explicitly integrate the effects of gene flow, possibly overestimating N_e (although the estimated values were concordant with other pinniped studies). Future studies should consider the use of genomic markers to increase statistical power to enable joint estimations of N_e and gene flow and better characterize the effects of metapopulation structure and dynamics on the resilience of otariid populations.

Finally, our study suggests that conservation and managing measures for this species should consider the existence of spatial genetic structure reflected in a northern and southern cluster of populations, the biogeographic importance of the zone around 40–42°S, as well as the role of high-density populations within each cluster for their potential to become source areas on immigrant to rescue other declining population along the coast.

CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13421.

DATA AVAILABILITY STATEMENT

Individual sample metadata of mtDNA haplotype and microsatellite results of the South American sea lion from Pacific coast are available on supporting information. D-loop mtDNA sequences were deposited in GenBank under accession numbers JQ434428 to JQ434457.

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BIOSKETCH

Constanza S. Weinberger was a PhD student developing conservation research on marine mammals, specifically investigating the effects of hunting and competition with fishermen on the resilience of the South American sea lion. Her thesis was co-supervised by **Pablo A**. **Marquet**, who is a theoretical ecologist and macro-ecologist, and **Sylvain Faugeron**, who is an evolutionary ecologist of marine species. **Juliana A. Vianna** is a specialist in conservation genetics of marine mammals and birds. As a team, the authors aim at integrating temporal and special scales of the processes affecting biodiversity and resilience of marine species.

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