# Latin American aquatic mammals: an overview of 12 years focusing on molecular techniques applied to conservation

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## Abstract

Ecological information useful for conservation purposes have benefitted from recent and rapid advancements in genetic techniques, revealing unknown aspects of behavior, natural

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Loizaga, R., Caballero, S., Cunha, H. A., Gravena, W., Herrerra-Trujillo, O., Lopes, F., Milmann, L., Ott, P. H., Pérez-Alvarez, M. J., Túnez, J. I., Durante, C. A., & Oliveira, L. R. (2023). Latin American aquatic mammals: an overview of 20 years focusing on molecular techniques applied to conservation. *Latin American Journal of Aquatic Mammals, 18*(1), 66-95. <u>https://doi.org/10.5597/lajam00303</u> mammal species, many of them with conservation concerns. Molecular markers have been used to define management units, settle taxonomic uncertainties, and control illegal wildlife trade, among others, providing valuable information to decision-making to conserve and manage aquatic mammals. We review genetic studies applied to conservation-related issues involving natural populations of more than 40 species of aquatic mammals in Latin America, covering four taxonomic groups. The main goal was to assess which genetic approaches have been used and to identify gaps in genetic research relating to geographic areas and species. We reviewed studies published in peer-reviewed journals between 2011 and 2022, and found that most were focused on population structure, phylogeography, gene flow and dispersal movements. The review revealed that researchers need to increase and improve the knowledge in those species which face major conservation concerns. Scarce findings were related to forensics and its application to wildlife trade. In the era of next-generation-sequencing techniques, just a few studies used genomics as a tool for monitoring gene diversity, an important goal to help us predict how species will cope with climate change events. Looking to the future we suggest which species, geographic areas and genetic studies should be prioritized in a scenario of climate change and increased human threats (e.g., fisheries bycatch, habitat degradation) and the urgent need for conservation actions. Finally, we highlight the benefits of the collaborative works and the necessity of generating a conservation genetic network, with an open

history, population structure and demography of several aquatic

agenda to discuss the local and regional problematics. All in all, we strongly emphasize the generation of critical information toward the effective conservation and management of aquatic mammals in Latin America.

## Introduction

Conservation genetics deals with understanding genetic factors causing rarity, endangerment, and extinction (such as inbreeding and loss of genetic diversity), applying geneticbased management to minimize these impacts, and using genetic markers to aid in resolving taxonomic uncertainties, to better understand species' biology, as well as in wildlife forensics (Frankham et al., 2019). It is an applied discipline based on evolutionary and molecular genetics and genomics. Ultimately, conservation genetics is the application of genetics to understand and reduce the risk of population and species extinctions (Frankham, 2019). The impact on genetic diversity is guite critical, as genetic variation is needed for species adaptation and taxa speciation (Hughes et al., 1997). Biodiversity is rapidly being lost due to direct or indirect human activity, therefore there is an urgent need to preserve and conserve species and their habitats.

Aquatic mammals have a long history of direct hunting and are subjected to negative effects of anthropogenic activities (Crespo, 2021). During the last decades, fisheries have grown exponentially in Latin American countries, resulting in overexploitation of several species (Salas et al., 2007; 2019). Some marine organisms have in fact been driven to extinction due to direct hunting, such as Steller's sea cow (Turvey & Risley, 2006). Others are close to extinction because of indirect catch; for example, the vaquita (Phocoena sinus) with only an estimated 10 individuals remaining, although not biologically extinct, is functionally so. These animals have become too rare to fulfill their natural roles in ecosystem function (Dayton et al., 1995; 1998). Nonetheless, genomic comparisons with other cetacean species and modeling indicated that vaguitas are unlikely to suffer from inbreeding depression. Therefore, if the risk of bycatch mortality could be eliminated there is a chance that this species will not go extinct (Robinson et al., 2022). Aquatic mammals play an important role in ecosystems as high trophic level predators, keystone species, and by their function in the transference and recycling of nutrients (Bowen, 1997). The extirpation of aquatic mammals can cause ecosystems imbalance and compromise their existence. The Atlantic and Pacific waters of Latin America are rich in aquatic mammals, totalizing 70 species: 50 cetaceans, 12 pinnipeds, four mustelids, and two sirenian species (Crespo, 2002; SOLAMAC, 2021). These two ocean basins comprise about 58% of all known living aquatic mammal species, including 20 species that are found nowhere else (Crespo, 2002). These mammals occupy a variety of habitats, from the pelagic continental shelf and coastal marine waters to estuarine, riverine, and lacustrine areas. Most of the species suffer some degree of interaction with human-based activities and their current distributions, dispersal patterns, breeding, and reproductive success are being influenced due to the strong exposure to these activities.

Oliveira et al. (2012a) reviewed studies published in peerreviewed journals between 1993 and 2010, in which genetic approaches had been applied to conservation-related issues involving natural populations of 25 species of aquatic mammals in South America. The authors found that most of the studies dealt with population structure, phylogeography, gene flow and dispersal movements, and just a few focused on evolutionarily significant units, management units, forensics, and conservation policy. It is fundamental to acknowledge that scientific research in general and conservation science in these South American countries are historically underfunded due to socio-economic and political difficulties. Despite so, conservation genetics research is an essential tool for a comprehensive approach, not only to increase the knowledge of individual species, but mainly to support more realistic conservation strategies and policies for Latin American aquatic mammals.

In this manuscript, we consulted all peer-reviewed studies using molecular genetic techniques, including new applications such as genomic studies and environmental DNA, that have been conducted on aquatic mammals in the period between 2011 and 2022, aiming at generating key information for management of these populations in Central and South America, and the Caribbean. Moreover, the present review compares results from the last 12 years to those compiled by Oliveira et al. (2012a) during the two decades before, recognizes in which genetic approaches the Latin-American research has moved forward, and identifies knowledge gaps in genetic research relating to geographic areas and species. All in all, the main goal was to discuss the future of molecular studies and to highlight priorities for the conservation of aquatic mammals in Latin America.

## Methods

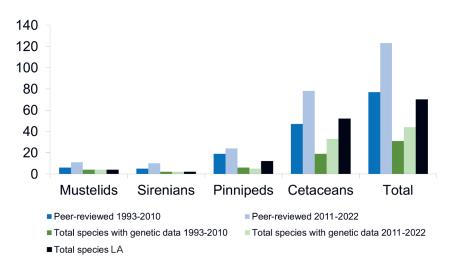
We reviewed studies published in peer-reviewed journals in the last decade, between 2011 and 2022, in which genetic approaches were applied to conservation-related issues involving natural populations of 44 species of aquatic mammals in Latin America and compared with the information in Oliveira et al. (2012a) (Fig. 1, Table 1). In addition, a more detailed comparison was made considering each species separately (Fig. 2). The results are divided into a summary of research in conservation genetics (according to order, suborder, family, species), molecular phylogenetics, barcoding, and wildlife forensics. Nevertheless, considering the current discussion about the taxonomic ranking of Cetacea, Mysticeti and Odontoceti (*e.g.*, Prothero et al., 2022), for simplicity, we mention these groups as unranked taxa.

## Results

**Conservation genetics** 

Cetacea, Mysticeti, family Balaenopteridae

*Megaptera novaeangliae*. Two of the seven stocks of humpback whales recognized by the International Whaling Commission in the Southern Hemisphere (SH) overwinter and breed in the tropical waters of the Atlantic and Pacific coasts of South America (Donovan, 1991). Information about the migratory



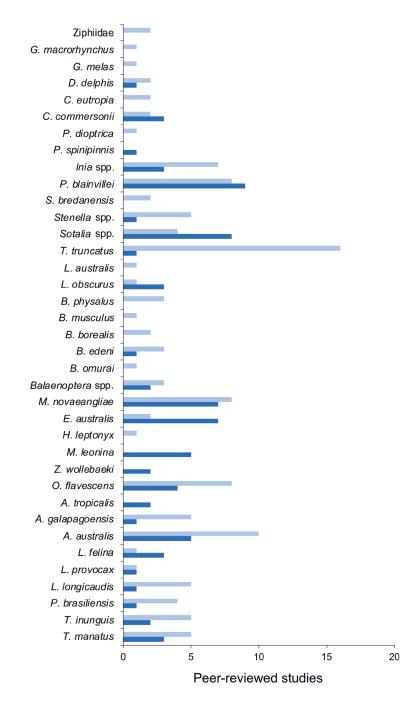
**Figure 1**: Aquatic mammal species richness worldwide (black bars); total species with genetic data in Latin America in two periods: dark blue bars: peer-reviewed studies during 1993-2010 and light blue bars during 2011-2022, shown in total, and broken down into mustelids, sirenians, pinnipeds, and cetaceans. Dark green bars show total peer-reviewed studies between 1993-2010, and light green peer-reviewed between 2011-2022.

Table 1: Latin American aquatic mammal species with genetic data, their IUCN status, and the number of genetic studies published in two periods of time (1993 – 2020 and 2011 – 2022).

Taxon	Species	Number species <sup>a</sup>	Category by IUCN <sup>ь</sup>	Peer-reviewed manuscripts 1993-2010	Peer-reviewed manuscript 2011-2022
Sirenia	Trichechus manatus	2 (2)	VU	3	4
	Trichechus inunguis		VU	2	5
Mustelidae	Pteronura brasiliensis	4 (4)	EN	1	4
	Lontra longicaudis		NT	1	1
	Lontra provocax		EN	1	2
	Lontra felina		EN	3	1
Pinnipedia	Arctocephalus australis	12 (4)	LC	5	8
	Arctocephalus galapagoensis		EN	1	4
	Arctocephalus tropicalis		LC	2	
	Otaria flavescens		LC	4	7
	Zalophus wollebaeki		EN	2	
	Mirounga leonina		LC	5	
	Hydrurga leptonyx		LC		1
Cetacea*	Eubalaena australis	52 (33)	LC	7	2
	Megaptera novaeangliae		LC	7	3
	Balaenoptera acutorostrata		LC	2	2
	Balaenoptera bonaerensis		NT	_	
	Balaenoptera omurai		DD		1
	Balaenoptera brydei		LC	1	1
	Balaenoptera borealis		EN		2
	Balaenoptera musculus		EN		1
	Balaenoptera physalus		VU		3
	Lagenorhynchus obscurus		LC	3	1
	Lagenorhynchus australis		LC		1
	Tursiops truncatus		LC	1	12
	Sotalia fluviatilis		EN	8	4
	Sotalia guianensis		NT		
	Stenella clymene				
	Stenella attenuata				
	Stenella coeruleoalba		LC	1	4
	Stenella longirostris				
	Stenella frontalis				
	Steno bredanensis		LC		2
	Pontoporia blainvillei		VU	9	7
	Inia spp.		EN	3	7
	Phocoena spinipinnis		NT	1	
	Phocoena dioptrica		LC	·	1

Taxon	Species	Number species <sup>a</sup>	Category by IUCN <sup>ь</sup>	Peer-reviewed manuscripts 1993-2010	Peer-reviewed manuscript 2011-2022
	Cephalorhynchus commersonii		LC	3	2
	Cephalorhynchus eutropia		NT		2
	Delphinus delphis		LC	1	3
	Globicephala melas		LC		1
	Globicephala macrorhynchus		LC		1
	Mesoplodon layardii		LC		1
	Mesoplodon densirostris		DD		,
	Ziphius cavirostris		LC		I

<sup>a</sup>Total number of species presents in Latin America and in parenthesis the number of studied species between 2011-2022. <sup>b</sup>Categories (IUCN 2022): DD, data deficient; EN, endangered; VU, vulnerable; LC, least concern.



**Figure 2**: Numbers of peer-reviewed papers on aquatic mammal species in Latin America published in two different time periods: dark blue bars showing data between 1993-2010 and light blue bars showing genetic data between 2011-2022.

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destination of these stocks has been investigated for a couple of decades using photo-identification and genetic information (Caballero et al., 2001; Andriolo et al., 2010). Genetic connectivity between the whales breeding in the Pacific coast of South America (breeding stock G) and the western Antarctic Peninsula (WAP) has been confirmed using mitochondrial DNA (Caballero et al., 2001, Olavarría et al., 2007) and genetic connectivity between the population that overwinters in the Brazilian coast (breeding stock A) and feeds around South Georgia and South Sandwich Islands (Engel et al., 2008). Mixed stock analyses and mitochondrial control region (CR) haplotype frequencies in an 18-year window confirmed temporal stability in the migratory connection between the Colombian breeding grounds (stock G) and the WAP feeding grounds (Albertson et al., 2017). However, little was known regarding the population structure, and population differentiation and levels of gene flow between the two breeding areas in South America. Cypriano-Souza et al. (2016) investigated the population structure and patterns of gene flow between these two breeding areas based on the analyses of mitochondrial DNA CR and 16 microsatellite loci (msDNA), finding significant genetic differentiation between these two areas for both markers. Some gene flow was found, being it low to moderate, asymmetrical, and mediated mostly by males. Nevertheless, the comparison of catalogues of individuals photo-identified in Puerto Cayo (Ecuador) and Abrolhos Bank (Brazil) revealed an inter-oceanic movement of an adult female humpback whale between these two breeding grounds off South America (Stevick et al., 2013). For the stock that breeds in the Eastern Pacific Ocean (stock G), some stratification has been found, with some whales feeding in the Strait of Magellan and Corcovado Gulf, off southwestern South America. Félix and collaborators (2012) studied the genetic diversity of humpback whales breeding in the Galápagos Islands and in the Ecuadorian coast, finding high genetic diversity and haplotypes shared with both the Antarctic Peninsula and with whales sampled in the Strait of Magellan, as well as changes in haplotype frequencies supporting stratification in these breeding grounds.

Rosenbaum et al. (2017) conducted the first circumglobal assessment of mitochondrial genetic population structure of humpback whales in the SH and Arabian Sea. The analysis of the (mt)DNA control region (311 bp) of 3,009 individuals sampled across the species' range in the SH, including Brazil (n = 164) and Colombia (n = 148) concluded, among other findings, that the breeding stocks A and G represent genetically differentiated population units that should be considered as separate units for management and regulatory assessments.

Recently Caballero et al. (2021a), based on the analysis of 15 microsatellite loci, evaluated the genetic connectivity at the individual level between the Colombian and Ecuadorian breeding grounds (n = 114), and the WAP (n = 578). This study evidenced individual recaptures for three whales sampled in Colombia and resampled in the western Antarctic Peninsula, as well as one recapture of a sample from Ecuador, from a whale also sampled in the WAP. Some of these recaptures came from a whale sampled in 1996 in the Pacific of Colombia, resampled in 2014 in the WAP, and one female sampled in 1997 in the Pacific of Colombia and resampled again in 1997 in the WAP. These data are important because they inform about longevity of these animals.

Balaenoptera borealis. The sei whale presents a disjoint geographic distribution (Rice, 1998). Significant genetic divergence between sei whales from the North Atlantic (NA) and North Pacific (NP) has been recorded, but limited samples from the SH have precluded a global analysis. Recently Taguchi et al. (2021) analyzed a sample from a stranded individual in southern Brazil, and revealed genetic structure, based on mitochondrial DNA (mtDNA) and microsatellite loci (msDNA) analyses, for the species with the population from the SH being genetically closer to the NP population than to the NA population. Pérez-Álvarez et al. (2021a) undertook a global mitochondrial DNA phylogeographic study based on samples from the mass mortality event occurred in southern Chile and new sequences from the NP. A marked phylogeographic structure was observed between the three ocean basins (NA, NP, and SH) with the highest genetic structure between NA-NP and NA-SH and, similarly to Taguchi et al. (2021), lower values between SH-NP. The results suggest a more recent separation between SH-NP and an absence of recurrent gene flow among all three populations, supporting an ongoing phylogeographic differentiation between them. Demographic analyses detected a recent reduction of population size in the SH and estimated effective population sizes larger than estimated census sizes, suggesting that most of the genetic diversity of pre-whaling populations is still retained. As mentioned in Pérez-Álvarez et al. (2021a), from a conservation point of view, the identity of each population and the importance of independent management is highlighted, being crucial to prioritize the recovery of population size of this species to limit any future loss of genetic diversity.

**Balaenoptera omurai**. The known distribution of the Omura's whale was limited to the western Pacific Ocean and the eastern Indian Ocean (IO). This species is difficult to identify and is often confused with the small form of Bryde's whale (Sasaki et al., 2006). Cypriano-Souza et al. (2016), using mitochondrial markers (CR, cytochrome *b*, and cytochrome *c* oxidase subunit 1 (*cox* 1)), identified as *B. omurai* a carcass of an individual stranded on the northeast coast of Brazil, representing the first record of the species in the South Atlantic Ocean, and expanding its global distribution range. The authors suggested the existence of an autochthonous Atlantic population of Omura's whale and highlight the importance of reassessing specimens previously identified as Bryde's whale in the area.

**Balaenoptera brydei**. For the study of taxonomy and population structure of Bryde's whale in South America, samples from Brazil, Chile, and Peru were gathered for mtDNA analysis (Pastene et al., 2015). Results suggested that whales from Peru, Chile and Brazil belong to *B. brydei* according to the taxonomic classification suggested by Wada et al. (2003). The Bryde's whale haplotypes from South America were clustered together with *B. edeni* brydei and clearly separated from *B. e. edeni*, and significant genetic differences between the population from Brazil and those from Chile and Peru were found. These results elucidate important aspects regarding the classification of individuals from the species in South America and its stock structure, indicating that individuals from Chile and Peru are connected but separated from those in the Atlantic Ocean (Pastene et al.,

2015). Although individuals are probably isolated because their range does not extend further than southern Brazil (~32°S) at the Southwest Atlantic Ocean (SWAO) (Milmann et al., 2020), future studies should include msDNA analysis and greater number of individuals, specially from the area to elucidate whether the isolation of this population is historical or still ongoing. There is also interest on a better understanding of stock structure of the species in the SWAO because an increase in stranding numbers of Bryde's whale was noticed in southeastern Brazil (Moura & Siciliano, 2012; Milmann et al., 2020). In this context, there is also a need for molecular identification of stranded whales that were decomposed, and not identified or previously identified as Bryde's whale, as they may be from Omurai's whale, which may look similar and had its occurrence only recently described in the area (Cypriano-Souza et al., 2016; see above). Since previous work with the species was from stranded individuals, it is important that future molecular analysis include more samples and biopsies from Bryde's whales in offshore areas, to confirm if there is either one form of *B. brydei* in the area or offshore and inshore ecotypes, such as in South Africa (Penry et al., 2018).

Balaenoptera bonaerensis and Balaenoptera acutorostrata. There are two recognized minke species, the larger Antarctic minke whale (B. bonaerensis), which is restricted to the SH, and the cosmopolitan common minke whale (B. acutorostrata). Additionally, three subspecies of the common minke whale are currently recognized: B. a. scammoni from the NP, B. a. acutorostrata from the NA, and the dwarf minke whale B. acutorostrata unnamed subsp. from the SH. After the study by Pastene et al. (2009), for the first time both the Antarctic minke whale and the three subspecies were included in msDNA analysis, and the results were congruent with those from mtDNA analysis, showing significant genetic differences among SWAO and Western South Pacific (WSP) dwarf common minke whales (Glover et al., 2013). Regarding the need for more samples from the common minke whale from the SWAO and for the use of both msDNA and mtDNA markers (Pastene et al., 2007, 2009; Glover et al., 2013), further genetic investigation using previous data from subspecies and species of minke whale (Pastene et al., 2009) was performed to verify genetic differences between the SWAO and the WSP common minke whale. Milmann et al. (2021) analyzed new samples of stranded common minke whales from Brazil (n = 18) and compared with samples from other oceanic basins (NP, Sea of Japan, NA, and WSP) analyzed in previous studies (Pastene et al., 2009). The SWAO population exhibited the lowest estimates of diversity for both genetic markers (msDNA and mtDNA) and the difference between populations was still evidenced. There were no shared mtDNA haplotypes among common minke whales from different locations. Moreover, the phylogenetic analyses placed SWAO in a different cluster from WSP and closer or within the NA clade. Based on the net nucleotide substitutions criterion (see Rosel et al., 2017), both populations of common minke whales in the SH were proposed as subspecies level (dA = 0.026). These results also showed a trichotomy between the SWAO and NA common minke whales, and authors suggested that taxonomy should be re-accessed for common minke whales globally, with new data from other localities in the SH, such as the western IO. For conservation

measures both populations should be considered as different Management Units (MU) (Milmann et al., 2021).

Atypical migrations of the Antarctic minke whale to the Northern Hemisphere (NH) and gene flow between species in the NA have also been identified. Glover et al. (2013) analyzed two hybrids, one of which was confirmed to be between the Antarctic minke whale and the common minke whale from the NA, which was pregnant from another common minke whale from the NA, showing hybrids between these two species are fertile and have the potential to reproduce. Subsequently, Malde et al. (2017) used whole-genome resequencing to identify a panel of diagnostic single-nucleotide polymorphisms (SNPs) permitting highly accurate identification of species, subspecies, F1 hybrids, and back-crossed whales in this species complex. Five panels of putatively diagnostic markers were established on a genotyping platform for validation of allele frequencies: two panels (26 and 24 SNPs) separated the two species of minke whale, and three panels (22, 23, and 24 SNPs) differenced the three subspecies of the common minke whale. The panels demonstrated the ability to accurately identify back-crossed whales up to three generations. The results and data derived from this study will allow us to address evolutionary questions related to the connectivity between this complex of species in all regions of the world.

Balaenoptera musculus. Two recognized subspecies of blue whales are present in the SH: the pygmy blue whale (B. m. brevicauda) and the true-blue whale (B. m. intermedia). Additionally, Branch et al. (2007) highlight that the Chilean blue whales (Southeast Pacific) are recognizably different in mean length, call type, and genetics, and are geographically distinct from the other SH subspecies, and therefore should be considered a different subspecies. Torres-Florez et al. (2014) analyzed msDNA and mtDNA data from southern Chile (SCh) waters and compared with blue whales from Antarctica (ANT), northern Chile (NCh) and the Eastern Tropical Pacific (ETP). No significant differentiation in haplotype frequencies (mtDNA) or among genotypes (nDNA) was found between SCh, NCh and ETP, while significant differences were found between those three areas and ANT; thus, the authors suggested the existence of at least two breeding population units (or subspecies). The lack of differences detected between SCh/NCh/ETP areas supports the hypothesis that eastern South Pacific (ESP) blue whales are using the ETP area as a possible breeding area. Later, Leduc et al. (2017) presented a comparison of blue whale samples from different parts of the Eastern Pacific and provided a context of their relationship within the pattern of variation in the SH. For it, they analyzed msDNA and mtDNA sequences on blue whale samples from ANT, IO, ESP, eastern North Pacific, and ETP. The authors found that the ETP is differentially used by blue whales from the northern and southern eastern Pacific, with the former showing stronger affinity to the region of Central America known as the Costa Rican Dome, and the latter favoring the waters of Peru and Ecuador. They also found a high degree of differentiation between Chilean blue whales and those from other regions of the SH, being compatible with the recently proposed subspecies status, but not all blue whales in Chilean waters can be assumed to be of this type. The authors also suggested that

the range of the proposed Chilean subspecies should include, at least seasonally, the waters of Peru and Ecuador.

**Balaenoptera physalus**. Fin whales are distributed across the temperate to subpolar waters of the world. Genetic studies of this species considering samples from Latin America have focused on understanding the population structure and taxonomy in the main oceanic basins. By 2018, three subspecies were recognized (Committee on Taxonomy, 2018), *B. p. physalus* in the NH, *B. p. quoyi* in the SH, and the pygmy fin whale, *B. p. patachonica* that was originally described from a specimen that stranded at the mouth of Rio de la Plata, Argentina, and later reported to the SA and the ETP off Ecuador, suggesting they may occur farther north as well (Archer et al., 2013; 2019).

To test if all NH fin whales belong to the same subspecies (*B. p. physalus*), Archer et al. (2013; 2019) studied the phylogenetic relationship of fin whales from three of the primary ocean basins in which they occur. the NA, NP, and Southern Ocean (SO), analyzing mitogenome sequences and SNPs. The results of both studies showed a high differentiation between the populations of the NA, the NP, and the SO. The authors proposed the North Pacific fin whale be recognized as a separate subspecies, with the name *B. p. velifera*. They also highlight the importance of incorporating samples from the Atlantic and South Pacific in future studies to assess whether there is structuring within *B. p. quoyi* in the SH, and such samples would be valuable for examining the validity of the low- to mid-latitude pygmy fin whales, *B. p. patachonica*.

Pérez-Álvarez et al. (2021b) extended the samples used by Archer et al. (2013; 2019) with new mtDNA sequences from the southeastern Pacific, including samples from north-central Chile and the Gulf of California. The results of that study confirm the strong genetic differentiation between NA, NP, and the SH previously reported (Archer et al., 2013; 2019). The authors found no evidence of genetic structure within the SH, suggesting the existence of a single taxon, so the pygmy fin whale, B. p. patachonica, could not be a valid subspecies, and they proposed that until there is evidence to positively support the validity of this subspecies, all SH fin whales, including those found in the mid-latitudes of the southeastern Pacific, belong to the previously described subspecies B. p. quoyi. Thus, currently the Society for Marine Mammalogy's Committee on Taxonomy (2022) recognizes three subspecies, B. p. physalus for NA fin whale, B. p. velifera for NP fin whale and B. p. quoyi for Southern fin whales.

#### Cetacea, Mysticeti, family Balaenidae

**Eubalaena australis.** The Southern right whale was once widely distributed in the SH ocean basins, but its populations were drastically decimated due to whaling during the 19<sup>th</sup> century. In the decade 2011 - 2022, only two studies were published on connectivity and population structure of Southern right whales in the SH. Carroll et al. (2019; 2020) established a long-term, large-scale collaboration on genetics of the species in order to combine new and published mtDNA and msDNA genetic data from all major wintering grounds and, uniquely, the South Georgia feeding grounds.

Carroll et al. (2019) added new data to those already available

to estimate the diversity of both mtDNA and nuclear DNA and inferred for the first time the population structure of Southern right whales at a circumpolar scale. For this, the authors included samples of mtDNA haplotype sequences and nuclear DNA microsatellite genotypes from Argentina, South Africa, southwest Australia, and New Zealand sub-Antarctic. The results confirm previous findings of hierarchical global population structure in mtDNA haplotype data (Patenaude et al., 2007), showing low but statistically significant differentiation between the Argentinean and South African nursery grounds at nuclear loci (microsatellite FST = 0.001, Jost's D = 0.004, p < 0.01), and a stronger differentiation in mtDNA haplotype data. Additionally, Carroll et al. (2019) suggested that currently the species has recovered part of its original distribution, occurring in large wintering aggregations and areas with sporadic sightings. The authors found greater support for the scenarios considering secondary contact, indicating that populations in different ocean basins were largely isolated and entered secondary contact in the last 25,000 years. They further suggested that the Southern right whales in the two ocean basins should be considered distinct population segments.

Subsequently, Carroll et al. (2020) added samples from Brazil, South Georgia (SG), and Chile-Peru to the published data set, to investigate the position of these previously unstudied habitats in the migratory network. The results of this study showed connectivity between Brazil and Argentina, including the movement of one genetically identified individual between the South American grounds, information that was only previously revealed by photo-identification matches (Best et al., 1993). However, statistically significant genetic differentiation was found between Southern right whales sampled in Brazil and Argentina in both mtDNA and microsatellite markers. Nevertheless, the magnitude of this differentiation was lower than that used to define southeast and southwest Australian right whale wintering ground as distinct stocks (Carroll et al., 2019). The authors believe that the differences between Brazil and Argentina reflect differences in the demographic aggregation of whales using each region, which probably is linked to female philopatry. Moreover, the authors found a single sample from Chile-Peru that had an mtDNA haplotype previously only observed in the Indo-Pacific and had a nuclear genotype that seemed admixed between the Indo-Pacific and South Atlantic, based on genetic clustering and assignment algorithms. The SG samples were more like the South American than the South African wintering grounds. Before Carroll et al. (2020), only Patenaude et al. (2007) published a comprehensive genetic study of the Southern right whale including four calving grounds (Argentina, South Africa, western Australia, and the New Zealand sub-Antarctic) and two feeding grounds (SG and south of western Australia). Patenaude et al. (2007) found using a phylogenetic reconstruction of the Southern right whale that haplotypes revealed two distinct clades that differed significantly in frequencies between IP and SWA oceans. Carroll et al.'s (2019; 2020) and Patenaude et al.'s. (2007) studies highlighted the importance of international collaborations to provide context for Southern right whales populations recovering or emerging, like the SG feeding ground, and those that remain critically endangered, such as Chile-Peru Southern right whale populations.

#### Cetacea, Odontoceti, family Pontoporiidae

**Pontoporia blainvillei**. The franciscana (Gervais & d'Orbigny, 1844) is a coastal and endemic species that ranges from the state of Espírito Santo, Brazil (18°25' S) to Chubut province, Argentina (41°10' S) (Bastida et al., 2007). Due to their coastal and estuarine habits, franciscanas are threatened by anthropogenic activities that cause habitat loss and degradation, and incidental catch in fishing gillnets is a major cause of non-natural mortality (Secchi et al., 2021). Franciscanas are currently regarded as the most threatened small cetacean in the SWAO, being categorized as vulnerable in the Red List of the International Union for Conservation of Nature (Zerbini et al., 2017). Regional assessments also recognize their endangerment, and the species is listed as critically endangered in Brazil, vulnerable in Argentina, and priority species in Uruguay.

Genetic data have been successfully used to aid in the delimitation of franciscana populations for more than two decades. Secchi et al. (2003) integrated preliminary genetic data to other lines of evidence and proposed four MUs for the species, termed Franciscana Management Areas (FMA). In the following years, Méndez et al. (2008; 2010) and Costa-Urrutia et al. (2012) provided evidence of microscale genetic differentiation within FMAIV (Argentina) and FMAIII (southern Brazil and Uruguay), respectively, based on mitochondrial and microsatellite data.

Cunha et al. (2014) analyzed mtDNA sequences from throughout the species' distribution. Their data revealed genetic differentiation between franciscanas from Espírito Santo and northern Rio de Janeiro, indicating that FMAI should be split as FMAIa and Ib, respectively. In addition, preliminary data also suggested genetic subdivision in FMAII, and the authors therefore recommended the provisional recognition of two MUs, corresponding to franciscanas from southern Rio de Janeiro and northern São Paulo (FMAIIa), and from central São Paulo to northern Santa Catarina (FMAIIb). Considering their original data and previous results by Costa-Urrutia et al. (2012) and Mendez et al. (2008; 2010a), Cunha et al. (2014) recommended an update of the original FMA proposal, which included FMAIa and Ib, the provisional recognition of FMAIIa and IIb, of two populations in FMAIII and of three populations within FMAIV. More recently, population structure was further assessed by Gariboldi et al. (2015; 2016). Their results were consistent with the existence of population subdivision within FMAIV. Combined, the data provided by Mendez et al. (2008, 2010a) and Gariboldi et al. (2015, 2016) indicated that up to five populations exist within FMAIV (Cunha et al., 2020).

The analyses of genetic diversity across the distribution of franciscanas also revealed a strong divergence between the mtDNA lineages from the north (Espírito Santo and northern Rio de Janeiro), compared to the south (southern Rio de Janeiro southwards) (Cunha et al., 2014). The authors proposed that the two lineages should be regarded as Evolutionarily Significant Units (ESU) *sensu* Moritz (1994), to reflect their distinctiveness and emphasize the need to preserve each ESU. This finding was reexamined by Nara et al. (2022) in a phylogeographic study with a large number of sequences from the entire distribution, including for the first time a large sample from Espírito Santo. Besides confirming the strong differentiation between the two

ESUs, Nara et al. (2022) dated the evolutionary splitting of the main lineages, which roughly correspond to the four main FMA, and discussed how they could have been caused by Pleistocene events. Finally, their population structure analyses detected nine populations, and although limited by lack or small sampling in some areas and by being based in a single mtDNA locus, it is the most geographically comprehensive analysis conducted to date. Analyses largely confirmed all previous studies and detected genetic distinction of franciscanas from Babitonga Bay in Brazil. The single exception to the abovementioned pattern of fine scale genetic differentiation is a recent study on the microscale structure of franciscanas in the entire coastline of FMAIa (Espírito Santo), which used a large sample (n = 68) and mtDNA and microsatellites (de Oliveira et al., 2020). That study confirmed that FMAIa has the lowest genetic diversity among all franciscana populations but did not detect differentiation along 190 km of the Espírito Santo coast, suggesting a single population (de Oliveira et al., 2020). In summary, the refinement of management units based on genetic data is still underway, but a clear picture of microscale genetic differentiation has emerged in the last decade and should not be neglected.

Genetic studies have also investigated the social structure of franciscanas. Costa-Urrutia et al. (2012), as Mendez et al. (2010), and Valsecchi and Zanelatto (2003) before, suggested that the species has a matriarchal structure. Mendez et al. (2010) went a step further to propose female philopatry in the species. This is a general pattern in mammals and has been used to explain population structure in many cetaceans. A combination of female philopatry and habitat specialization could explain the genetic differentiation of franciscanas among geographically close localities in FMAIII and FMAIV (Mendez et al., 2008; 2010; Costa-Urrutia et al., 2012; Gariboldi et al., 2015, 2016) and would have direct consequences for conservation. As a methodological note, specific microsatellite loci were developed for franciscanas, increasing the number of nuclear loci that can be used in studies of social structure and population genetics (Cunha et al., 2021).

#### Cetacea, Odontoceti, family Phocoenidae

*Phocoena* spp. Limited information currently exists regarding conservation genetic studies on the two species of the family Phocoenidae found in South America: the spectacled porpoise (*Phocoena dioptrica*) and the Burmeister's porpoise (*P spinipinnis*). Between 2010 and 2022 we only found one study focusing on the spectacled porpoise. In this work, researchers sequenced a fragment of the mtDNA CR from 50 stranded individuals from Tierra del Fuego, Argentina (Pimper et al., 2012). Since most of the samples used in this study came from highly degraded samples, including dry skin, bones and teeth, a short fragment was sequenced (380 bp). The authors found comparatively high levels of mitochondrial genetic diversity, like those found for other phocoenids, such as the harbour porpoise (*P phocoena*) (Rosel et al., 1999) and Dall's porpoise (*Phocoenoides dalli*) (Hayano et al., 2003).

#### Cetacea, Odontoceti, family Iniidae

Inia spp. Considered the largest of the freshwater dolphins, with the widest distribution, there is not a consensus about

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its taxonomic organization (da Silva et al., 2023). Inia dolphins are distributed in almost all rivers of the Amazon, including the Itenéz-Mamoré, the Orinoco and the Tocantins-Araguaia River basins, the latter largely disconnected from the Amazon Basin, discharging its waters directly into the Atlantic Ocean at the Amazon Estuary. Inia distribution is only limited at headwaters, by the small size of rivers, and by impassable rapids or waterfalls (Best & da Silva, 1989). Several studies described morphological differences between Inia populations, suggesting that dolphins from Itenéz-Mamoré should be considered a distinct species (Inia boliviensis) from, and dolphins from the Orinoco basin, a subspecies (Inia geoffrensis humboldtiana) of, the Amazon River dolphin (Inia geoffrensis geoffrensis) (van Bree and Robineau, 1973; Trebbau and van Bree, 1974; Pilleri and Gihr, 1977). Although Casinos and Ocaña (1979) contested these results because the characters used were too variable, da Silva (1994) proposed the same taxonomy based on morphological analysis of cranial characters and number of teeth. Nevertheless, only Inia geoffrensis has been assessed in the IUCN Red List, following the Society for Marine Mammalogy's Committee on Taxonomy that recognizes a single species with two subspecies (I. g. geoffrensis and I. g. boliviensis). Since 2018, Inia geoffrensis is considered endangered, facing several threats, and showing decreasing population number trends (da Silva et al., 2018b).

Most of the genetic studies focus on parts of the distribution of the genus, mainly to determine the taxonomy, diversity, and estimated time of divergence; therefore, there is still a lot to discover about dolphins in this species complex. Almost all the studies retrieved the same results, that dolphins from the Itenéz-Mamoré River Basin have distinct haplotypes (mtDNA) (Hollatz et al., 2011a; Gravena et al., 2014; 2015; Hrbek et al., 2014; Siciliano et al., 2016; Ruiz-García et al., 2018), sequences from nuDNA (MHC genes, Y chromosome regions, or introns) (Martínez-Aguero et al., 2006; Ruiz-García et al., 2008), and alleles (microsatellites) (Hollatz et al., 2011a; Gravena et al., 2014; 2015; Hrbek et al., 2014). Pilleri and Gihr (1977) proposed that I. boliviensis and I. geoffrensis from the Madeira and Itenéz-Guaporé rivers experienced allopatric speciation, probably due to the presence of 18 rapids in a 350-km section between Guayaramerín and Porto Velho (Cella-Ribeiro et al., 2013). The first study using mitochondrial markers also estimated between 5.3 and 6.5 Mya of divergence between the two Inia lineages (Banguera-Hinestroza et al., 2002). After that, other studies using larger sequences of mitochondrial markers estimated the divergence time between the lineages in 2.87 Mya (1.31 - 4.90 Mya) (Hrbek et al., 2014), and of 3.85 Mya (2.87 - 5.28 Mya) (Ruiz-García et al., 2018). Although the results are slightly different, they agreed that I. boliviensis and I. geoffrensis did not share haplotypes and diverged in the late Pliocene. The genetic distinction between the species was also observed in nuclear markers, in both neutral and adaptive markers (Martínez-Aguero et al., 2006; Ruiz-García et al., 2008; Hollatz et al., 2011a; Gravena et al., 2014; 2015; Hrbek et al., 2014). Even though Gravena et al. (2015) observed that downstream the Madeira River rapids there are hybrid specimens between the lineages already described, I. boliviensis and I. geoffrensis are different species with independent evolutionary trajectories, as has been shown in several species of cetaceans (Crossman et al., 2016).

In 2014, a new species of *Inia, I. araguaiaensis*, was described using mitochondrial and nuclear markers, as well as morphological data. Dolphins from the Tocantins-Araguaia River Basin showed different haplotypes, not shared with the other two lineages already described, meaning that there is no current gene flow, or that there has been no historical gene flow between them. In addition to that, their distinctiveness is manifested by diagnostic alleles and distinct allelic frequencies (Hrbek et al., 2014). Moreover, haplotypes from *I. araguaiaensis* were found in the uncertainty area described by Hrbek et al. (2014), downstream of the Tucuruí dam, which was the potential limit of their distribution (Siciliano et al., 2016).

#### Cetacea, Odontoceti, family Delphinidae

Cephalorhynchus commersonii. The Commerson's dolphin has the largest distribution area in the genus with two subspecies, C. c. comersonii in South America and C. c. kerguelenensis in the Kerguelen Islands (Dawson, 2018). Cipriano et al. (2011) characterized the amount and distribution of genetic information in the species along the southern Argentina coastline, which ranged between Puerto Deseado (48° S) and Strait of Magellan (52° S). Using mtDNA CR sequences (D-loop) obtained from skin samples (n = 57), the authors reported genetic diversity levels (overall h =  $0.671 \pm 0.106$  and  $\pi = 0.396 \pm 0.280\%$ ) in the same order of magnitude that previous studies conducted in the area (see Oliveira et al., 2012a) and no evidence of potential deviations from neutrality in each sampling location (D and Fu's F<sub>s</sub> statistics, p > 0.05). In addition, the study provided more evidence of significant population structure (overall F<sub>st</sub> = 0.21, p < 0.001) with reduced gene flow between local subpopulations. For this reason, and framed on conservation implications, Cipriano et al. (2011) suggested considering each sampling location as a separate management unit, to identify and reduce potential threats over the species. Recently, Kraft et al. (2021) evaluated the dispersal model proposed for the species including genetic information of both subspecies at biogeographic scale. Using new tissue samples of skin and published data of D-loop sequences (n = 256), the authors estimated diversity indices, genetic and phylogeographic structure and migration rates. Commerson's dolphin from South America showed levels of haplotype and nucleotide diversities of 0.699 and 0.39%, respectively. Also, genetic differentiations were found among sampling areas of C. c. comersonii; but the greater percentage of variation was explained among subspecies. These results were supported by gene flow estimation, which indicated different migration rates within South America regions, but no migration between them and Kerguelen Islands (KI). The results are consistent with the model of post-glacial colonization of KI by South American C. commersonii, followed by an ongoing divergence process and subspecies status. Despite advances in genetic studies of Commerson's dolphin that increased the knowledge at a broader geographic scale, there is a lack of information in its northern distribution. Furthermore, the studies in this region were carried out only using mtDNA as a molecular marker, revealing a large gap of genetic information about microevolution processes at different time scales. Therefore, more studies should be conducted on the species, which include the entire distribution and the analysis of nuclear molecular markers.

Cephalorhynchus eutropia. The Chilean dolphin is endemic of South America, occurring only along the Chilean coast from 30° S to 56° S (Dawson et al., 2018). Genetic studies have been conducted relatively recently on the species, where nuclear markers and mtDNA sequences were analyzed. Pérez-Álvarez et al. (2015) used 53 samples and 21 microsatellites loci to characterize the gene diversity. In addition, genetic differentiation was explored, reporting a strong genetic break throughout the species' distribution, without current gene flow and evident physical barriers. Therefore, two genetic populations, proposed as MUs, were defined, highlighting the need of identifying the current threats to which each of the Chilean dolphin populations are exposed, and design management strategies adjusted to each area in future conservation strategies. Subsequently, using mtDNA, the historical dimension of this genetic differentiation was explored; and combining both markers past and recent demographic changes were evaluated (Pérez-Álvarez et al., 2016). The southern population exhibited lower genetic diversity and signal of demographic expansion, associated with the Last Glacial Maximum. In opposite, the northern population showed a signal of stable population size in the recent past, which suggests a process of colonization from north to south after ice retraction.

Lagenorhynchus australis. Peale's dolphin is an endemic species of South America, with the main distribution between 38° S and 59° S in the Pacific Ocean and 44° S as the northern limit in the Atlantic Ocean, including the Falkland (Malvinas) Islands. In general, little is known about the species in comparison with other small cetaceans of the region. As far as genetic studies are concerned, there is only one regional-scale study located at the north of its distribution in a Marine Protected Area from the SWAO, in which mtDNA CR sequences were analyzed (Durante et al., 2020). From 23 skin samples, the authors estimated levels of h = 0.6725  $\pm$  0.0898 and  $\pi$  = 0.53 ± 0.32%. Also, they evaluated different demographic tests, which showed no evidence of historical demographic changes. Finally, genealogical relationships among haplotypes, including sequences of individuals from Falkland (Malvinas) Islands (n = 11) and Tierra del Fuego (n = 2) available in an online repository, suggested potential population subdivision for Peale's dolphin in the Atlantic Ocean. This is the first study on the species, and because of this, genetic variability at the phylogeographic scale and population differentiation remain unknown, as well as gene information from nuclear markers.

*Lagenorhynchus obscurus*. The dusky dolphin is the most abundant species of the genus. Its distribution is only in the SH in a discontinuous pattern associated with temperate coastal and shelf waters (van Waerebeek & Würsig, 2018). A new study along the Argentine coast was carried out on the species to evaluate spatial genetic structure and regional genetic patterns to propose conservation strategies and management (Loizaga de Castro et al., 2016). Using mtDNA CR from 119 samples over six locations distributed along the entire Patagonian coast, the authors identified two genetic populations which correspond to the continental and island regions ( $F_{CT} = 0.774$ ). Furthermore, the results showed a strong regional phylogeographic genetic

structure, defining a minimum distance of 50 km at which dolphin pods are independent and can be considered as operational units in conservation issues.

Sotalia guianensis and Sotalia fluviatilis. These dolphins were confirmed as separate species based on genetic and morphometric evidence (Cunha et al., 2005; Caballero et al., 2007). Their divergence was dated at 2.3 Mya in an analysis of complete mitogenomes of several odontocetes and the first mitogenomes of Guiana dolphin S. guianensis and tucuxi S. fluviatilis using a relaxed molecular clock (Cunha et al., 2011). Initial genetic analyses of three mitochondrial gene fragments evidenced high genetic diversity in both species. For Guiana dolphin, higher nucleotide and haplotype diversity was found in populations in northern South America (Colombia, Venezuela, and French Guiana), with lower levels of diversity found on the coast of Brazil. Significant population differentiation was found for all populations studied, suggesting reduced gene flow among locations (Caballero et al., 2010). For tucuxi, high nucleotide and haplotype diversities were found for all populations sampled, and connectivity between sampled areas was found, suggesting gene flow among areas in the Amazon Basin (Caballero et al., 2010). One question that remained from initial species designations for Sotalia was about the need for taxonomic clarification of the Sotalia populations found in the Orinoco River. An analysis of seven samples collected in the Orinoco River in 2015, using three mitochondrial genes and two nuclear autosomal introns, confirmed that the population found in the Orinoco is of S. guianensis, likely the result of a colonization event into freshwater, from coastal populations during the Middle to Late Pleistocene (640,000 ya) (Caballero et al., 2018).

Studies using microsatellite analyses for Guiana dolphin samples collected in different locations along the Brazilian coast, including Paraty and Sepetiba bays (Hollatz et al., 2011b) and locations along the coast of Espírito Santo State (Ywasaki-Lima et al., 2017), revealed slight but significant population structure, suggesting that their small body size, coupled with restricted home ranges and limited dispersal may be important factors shaping the population structure of this species. A more comprehensive study about the population structure, using both mtDNA CR sequences and 10 microsatellite loci on a higher number of samples from across their distribution confirmed strong population differentiation for Guiana dolphins, particularly north and south of the Amazon River mouth, suggesting that as a strong geographical barrier for this species. No measurable migration was evidenced among the S. guianensis populations sampled, suggesting that each of these needs to be managed as a separate conservation unit. Genetic diversity levels were higher in tucuxi than in Guiana dolphin and a west-east population structure pattern was evidenced for tucuxi, suggesting current gene flow occurring between neighboring groups.

The potential for hybridization between both *Sotalia* species has been suggested for their area of sympatry in the Amazon Estuary. Dos Santos et al. (2018) analyzed 51 samples from the region using a diagnostic PCR-RFLP system based on two nuclear introns, and all individuals were genetically identified as *S. guianensis*. Thus, up to date, no genetic evidence exists supporting the existence of hybrids. Only Guiana dolphin has

a confirmed distribution in the Amazon Estuary, suggesting that tucuxi is not distributed in the Amazon Delta (dos Santos et al., 2018).

Steno bredanensis. A first study by da Silva et al. (2015) investigated the phylogeography and population structure of the rough-toothed dolphins using mtDNA CR and cytochrome b sequences as well as mitogenomes. These analyses revealed significant differentiation among populations from different ocean basins (Atlantic vs. Pacific/Indian Ocean) but results were not conclusive regarding potential speciation within the genus. Additionally, these authors found significant differentiation also at the regional level between samples from the Caribbean, southeastern, and southern Brazil. Recent analyses with increased sample sizes and sequences from autosomal introns, which also included additional samples from the Eastern Pacific and an increased sample size from the Caribbean, confirmed these initial results, showing oceanic basin divergence and diagnostic characters suggesting recognition of two subspecies within S. bredanensis, one exclusively distributed in the Atlantic Ocean (Albertson et al., 2022).

Tursiops truncatus. This species has a worldwide distribution and is probably the most studied dolphin. However, its taxonomy is still controversial and recent publications have suggested new species designations for this genus, based on genetic and morphological evidence, one of them in the SWAO (Charlton-Robb et al., 2011; Wickert et al. 2016; Costa et al., 2022). Nevertheless, these taxonomic changes are still under debate, including the recognition of the Lahille's bottlenose dolphin, which inhabits the coastal waters of southern Brazil, Uruguay, and Argentina, as a valid species (Tursiops gephyreus) (Wickert et al., 2016). Currently, the Society for Marine Mammalogy's Committee on Taxonomy recognizes this coastal form as a subspecies (T. t. gephyreus). In recognition of the distinctness of this coastal form, the IUCN proceeded a separate assessment and recently classified the Lahille's bottlenose dolphin as vulnerable to extinction (Vermeulen et al., 2019).

In the last ten years, several publications have dealt with the genetic diversity and population structure of Tursiops truncatus around South America and in the Caribbean. Caballero et al. (2012), in a first comprehensive study that included samples from the wider Caribbean, showed the presence of two forms in this region. The "worldwide distributed form" and the "inshore" ecotype (following Tezanos- Pinto et al., 2009) were found, showing distinct haplotypes for each of these groups. The presence of the two forms varied according to the geographic location sampled, with the inshore ecotype being more common in the Bahamas, Cuba, and Mexico, whilst the worldwide distributed form was found more commonly in Puerto Rico, Colombia, and Cuba. Populations with a higher proportion of worldwide distributed form showed, in general, higher levels of genetic diversity, while populations with a higher proportion of inshore ecotype had relatively lower levels of diversity. Low female-mediated gene flow was detected but male-mediated gene flow seems to be happening between these areas. Population structure at both mtDNA and nuclear DNA was found, with Mexico showing significant differentiation.

Results from this study are relevant considering that Cuba sells dolphins captured in their waters to oceanaria around the world and knowing the genetic characteristics of these animals is important for their correct management in captivity, and to improve their local population management and capture sustainability.

Another study on the genetic diversity and population structure of *T. truncatus* in the Caribbean was carried out in the Archipelago of Bocas del Toro in Panama (Barragán-Barrera et al., 2017). This population has been negatively impacted by dolphin watching tourism, with animals moving away from their main feeding areas (Kassamali-Fox et al., 2020). In this population, only one haplotype was found, belonging to the inshore ecotype, and significant genetic differentiation was found between this population and all other researched populations in the Caribbean. No gene flow was evidenced even with a population in Costa Rica, the closest in proximity to Bocas del Toro. This result suggests that this population has been isolated in this area of Panamá for a long time and it may be more prone to extirpation over time if threats continue.

In the Pacific coast of South America, Bayas-Rea et al. (2018) investigated the phylogeographic patterns and population structure of bottlenose dolphins from the Gulf of Guayaquil, Ecuador, using both mtDNA CR sequences and partial mitogenomes. This study evidenced population differentiation between bottlenose dolphins from the outer estuary in the Gulf and the ones in the inner estuary. It also revealed lower levels of genetic diversity in the inner estuary dolphins. Results from this study agree with the latter studies on small coastal T. truncatus populations, suggesting that although the species may be widely distributed, a smaller coastal population may be at high risk due to anthropogenic activities. A second genetic study on common bottlenose dolphins along the Pacific coast of South America was carried out by Pérez-Álvarez et al. (2018). Coastal resident and pelagic non-resident T. truncatus have been described in north-central Chile. Using long-term residence data (over 13 years of photo-identification) and mtDNA data, higher levels of genetic diversity were found in the pelagic non-resident dolphins and a significant genetic structure was detected between both groups. The study proposed a population dynamic model for the resident population that may help limit inbreeding in this population. Additionally, the authors proposed a peripatric model of population differentiation with resident groups sporadically connected to the pelagic population, potentially explaining the origin of this unique resident population of bottlenose dolphins along the Chilean coast (Pérez-Álvarez et al., 2018).

In recent years, several studies have looked at the genetic diversity and population structure of bottlenose dolphins in the SWAO. Fruet et al. (2014), using information from both the mtDNA CR and microsatellites, found extremely low genetic diversity in a population found in southern Brazil, Uruguay, and northern Argentina. The authors also found significant genetic differentiation between bottlenose dolphins from southern Brazil-Uruguay and those from Bahía San Antonio in Argentina, suggesting that these groups represent distinct ESUs. This study was very relevant, since this population has been showing decline in abundance over the last two decades (Coscarella et al., 2012; Vermeulen & Brager, 2015). Moreover, a significant

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genetic population structure was found within Brazil-Uruguay, encompassing five coastal populations recognized as distinct MUs (Fruet et al., 2014). A fine-scale population structure among distinct groups of coastal bottlenose dolphins in southern Brazil was also revealed by Costa et al. (2015) and Genoves et al. (2020). Both studies found a high genetic structure and reduced gene flow among close populations despite the lack of visible geographic barriers. The existence of specialized feeding behavior associated with high natal philopatry of bottlenose dolphins in some of the studied estuaries was pointed out as an important component in promoting genetic structure in this region.

In a broader geographical scale, Fruet et al. (2017) analyzed genetic data (mtDNA and nuclear microsatellites) of common bottlenose dolphins with different external morphology collected in coastal and offshore waters in southern Brazil and Argentina. The authors found a high genetic differentiation between these two populations, referred by them as ecotypes, and suggested that the offshore ecotype should be considered as an additional ESU in the SWAO. Loizaga et al. (2020) analyzed new mtDNA sequences of the two bottlenose dolphin forms found along the northern Patagonian coast, Argentina. They found three new haplotypes recovered from nine samples; the most frequent haplotype represented the coastal morph (referred to as the endangered population of T. t. gephyreus), also two haplotypes showing falcate dorsal fin, a characteristic describing the oceanic morph (referred to as T. t. truncatus, which is classified as data deficient). This finding suggests that both morphs may exist in sympatry in Argentina, and despite being preliminary, hints at an unexpectedly higher genetic diversity of matrilines than previously anticipated (Loizaga et al., 2020).

A comprehensive study of bottlenose dolphins in Brazilian waters was carried out by Oliveira et al. (2019). The authors analyzed mitochondrial and nuclear data of 109 bottlenose dolphins from tropical and subtropical waters of the SWAO, including both offshore and coastal populations. It was also the first genetic study that included individuals that were morphologically identified as belonging to T. truncatus and the putative T. gephyreus. A clear mitochondrial genetic difference was found between the two forms, with the specimens identified morphologically as T. gephyreus forming an exclusive clade. Nevertheless, the nuclear data indicates the existence of some current or recent mixing between the two forms, precluding a clear decision about the validation of *T. gephyreus* as a full species status. The authors also found a strong population genetic structure among the specimens morphologically identified as T. truncatus, revealing at least three distinct management units: 1) Saint Paul's Rocks; 2) north and northeast of Brazil; and 3) Campos and Santos basins, extending at least to the southernmost part of Brazil. The specimens morphologically identified as T. gephyreus were found exclusively in the southern region of the SWAO and seem to be endemic of very coastal (< 10 m depth) and estuarine waters. Costa et al. (2021) also compared morphological and genetic data (mtDNA CR and 10 microsatellite loci) from samples collected from two forms in southern Brazil and found strong congruence between morphological and mitochondrial and nuclear divergence. Nevertheless, the authors suggest that the two forms seem to

be in a process of ecological divergence leading to speciation, since it was not possible to rule out some gene flow. In view of that, the authors support the recognition of the two forms as the subspecies *Tursiops t. gephyreus* (SWAO coastal ecotype) and *T. t. truncatus* (offshore ecotype, which includes the SWAO and Western North Atlantic offshore dolphins) (Costa et al., 2021). Regardless of the taxonomic issue above, both studies (Oliveira et al., 2019 and Costa et al., 2021) reinforced the importance to recognize this coastal form as a distinct management unit.

Stenella spp. Some species within the genus Stenella have been studied in South America and in the Caribbean. An initial study by Caballero et al. (2013) presented information on the population structure of the Atlantic spotted dolphin (Stenella frontalis) that included samples from the Caribbean (n = 6; Puerto Rico, Colombia, British Virgin Islands, Bahamas, and Dominica) and southeastern Brazil (n = 9). The CR of the mtDNA and an intron of the autosomal alpha-lactalbumin gene were used in this study. When compared with CR sequences previously obtained from samples from the Azores, Madeira, Gulf of Mexico and Northeastern Atlantic, five new haplotypes were found for the Caribbean samples and three new haplotypes were detected in samples from southeastern Brazil. For the alphalactalbumin intron, six alleles were detected in total, four of which shared between southeastern Brazil and the Caribbean. Population differentiation was detected between the Caribbean and southeastern Brazil at the  $F_{st}$  level, but not at the  $\Phi_{st}$  level. Southeastern Brazil did not show significant differentiation when compared to the Azores and Madeira. In a recent study that included a higher number of mtDNA sequences from both the Caribbean and from northeastern and southeastern Brazil as well as from Uruguay, population structure was found between a group of samples from oceanic origins: those from Azores, Madeira, the Canary Islands and the Mid-Atlantic Bight; those from the Caribbean and northeastern Brazil; and those from southeastern Brazil and Uruguay (do Amaral et al., 2021). Such population differentiation pattern could be explained due to isolation by distance, in which genetic distance can be correlated with the geographic distance between sample locations. Environmental heterogeneity was found to explain the population differentiation.

The second *Stenella* species that has been more widely studied in South America is the spinner dolphin (*S. longirostris*). A study investigating the genetic diversity and population structure of this species in the Fernando de Noronha Archipelago in Brazil by analyses of the mtDNA control region and 10 microsatellite loci found no population structure among sampling locations but identified two unique haplotypes only found in samples from this location when compared to previously published sequences worldwide and what appears to be two distinct genetic lineages in the Archipelago (Faria et al., 2020).

A recent study (Faria et al., 2022) analyzed the population structure of five *Stenella* species (*S. longirostris*, *S. attenuata*, *S. clymene*, *S. frontalis* and *S. coeruleoalba*) along the Brazilian coast and in Fernando de Noronha Archipelago. The authors analyzed three mitochondrial gene fragments (COI, cytochrome *b* and CR) and found high haplotype and nucleotide diversity overall for all species. Clear haplogroups were formed for *S.* 

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attenuata, S. frontalis and S. longirostris, but S. clymene and S. coeruleoalba shared haplotypes. For that reason, the study suggested that introgression and current gene flow is still occurring within species belonging to this genus along the Brazilian coast. The striped dolphin has also been studied using mtDNA sequences (COI, cytochrome *b* and CR) from specimens collected in northeastern Brazil, Gulf of Mexico and the northwestern Atlantic (Nara et al., 2017). Although results are preliminary due to small sample sizes, they suggested the existence of differentiated populations in those three areas. Phylogenetic trees built using COI and cytochrome *b* markers and sequences from the other four *Stenella* showed paraphyly of *S. clymene*, a finding consistent with the introgression hypothesis mentioned above.

Delphinus delphis. Until recently, the common dolphin included two species, the short-beaked common dolphin (Delphinus delphis) and the long-beaked common dolphin (Delphinus capensis) (Committee on Taxonomy, 2022). Two genetic studies were conducted with common dolphins over the last decade in Latin America, mainly focusing on taxonomic identity. Cunha et al. (2015) analyzed 37 samples from Brazil and Argentina's coasts, including specimens with the long- and short-beaked morphotypes, along with 260 cytochrome b sequences from all the ocean basins (southeastern, northeastern, northwestern, and central Atlantic; northeastern and southwestern Pacific, Indian "tropicalis form") including the type localities of *D. delphis* and D. capensis. Results indicated a single species in the Atlantic, D. delphis, and suggested that D. capensis was an invalid taxon. This conclusion was recognized by the Committee on Taxonomy of the Society for Marine Mammalogy, that endorsed the discontinuation of the use of D. capensis. Finally, Farías-Curtidor et al. (2017) determined the taxonomic identity of specimens collected in northern Colombian waters. Genetic barcoding and phylogenetic analyses using two mtDNA markers, D-loop, and cytochrome b, also indicated that these specimens are genetically closer to the short-beaked common dolphin. Further studies in areas of South America that are still unsampled or have been poorly sampled should be conducted.

Globicephala spp. Two studies have been conducted on species of the genus Globicephala in South America and the Caribbean. A first study analyzed mitochondrial DNA CR sequences and microsatellites for Globicephala macrorhynchus, the short-finned pilot whale, in the Caribbean. Samples were collected from various stranding events in Puerto Rico, the British Virgin Islands, Jamaica, and Trinidad and Tobago. This study found low genetic diversity overall in these groups, but one unique haplotype was found for the Caribbean, when sequences obtained in this study were compared with sequences from other studies that included samples from the Western North Atlantic, Hawaii, and the South Pacific. Low mean relatedness was found among stranded animals in each event (Téllez et al., 2014). The second study was conducted for the long-finned pilot whale Globicephala melas. This work investigated the global phylogeography for this species, including new data from the Southeastern Pacific, obtained from animals from two mass strandings in southern Chile. Significant genetic differentiation was found among sampling locations compared to the Mediterranean, SH and NA. Samples from southern Chile were clustered with samples from Tasmania and New Zealand, and low levels of genetic diversity, both at the mitochondrial and nuclear level, were found but higher than those found for the NA and Mediterranean populations (Kraft et al., 2020).

#### Cetacea, Odontoceti, family Ziphiidae

Information about genetics of beaked whales in Latin America is almost inexistent. The few studies found involve stranded specimens from Chile and basically are related to the use of genetic tools to confirm species identity or to analyze the phylogeography of the specimens in a global perspective. Español-Jiménez et al. (2020) provided the first genetic information (mtDNA CR sequence) of the strap-toothed beaked whale (*Mesoplodon layardii*) in Chilean Patagonia. Single samples from Cuvier's beaked whale (*Ziphius cavirostris*) and Blainville's beaked whale (*M. densirostris*) from Chile were also recently included in genetic global analyses, using both double-digest restriction associated DNA (ddRAD) and whole mitochondrial genome (mitogenome) (Onoufriou et al., 2022).

#### Order Sirenia, family Trichechidae

Several studies over the last decade have presented results of genetic analyses conducted in both the Antillean (Trichechus manatus) and Amazonian (T. inunguis) manatees. The work by Satizábal et al. (2012) presented a comprehensive analysis on the genetic diversity and phylogeography of both species using samples from Peru and Colombia and control region sequences as well as 15 microsatellite loci. In Colombia, the Antillean manatee is found mainly in the Magdalena, San Jorge, Sinu, and Orinoco rivers. Strong mitochondrial genetic structure was found for different river basins in Colombia, as well as in the Amazon. Females were philopatric, while males dispersed, demonstrating male-biased gene flow for both species. Such pattern was in contrast with previous findings in manatee populations inhabiting marine environments, suggesting less environmental restrictions for dispersal than those found in coastal habitats. These results were relevant for conservation and management, as animals should be reintroduced to areas in which their mitochondrial lineage was detected. Also, previous studies suggested T. inunguis as a panmitic population (Vianna et al., 2006).

Some recent studies have focused on hybridization between *T. manatus* and *T. inunguis*. Hybridization between these two manatee species was first confirmed by Vianna et al. (2006), using microsatellite markers and mitochondrial control region sequences. The study by Lima et al. (2019) used both mitochondrial control region sequences and sequences from the nuclear intron RAG1. This study demonstrated that the wild manatee population along the Guianas coastaline and Amapá State (Brazil) is the result of hybridization and introgression between Antillean and Amazonian manatee. The authors suggested that this particular population is probably locally adapted to an estuarine habitat that is under the influence of the Amazon River plume. Another study investigated this same phenomenon in these areas using genomic tools such as SNPs derived from ddRAD and sequences from nuclear and

mitochondrial genes (Vilaça et al., 2019). This study presented a hypothesis on how *T. inunguis* may have inhabited the Amazon River plume and this allowed them to colonize streams in the Guiana coastline. These authors suggested the need to define this area as a special conservation area for this hybrid population.

Another study by Luna et al. (2021) investigated the genetic diversity and population structure of both Antillean and Amazonian manatees in the Amazon River, the Brazilian coast, and Venezuela and the Guianas by means of mitochondrial control region sequences and microsatellite loci. This study found differentiation between the Venezuela/Guianas samples and the Brazilian coast, as well as strong differentiation between the Amazonian and Brazilian coast samples. This study did not find evidence of hybridization in the samples analyzed.

Lastly, a recent study by Caballero et al. (2021b) presented an update on the phylogeography of *T. manatus* and *T. inunguis* in Colombia, using samples from new geographic regions that were not sampled in the earlier study by Satizábal et al. (2012). This study improved resolution confirming strong genetic differentiation between the Magdalena, Sinu, and Orinoco rivers. This study also identified newly described haplotypes found in Canal del Dique, an artificial channel connecting the Magdalena River with the Bay of Cartagena, constructed in the 16th century. The Canal del Dique is highly polluted, which makes for a surprising discovery of manatees living in this region. This study also presented information about the use of a relatively new molecular tool, environmental DNA, to detect the presence of manatees in different regions. This tool implies the collection and filtering of water through filters of 0.8 µm. These filters are then used to extract DNA and to amplify fragments for particular genes, for example the mitochondrial 12S gene, allowing for metabarcoding and species identification from these environmental samples. In this study, eDNA allowed detection of manatee DNA in the mouth of the Atrato River and Canal del Dique. Such information is important to identify areas of the country in which to start conservation initiatives and programs.

#### Carnivora, family Mustelidae

Pteronura brasiliensis. The giant otter is found in the Orinoco, Amazonas, and Parana basins, and the hydrographic networks of the Guianas. It is currently classified as endangered as a direct consequence of overhunting during the last century (Groenendijk et al., 2021). Pickles et al. (2012) assessed levels of genetic diversity and investigated patterns of population structure in several remnant populations along the distribution range of the species using fecal and museum samples, and 13 microsatellite loci. All populations displayed moderate to low levels of heterozygosity and allelic richness, and low effective population sizes. Population structure analyses were congruent with previous mtDNA results (Pickles et al., 2011) which suggested the Itenéz population in Bolivia as the only exhibiting a genetic bottleneck signature, and the northern South American populations constituting two ESUs. Caballero et al. (2015) also studied genetic diversity and population structure of giant otters in the Colombian Orinoco basin using fecal and tissue samples, and the mtDNA control region. Most of

the 15 haplotypes found defined one not previously described phylogroup with high genetic diversity in the Colombian Orinoco. This phylogroup, together with a second one defined from a few Colombian Orinoco and Amazon samples, should be considered a distinct genetic management unit. Finally, Ribas et al. (2016) combined genetic data obtained from 50 otters and 12 specific microsatellite loci (Ribas et al., 2011) and long-term ecological information to determine genetic relatedness within and between cooperative otter groups to test the hypothesis these groups are composed of a dominant reproductive pair and their offspring of previous years. The average relatedness within groups was high but highly variable in each group, including groups of unrelated individuals and contradicting the hypothesis of an exclusively parent-brood model. The authors concluded that direct benefits, such as alloparental care, and the acquisition, inheritance, and defense of high-quality territories, may drive the evolution of group-living in this endangered social carnivore.

Lontra provocax. The Southern river otter, or huillín, is an otter species endemic to southern Chile and Argentina and is currently classified as endangered by the IUCN (Sepúlveda et al., 2021). Despite being a threatened species and the urgent need to determine the existence of conservation units, corridors, and geographic barriers (Valenzuela et al., 2019), only one genetic study has been published since the work of Vianna et al.'s (2011). Pizarro et al. (2021) assessed for the first-time variation and signature of selection in MHC class I and II loci in Chilean wild populations. Low genetic diversity was found, whereas signatures of historical positive selection are inconclusive. This is possibly due to a recent population bottleneck caused by anthropogenic pressures that might have unchained a strong genetic drift that overcomes the effects of positive selection in the MHC loci. These results suggest that L. provocax has a low adaptive capacity and therefore a great susceptibility to the spread of diseases from domestic and invasive animals.

Lontra felina. The marine otter can be found disjunctively distributed on rocky shores from the northern coast of Peru to the extreme south of Argentina (Lariviére, 1998). It is currently classified as endangered (Valqui & Rheingantz, 2021), and little information is available on population size because marine otters are very difficult to observe and count. Only one genetic study has been published since 2010. Biffi and Williams (2017) used non-invasive techniques, five to seven microsatellite loci, and a sex-linked marker to determine the population size in two regions of Peru separated by ~730 km. A minimum of 80 individuals was identified across all locations, corresponding to a density estimate of 4.4 otters per km, a value two times higher than estimates based on visual counts. There was also a strong positive relationship between the number of fresh scats and unique genotypes, suggesting scat counts might be used to estimate the minimum number of otters at a site. The authors concluded that both methods - non-invasive genotyping and scat counts - will be valuable tools for estimating population sizes and monitoring movements of this secretive species.

*Lontra longicaudis*. The Neotropical river otter is a top predator in many South and Central American freshwater systems.

It is distributed from northern Mexico to central Argentina (Rheingantz & Trinca, 2015). Despite its wide distribution, it is currently categorized as a near threatened species (Rheingantz et al., 2021). In the last ten years, several studies have analyzed the genetics of the species. However, the total of studies is not very representative of its enormous distribution area. Trinca & Eizirik (2012) reported a noninvasive standardized protocol for molecular sexing of Neotropical otter samples collected in the field that resulted in reliable gender determination for 95% of samples. Trinca et al. (2012) investigated the genetic diversity, population structure, and demographic history of the species across a large portion of its geographic range by analyzing three segments of the mtDNA genome from 52 individuals. They found high levels of genetic diversity and at least four distinct evolutionary lineages, partially congruent with the subspecies classification previously proposed for this species, in Colombia, Bolivia, Amazon/French Guiana, and Eastern South America, although a single sample represented Colombia and Bolivia. Also, a recent population expansion was identified in eastern South America. Trinca et al. (2013) employed non-invasive genetic analysis and eight microsatellite loci to estimate ecological and population parameters in a Neotropical otter population in the Maquiné Valley, southernmost Brazil. The authors directly identified 28 individuals and estimated a high genetic diversity and population density. Inbreeding and parentage values were low, evidencing that the Maquiné Valley's constitutes a healthy population. Spatial organization analysis indicated that male cumulative displacement was higher than that of females, with the latter sex showing evidence of philopatric behavior. Trigila et al. (2016) analyzed the genetic diversity and individual relatedness in a L. longicaudis population located at the lower delta of Paraná River, Argentina, using eight microsatellite loci, fecal samples, and tissue samples collected from roadkilled animals. Their results, together with genetic and habitat suitability data previously obtained, were used to test whether genetic diversity, inbreeding, and parentage coefficients are related to habitat suitability both at landscape and at regional scale. The levels of heterozygosity found in the lower delta were the lowest reported to that date, and a positive association between habitat quality and levels of heterozygosity, both at landscape and regional scale, was found, suggesting that in highly suitable habitats, the otters are genetically more variable. Hernández-Romero et al. (2018) combined phylogeographic, morphometric and environmental niche modelling analyses to examine whether genetic and morphologic variation is associated with geographic and environmental variation and if the observed variation corresponds to the previously defined subspecies. They found strong phylogeographic structure between the northern (L. l. annectens) and the two southern subspecies (L. I. longicaudis and L. I. enudris), and although weaker, a genetic differentiation between the two South American

subspecies corresponding to hydrography and geographical barriers characteristic of the distributional area of the species. Taken together, all these results provide novel insights on the ecology, taxonomy and evolutionary history of this largely unknown Neotropical mustelid and should be useful to design conservation and management policies on behalf of this species and its habitats.

#### Carnivora, family Otariidae

**Otaria flavescens**<sup>1</sup>. The South American sea lion is one of the most widely distributed South American otariid species, occurring along both the Atlantic and the Pacific coasts of South America (Vaz-Ferreira, 1982a). The species is currently listed as least concern by the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN) (Cárdenas-Alayza et al., 2016a).

Seven articles dealing with the study of genetic diversity, population structure, phylogeography, phylogeny and/or breeding behavior of the species have been published between 2012 and 2022. Franco-Trecu et al. (2015) proposed to quantify the breeding success of South American sea lion males according to their breeding location (tide line vs. internal pool) and the fine-spatial kin structure during the breeding season. Using 12 microsatellite loci and DNA samples obtained from 21 adult males, they found that close kin males were only present at the tide line, suggesting a fine-scale kin structure in the study area, which could be a mechanism for decreasing agonistic interaction at the tide line. One year later, Hoffman et al. (2016) genotyped 259 animals from 23 colonies across the Malvinas (Falklands) Islands at 281bp of the mtDNA control region and 22 microsatellites to study the local genetic diversity and evaluate hypotheses for the catastrophic decline of the species in the islands. Moreover, the authors also compared their results with other populations, to establish the current population structure scenario in South America. As a result, they found a weak signature of population structure, a moderately high genetic diversity, and no evidence for the decline being associated with a strong demographic bottleneck. In addition, by combining the mitochondrial data obtained with published sequences across the geographical range of the species, they found a strong maternally directed population structure, with high levels of genetic differentiation between oceans, supporting previous results obtained using both genetic and morphologic data (Drehmer, 2005; Túnez et al., 2007).

Oliveira et al. (2017) evaluated the population genetic structure and the evolutionary history of the species along its entire distribution analyzing 147 sequences of the mtDNA control region and 10 microsatellite loci in 111 individuals. In agreement with what was reported by Hoffman et al. (2016), they observed that haplotypes from the two oceans comprise two very divergent clades, suggesting a period longer than 1 million years of low

<sup>&</sup>lt;sup>1</sup>We consider *Otaria flavescens* (Shaw 1800) as the legal and valid species name for the South American sea lion, following most South American marine mammalogists and several works: Cabrera (1940), Vaz-Ferreira (1984), Crespo (1988), Rodríguez & Bastida (1993), Rice (1998), and Lucero et al., (2019). Moreover, there is a tendency to consider that *Otaria flavescens* is mainly used by South American authors, while *Otaria byronia* is preferred among authors from other regions. We conducted an analysis of papers published in the last 10 years (2010-2020; n = 436) in which South American sea lion was included as a study species, based on hits in Google Scholar (database available upon request). The results indicate that in more than 80% of the papers (n = 354) the name used is *Otaria flavescens*, a percentage that has roughly fluctuated between 60 and 90%. Likewise, the majority use of *Otaria flavescens* is not restricted to papers with South American authors, but also in contributions from non-South American and mixed authors (Diego Rodriguez, pers. com.). Another aspect to be considered is that the name *Otaria flavescens* is officially used by all the countries where the species is distributed. This includes both the laws, decrees, and official lists of priority species for conservation, as well as the red lists of Brazil, Uruguay, Argentina, Chile, Peru, and Ecuador.

inter-oceanic female gene flow. These two ESUs, composed of at least two MUs in each ocean, would have gone through a large population expansion ~10,000 years ago, suggesting a very similar influence of historical environmental factors, such as the last glacial cycle, on both regions. These results are supported by previous studies in which skull morphology was analyzed throughout the entire distribution of the species and by mitochondrial and nuclear markers analyzed in the Atlantic coasts (Drehmer 2005; Túnez et al., 2007; 2010; Feijoo et al., 2011). Microsatellite analysis also supported significant genetic structure between Pacific and Atlantic populations, with some inter-oceanic gene flow mediated mainly by males.

Peralta et al. (2021) complemented these two previous studies by conducting an exhaustive phylogeographical analysis using the mtDNA control region and including, for the first time, data from colonies located at the southernmost limit of the species distribution, where gene flow between oceans would occur. The authors reported the existence of five MUs across the distribution range of the species and suggested that the Patagonian population must have expanded about 150,000 YBP. In addition, they found evidence for gene flow across the entire distribution range, supporting a scenario of secondary contact between Atlantic and Pacific populations in Tierra del Fuego and suggesting that the species constitutes a single ESU. Later that year, Weinberger et al. (2021) investigated South American sea lion population changes associated with interglacial expansion and overexploitation on the Chilean coast using 85 samples, eight microsatellites, and mtDNA control region sequences. Mitochondrial DNA showed high diversity and corroborated the divergence between Pacific and Atlantic populations and the existence of a secondary contact zone at the southernmost area of the species distribution range. Microsatellites supported a genetic discontinuity at 40° S, a reduction in effective population size during the glacial period, and a strong reduction during the hunting period. Finally, the scale of female natal fidelity was analyzed by Grandi et al. (2018) in a context of a recovering population with population expansion and recolonization. The analysis of the mtDNA control region in 170 newborn pups from 10 breeding colonies in northern Patagonia suggested some level of genetic structure. The authors concluded that females display different strategies when they choose where to breed. While some are residents, others disperse within the study area. Thus, the recolonization pattern may be the effect of weak female philopatry attenuated and/or interacting with other ecological and behavioral factors.

The first genome available for the species was published by Lopes et al. (2021). Phylogenies were recovered for the whole family with several different approaches, but mainly multispecies coalescent models. *O. flavescens* was placed as the earliest otariid lineage that diverged from a common ancestor after the colonization of the SH around 3 Mya.

*Arctocephalus australis*. The South American fur seal occurs in the Atlantic Ocean from southern Brazil to Cape Horn (including the Falkland/Malvinas Islands), and in the Pacific Ocean from Cape Horn to Peru (Repenning et al., 1971; Vaz-Ferreira 1982b). It is listed as least concern by the Red List of Threatened Species of the IUCN (Cárdenas-Alayza et al., 2016b). After the review of Oliveira et al. (2012a) eight new papers were published on the conservation genetics for this species, mainly related to phylogeography and the sequencing of the complete mitochondrial genome.

Previous studies on South American fur seals based on the analyses of mtDNA sequences, microsatellite loci, and skull morphology suggested the existence of two ESUs in Atlantic and Pacific Ocean basins (Túnez et al., 2007; Oliveira et al., 2008), with a genetic bottleneck detected in the Peruvian population (Oliveira et al., 2009). Túnez et al. (2013) reinforced these results when the authors found no significant differences in haplotype frequencies of the mitochondrial control region of fur seals collected at Cabo Polonio and Isla de Lobos colonies, both in Uruguay, and suggested that they were remnants of a single ancient gene pool. The authors also found evidence of population expansion in Uruguay associated with the dynamics of Pleistocene glaciations, possibly related to the high ocean productivity in the South Atlantic during glacial maxima periods.

Crespo et al. (2015) also found no genetic subdivisions along the Atlantic populations and ancient gene flow among them, suggesting that fur seals from southern Brazil to Tierra del Fuego form a single population. However, Rodrigues et al. (2018) found six shared haplotypes between Isla Guafo and Atlantic populations, and no shared haplotypes with the Peruvian population. This study presented the first evidence of the genetic connectivity of the South American fur seal populations across the Atlantic and Pacific oceans. Recently, Gutierrez et al. (2021) provided a new set of 16 microsatellite markers tested in 128 fur seals from the same population of Isla Guafo. The authors found that this population is genetically diverse probably due to the gene flow with other colonies or even related to a potentially recent expansion. Moreover, the authors found the first genetic evidence of twins in South American fur seals.

The last phylogeography challenge to the South American fur seal is related to the analyses of the entire distribution of the species using both traditional molecular markers (mtDNA and microsatellite loci) or even genomics. The comparison of these results with morphological analyses shall provide information that probably will impact the systematics and taxonomy of the species. Moreover, based on these results, it will be possible to understand the historical process and evolutionary forces that shaped the current distribution of genetic diversity of South American fur seal populations, as well as to identify the real gaps in distribution and geographical points of contact or split between putative populations from Atlantic and Pacific oceans.

The paternity of South American fur seals was studied by Francu-Trecu et al. (2014) at Isla de Lobos in Uruguay, the largest breeding colony of the species. The study was based on behavioral observations and genetic analyses of 10 polymorphic microsatellite loci from 36 adult males and 220 pups, which represented ~50% of reproductive males in the 2010 breeding season and 85% of pups born during the following breeding season. The paternity of 47% of pups was determined at 80% and 95% confidence levels, with a surprisingly high proportion of territorial males with lower breeding success in comparison with satellite males. The results suggested that the current mating system at Isla de Lobos is consistent with a lek, due to the high variance in South American fur seal male breeding success and the high reproductive synchrony of females, and their spatial pattern of space. According to Vaz-Ferreira (1982b) the mating system of Uruguayan populations of fur seals was traditional harems or female-defense polygyny, with males defending groups of females. Lekking was reported previously only for the Peruvian population of fur seals (Majluf ,1987), where females moved freely in the colony, with no restrictions by males, assessing and choosing potential mates among them. In this context, the results presented by Francu-Trecu et al. (2014) represent novelty for the species in terms of breeding behavior.

Sequencing of the complete mitochondrial genome of the South American fur seal was recently published by two studies. Rodrigues et al. (2017) obtained the mitogenome with 16,372 bp in length, which included the genes coding for the two rRNA (12S and 16S), 13 protein-coding genes, and 22 transfer RNA genes, and the control region. Similar results were obtained by Tian et al. (2021) who reached the size of the mitogenome of 16,579 bp, comprising 37 genes, including 13 protein-coding genes, 22 tRNA genes, two rRNA genes, and one displacement loop (D-loop) region. Both studies commented on the usefulness of the description of the mitogenomes for future phylogeny and genetic studies on pinnipeds, but only Tian et al. (2021) conducted a phylogenetic analysis that suggested that A. australis has a close relationship with A. forsteri. By sequencing whole genomes of fur seals and sea lions, Lopes et al. (2021) recovered the phylogeny of the Otariidae family and estimated divergence times between species of the group. In this study, A. australis was confirmed as the sister species of the Galapagos fur seal (A. galapagoensis), with the origin from a common ancestor estimated to have occurred ~0.5 Mya. The mitogenome phylogeny in this study also grouped A. australis and A. forsteri as sister species, indicating that this relationship is the result of incomplete lineage sorting (Lopes et al., 2021).

**Otaria flavescens and Arctocephalus australis hybrids**. The existence of hybrids in pinnipeds was reported in captivity and in breeding colonies of sympatric species (Schaurich et al., 2012; Lopes et al., 2021). Franco-Trecu et al. (2016) reported the finding of a hybrid adult female and its offspring, a male pup, at Isla de Lobos in Uruguay. The results were confirmed by using morphological and genetic data. Morphological data included weight and length measurements of the putative hybrid pup that were compared with average measurements for pups of the same sex of both species. Genetic data included mitochondrial cytochrome *b* gene, glucosidase beta acid gene, and nine microsatellites, which were analyzed for the hybrid female and its offspring, and compared with data from 256 fur seals, and 86 sea lions.

*Arctocephalus galapagoensis.* The Galapagos fur seal is an endemic species to the Galapagos Archipelago and is considered endangered by the Red List of Threatened Species of the International Union for Conservation of Nature, mainly due to the decreasing in its population size in the last decades (Trillmich, 2015).

Until the review of Oliveira et al. (2012a) on the conservation

genetics status of aquatic mammals from South America, scarce molecular studies were published for this species. The Galapagos fur seals can disperse long distances influenced by environmental conditions, such as ocean currents and *El Niño* events, meaning that the application of mtDNA fragments is still a fast and cheap tool that helps researchers from the whole Latin America in the identification of vagrants stranded thousands of kilometers away from the original distribution area (*e.g.*, Félix et al., 2001; Páez-Rosas et al., 2020).

Despite receiving the status of an endangered species, it was only in 2015 that the Galapagos fur seal was granted the first study about population genetics and phylogeography (Lopes et al., 2015). In this study, the authors assessed the genetic diversity, population structure, and the consequences for the management of the species in the Galapagos Islands. The study was conducted by analyzing 18 microsatellite loci for 90 samples and 87 sequences of the mtDNA control region obtained from individuals living in the three main Galapagos fur seal breeding colonies: Cape Hammond (Fernandina Island), and Banks Bay and Cape Marshall (Isabela Island). An unprecedented matrilineal population structure was found ( $\Phi_{ST}$  = 0.34 among colonies), with the detection of exclusive haplotypes in all three colonies. This means that some exclusive haplotypes are present less than 70 km apart from each other (Banks Bay and Cape Hammond). The nuclear molecular markers showed a lack of population structure (R<sub>st</sub> = 0.03 among colonies), meaning that females are highly philopatric and males are responsible for gene flow. Additionally, despite the recent decline in census numbers due to hunting and strong events of El Niño, it was detected that the effective population size (Ne) of mitochondrial lineages is historically stable.

Recently, Chaves et al. (2022) expanded the number of localities of Lopes et al. (2015) for both mtDNA sequences and microsatellites. The authors added 69 mtDNA sequences to the previously published dataset (Lopes et al., 2015; Chaves et al., 2022), resulting in 156 sequences and nine sampled localities. A total of 26 new samples were also assembled with the nuclear DNA dataset of Lopes et al. (2015), resulting in 110 samples, eight microsatellite loci, and six sampled localities.

By expanding the previous dataset for nuclear DNA, it was found that the populations of the Galapagos fur seal are genetically structured across four islands and six rookeries, following three major groups comprising: a western cluster of individuals from Fernandina; a central group formed by the north and east Isabela, Santiago, and Pinta; and a third cluster in Pinta, the furthest colony in the northeast. The estimations of gene flow among the different localities showed that the migration is asymmetric and occurs predominantly from Banks Bay to Cape Hammond. Migration between the rest of the colonies was moderately low. No significant difference in the historical *Ne* was found between Chaves et al. (2020) and Lopes et al. (2015). This study also concluded that the population structure and migration are probably influenced by a gradient of marine productivity in the Galapagos Islands (Chaves et al., 2022).

Great advances in the field of phylogenomics and population genomics have been made lately as well. In a comparative work of demographic scenarios to assess oscillations in the *Ne* of several species of pinnipeds, Peart et al. (2020) used reduced-representation libraries of genomes (RAD-seq method) to detect signatures of a recent bottleneck in the Galapagos fur seal populations. The authors showed that the reduction in the number of breeding individuals (Nc) in the last century is compatible with a bottlenecked population, while the long-term Ne was not affected (Peart et al., 2020), which corroborates with the findings of Lopes et al. (2015) and Chaves et al. (2022). The species was also included in the most comprehensive molecular phylogeny of the Otariidae family published so far. By using whole genome sequencing and a suite of phylogenomic analyses, Lopes et al. (2021) confirmed the position of the Galapagos fur seal as a sister species of the South American fur seal and estimated that their divergence from a common ancestor occurred ~0.5 Mya. In this manuscript, it was shown that the previous topological discordance for the species reported in the literature (e.g., Yonezawa et al., 2009; Berta et al., 2018) is due to a massive incomplete lineage sorting (see Molecular Systematics section), with genomic introgression playing a small role. The main events of introgression would have occurred between the ancestral lineages of both Galapagos and South American fur seals and New Zealand fur seals, representing around 9-12% of the genomes assessed in the publication.

The species still needs further investigation despite the great advances since Oliveira et al. (2012a). For example, some Galapagos fur seals of different stages of life have been identified on the northern Peruvian coast (Oliveira et al., 2012b) and the biological and evolutionary consequences of the extra range findings are not known.

#### Carnivora, family Phocidae

**Hydrurga leptonyx**. Leopard seals have been scarcely studied at the genetic level. Recently, Hernández-Ardila et al. (2021) published the first study on the genetic diversity of leopard seals around Danco Island in WAP, based on mitochondrial CR sequences from 13 samples collected between 2011 and 2012. Results from this study evidenced high levels of genetic diversity with almost each individual having a unique haplotype. This may be the result of high dispersal abilities in these seals, mediated by their pagophilic habits. A thorough study on their genetic diversity and population structure is warranted.

## Barcoding in Latin American aquatic mammals

In the last decades, DNA barcoding is becoming an important tool in wildlife forensics, molecular phylogeny, taxonomy, and conservation of marine biodiversity. Nevertheless, only a handful of studies have been published on this topic in Latin America in the last ten years. The work of Chaves et al. (2012) evaluated the potential of two short mtDNA fragments, the ATP6 (126 bp) and the cytochrome oxidase I gene (COI, 187 bp) to serve as standardized mini-barcode markers for species assignment of carnivore non-invasive samples. Samples of 66 species, including three Otariidae, one Phocidae, and two Mustelidae from South America, were sequenced for both segments. Intraspecific genetic distances were generally lower than between-species distances, resulting in diagnosable clusters for 86% (ATP6) and 85% (COI) of the species. Case studies with fecal samples supported the suitability of the two focal markers for poor-quality DNA and allowed an assessment of prey DNA co-amplification. Overall, results indicate that these segments hold good potential as standard markers for accurate species-level identification. Years later, Valsecchi et al. (2020) described the design and validation of two new sets of primers targeting hypervariable regions of the vertebrate mitochondrial 12S and 16S rRNA genes, which have conserved priming sites across virtually all cetaceans, pinnipeds, and other marine taxa, and amplified fragments with consistently high levels of taxonomically diagnostic sequence variation. The study included more than ten genera of Latin American aquatic mammals. In silico validation showed the two new loci outperformed most existing vertebrate barcode loci for taxon detection and resolution. Also, sequence diversity and taxonomic resolution of the new barcode loci in 680 complete marine mammal mitochondrial genomes demonstrated that they are effective at resolving amplicons for most taxa to the species level. According to the authors, these new primers will potentially allow surveys of complete marine vertebrate communities in single high throughput sequencing (HTS) metabarcoding assessments, simplifying workflows, reducing costs, and increasing accessibility to a wide range of investigators. Since 2012, three new studies evaluated the using of DNA barcoding to identify cetacean species along the coasts of South America. Falcão et al. (2017) evaluated the usefulness of an additional region of the COI gene - the E3-I5 region (loci 685 to 1179; 495 bp) - as a marker for identification of cetaceans from northeastern Canada and northeastern Brazil. The study encompassed seven species, including samples of four species collected in Brazilian waters: Physeter macrocephalus, Peponocephala electra, Sotalia guianensis, and Tursiops truncatus. The identification markers were successfully obtained, and the authors highlighted the importance of using multiple mitochondrial regions for taxonomic identification of some difficult taxa, as the Delphininae species. In the same year, Farías-Curtidor et al. (2017) carried out genetic barcoding and phylogenetic analyses to study taxonomic identity in common dolphins from Colombia (see "Delphinus spp." section for more details). DNA barcoding using a fragment of the mtDNA also allowed species identification confirmation for a live-stranded Clymene dolphin (S. clymene) in the Caribbean of Colombia. This species is endemic to the Atlantic Ocean, but scarce information exists for it in the Caribbean (Mignucci-Giannoni et al., 2021). Finally, Silva et al. (2021) generated COI sequences from 150 specimens of cetaceans of the Brazilian coast, comprising 33 species. This effort was part of the Brazilian Barcode of Life (BrBOL) initiative and encompassed around 70% of the cetacean species reported for Brazilian waters. Most of the specimens used in the study included voucher material deposited in scientific collections, allowing a direct comparison between the morphological and molecular identification. It is worth mentioning that Arnoux's beaked whale and spectacled porpoise (Berardius arnuxii and Phocoena dioptrica) were sequenced for cox 1 for the first time. The authors found that COI sequences correctly identified ~93% of the samples. The exceptions were two dolphin species (Stenella coeruleoalba and S. clymene) and

the Southern right whale, for which *cox* 1 failed to identify the species due to overlapping distributions of intra- vs. interspecific divergences. As mentioned by the authors, the dolphins of the genus *Stenella* present extensive sympatry and potential interspecies hybridization, probably requiring nuclear markers for their reliable identification. In the case of Southern right whale, the erroneous identification as *E. glacialis* when using one of the main public databases of DNA barcode data (BOLD) was a minor problem, since the designated species only occurs in the North Atlantic. The authors highlighted that DNA barcoding can reliably identify most cetaceans in the SWAO and emphasize the importance of voucher materials to validate the construction of a reliable DNA-based identification system.

## Molecular phylogenetics in Latin American aquatic mammals

The phylogeny and systematics of fur seals and sea lions have been exhaustively studied, but despite the increasing size of the molecular data (e.g., Yonezawa et al., 2009; Rodrigues et al., 2017; Tian et al., 2021), only a few relationships reached acceptance (Berta & Churchill, 2012; Churchill et al., 2014). The phylogenetic relationship between genera and some species within the family was highly discordant between studies published across time and the monophyletism of Arctocephalus remained unclear for a long time (Yonezawa et al., 2009; Berta & Churchill, 2012; Nyakatura & Bininda-Emonds, 2012; Churchil et al., 2014; Berta et al., 2018, Tian et al., 2021). The lack of resolution also hindered the understanding of the biogeographical history of the Otariidae family, such as when and how the trans-hemispheric dispersal occurred (Churchill et al., 2014). The popularization of NGS, such as the sequencing of whole genomes, made it possible to build high-quality reference genomes for a wide diversity of organisms, including pinnipeds (Foote et al., 2015; Humble et al., 2018, Lopes et al., 2021). With whole genomes available on GenBank and the new genomes sequenced for several species of fur seals and sea lions, Lopes et al. (2021) unraveled the phylogeny of the Otariidae and its bearing on the taxonomy and biogeographical history. Despite extreme topological discordance among gene trees across genomes, the authors found a fully supported species tree that agreed with the well-accepted relationships and resolved all prevalent uncertainties, such as the monophyly of Arctocephalus. The divergence times estimates found a relatively recent trans-hemispheric dispersal that originated the southern clade, from which rapidly diversified six major lineages between 3 to 2.5 Mya, a result that matches the fossil record from the Pacific coast of South America (Ochoa et al., 2021). It was also found that the almost simultaneous speciation of the southern clade was driven by the complete closure of the Isthmus of Panama and a period of global cooling that characterized the Plio-Pleistocene transition. The short period of diversification in the southern clade led to an extensive incomplete lineage sorting throughout the genomes and resulted in a high level of genealogical discordance, explaining the incongruence among and within prior phylogenetic studies of the Otariidae (Lopes et al., 2021).

## Wildlife forensics of Latin American aquatic mammals

Several studies before 2010 revealed that river dolphin lovecharms sold in popular markets in the Amazon did not belong to *Inia* spp.; such talismans belonged to *S. guianensis* (Cunha & Solé-Cava, 2007; Sholl et al., 2008; Siciliano et al., 2018), and this was confirmed by dos Santos et al. (2018). Ruiz-Garcia et al. (2013) analyzed 78 genital samples from the Amazon estuary that were in possession of sorcerers who would prepare them as love-charms. Using the mtDNA control region, they identified 75 as *S. guianensis*, and the others as *Steno bredanensis*, *Stenella frontalis* and *Tursiops truncatus*. *S. guianensis* sequences showed high diversity and were compatible with demographic expansion events during the Pleistocene.

Another conservation issue regarding dolphins in the Amazon is the piracatinga fishery. Amazon River dolphins, tucuxis, and caimans are illegally killed to be used as bait for this fish (da Silva et al., 2018a). The directed killing has implicated in the reduction of apparent survival of Amazon River dolpins in the Central Amazon (Mintzer et al., 2013) and justified the reassessment of the species to endangered status in the Red List of IUCN (da Silva et al., 2018b).

The fishery for piracatinga was boosted in Colombia, where this fish (locally called mota) replaced the much appreciated and overfished "capaz". Salinas et al. (2014) used COI sequences to prove the illegal selling of piracatinga as capaz in three large Colombian cities. In Brazil consumers do not like piracatinga because of its scavenger habitats, but suspicions about their sale arose when mysterious fish fillets named "douradinha" and other deceptive names emerged in local markets. Cunha et al. (2015) analyzed the cytochrome b of 62 fillets from douradinha and other suspicious names sold at markets in the Brazilian Amazon and found that 60% were actually piracatinga. Besides, the authors confirmed the presence of dolphin tissue in the stomach contents of three piracatinga, using DNA control region sequencing. Those results formed the scientific basis for a moratorium on the fishing and fraudulent selling of piracatinga, jointly issued by the Brazilian ministries of the Environment and Fisheries in 2014. This fraud was exposed in the mass media in Brazil and abroad to help end the illegal use of dolphins as bait.

## Discussion

Conservation genetics of aquatic mammals is a very stimulating, promising field of study that uses molecular tools, statistics, and bioinformatics to answer biological and ecological questions directly related to the conservation of particular populations/species. The ever-increasing human impact on marine, lacustrine, and river habitat makes conservation concerns a priority. Since the last review of molecular studies from aquatic mammals of South America (Oliveira et al., 2012a), which included publications until 2010, substantial genetic research has been done, expanding to new species, and exploring new techniques and technologies (Figs 1 and 2). Technological advances in DNA markers have had a revolutionary impact on the field of aquatic mammals' genetics, encompassing molecular systematics, evolutionary biology, molecular ecology, and conservation genetics. The numerous genetic markers currently available enable rapid access to intra and interpopulation genetic variability and allow the study of population structuring, kinship, and identification of both individuals and species alike. Thus, DNA markers are extremely useful to the development of more adequate management plans for natural Neotropical aquatic mammal populations.

The comparison of genetic conservation studies published during 1993-2010 and 2011-2022 demonstrated an increase in the number of studies for all taxonomic groups except pinnipeds, almost doubling the number of scientific papers. The number of studied species increased for cetaceans, the only group in which there were species not studied during 1993-2010 with first studies published during the last decade (Balaenoptera musculus, B. borealis, B. physalus, Lagenorhynchus australis, Phocoena dioptrica, Cephalorhynchus eutropia, Globicephala melas and G. macrorhynchus). Some cetacean species remain without any published information, except for DNA barcoding, but many of them have studies on conservation genetics that are currently underway (e.g., Physeter macrocephalus, Kogia breviceps, K. sima, Orcinus orca, Peponocephala electra, Pseudorca crassidens, Lagenodelphis hosei). Among the main gaps are studies related to rare or oceanic species, such as the beaked whales (family Ziphiidae) and the pygmy right whale (Caperea marginata). Nevertheless, some coastal and relatively common species still need further studies, including a better determination of the geographic boundaries of the proposed stocks (e.g., Phocoena spinipinnis, Tursiops truncatus).

The last decade has also experienced a slow but clear move of conservation studies toward genomic techniques. None of the studies published during 1993-2010 had used genomic data. Future studies should apply progressively more genomic techniques as Latin American laboratories have begun to produce genomic data and now do not depend entirely on collaboration with researchers from the USA and Europe, for instance.

Knowledge on the population structuring of a particular aquatic mammal population is fundamental to the establishment of Evolutionary Significant Units and Management Units, which are delimited with the aim of conserving genetic integrity and should be used by stakeholders to delineate management plans and improve the species conservation in the future. Thus, DNA markers are extremely useful to the development of more adequate management plans for natural Neotropical aquatic mammal populations. Understanding how species biodiversity in Neotropical freshwaters and marine habitats is generated and maintained is highly important, as these habitats are transformed by human development which deeply impact and jeopardize those species. As a result, most aquatic mammals are threatened or nearly so. Besides, aquatic mammal species and communities are also being increasingly exploited by tourism based on nature, a recently emerged economic activity developed to sustain growing human populations, theoretically in a more environmentally friendly way. Conserving aquatic mammal species and their habitats in a world with increasing demand for natural resources and consumerism is a very hard challenge. As this review has shown Latin American conservation geneticists dedicated to aquatic mammals are doing their job. To improve it during the next decade, they basically need adequate funding.

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