

REVIEW

Conservation genetics of South American aquatic mammals: an overview of gene diversity, population structure, phylogeography, non-invasive methods and forensics

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ABSTRACT

1. Most aquatic mammals have high dispersal potential, and there are often severe conservation concerns related to their legal or illegal harvesting. Therefore, economic, social and forensic factors often arise in decisions relating to their population management. Molecular markers are essential tools in modern conservation genetics, revealing previously unknown aspects of aquatic mammal behaviour, natural history, population structure and demography. Molecular markers also have been used to define management units, to recognize taxonomic units, to conduct forensic analyses and to control illegal wildlife trade, providing valuable information for decision-making in wildlife conservation and management.

2. We review studies published in peer-reviewed journals between 1993 and 2010, in which genetic approaches have been applied to conservation-related issues involving natural populations of 25 species of aquatic mammals in South America. These studies cover just 34% of the 70 aquatic mammal species recorded in South America.

3. Most of the studies are related to population structure, phylogeography, gene flow and dispersal movements. In addition, recent findings relate to evolutionarily significant units, management units, forensics and conservation policy.

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4. Finally, we look to the future and, based on numbers of studies and conservation concerns, suggest which species, geographic areas and genetic studies should be prioritized. Moreover, we discuss constraints on research and suggest collaborative works that would provide critical information towards the effective conservation and management of aquatic mammals in South America.

Keywords: Cetaceans, molecular markers, pinnipeds, sirenians, South America

Mammal Review (2012), **42**, 275–303
doi: 10.1111/j.1365-2907.2011.00201.x

INTRODUCTION

Conservation genetics is the application of molecular methods to preserve species as dynamic entities capable of coping with environmental change. The main goal of researchers in this field is to study molecular diversity in natural populations of species under anthropogenic impact, in order to reduce current rates of extinction and preserve biodiversity.

Conservation genetics encompasses genetic management of small populations, resolution of taxonomic uncertainties, assessment of management units (MUs) within species, molecular forensics and the identification of certain aspects of species' biology or social structure through the use of molecular markers (Frankham et al. 2002). The primary factors contributing to population reduction leading to extinction are habitat loss, competition with introduced species, overexploitation and pollution (Primack 2008). These factors are related to human population growth that reduces other species' population size. Reduced populations become susceptible to stochastic effects (Primack 2008). These include environmental, demographic or genetic stochasticities (inbreeding depression and loss of genetic diversity), and catastrophes. Although the role of genetic factors in extinctions of wild populations has been controversial, evidence now shows that genetic factors are important contributors to extinction risk (Frankham et al. 2002).

During the last 30 years, fisheries have grown exponentially worldwide and particularly in Latin American countries, resulting in overexploitation of several species (e.g. Vidal 1993, Crespo et al. 2000, Dans et al. 2003a, b). Populations of many of the world's largest marine mammals, reptiles, birds, fishes and invertebrates have been severely depleted or forced to extinction due to harvesting by humans (Malakoff 1997). In the past 50 years, the majority of marine mammal populations have been severely reduced to very low levels, and fisheries have been implicated as one of the major factors directly affecting recovery rates (Bowen 1985, Crespo et al. 1997). The impact of fishing operations on marine mammals and other components of marine ecosystems is a major conservation concern. As top predators of food webs, aquatic mammals suffer mortality by incidental entanglement in fishing gear (Northridge 1985, 1991, Crespo et al. 1997, 2000, Dans et al. 2003a, b), through competition for food resources (Bowen 1985, Trites et al. 1997), and due to by-catch interactions (Bratten & Hall 1996, Baird et al. 2002). In recent years, molecular methods have been used to address a number of conservation-relevant genetic issues for a wide variety of marine organisms ranging from zooplankton to whales. Molecular markers have revealed illegal whaling (Baker & Palumbi 1994) as well as previously unknown aspects of the behaviour, natural history and population demography of diverse

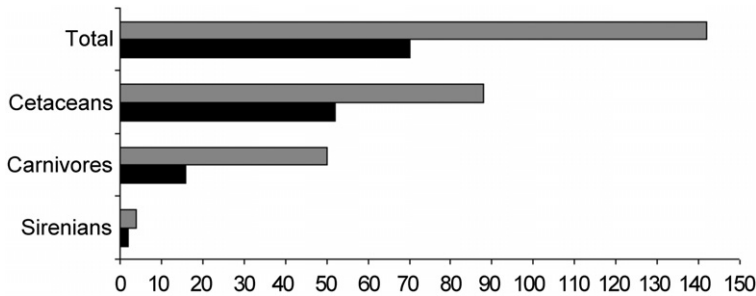


Fig. 1. Aquatic mammal species richness worldwide (grey bars) and in South America (black bars), shown in total, and broken down into cetaceans, carnivores and sirenians.

taxa, providing valuable information for decision-making in conservation and wildlife management (Awise 1998).

At least 70 species of aquatic mammals (orders Cetartiodactyla, Carnivora and Sirenia) are found in the waters of South America (Fig. 1; Crespo 2002), including eight species of baleen whales, 44 species of toothed cetaceans, 12 species of pinnipeds, four otter species and two species of sirenians. These comprise about 58% of all known living aquatic mammal species, and include 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.

The goal of this study is to review all publications in which genetic approaches have been applied to conservation-related issues involving natural populations of aquatic mammals in South America. Using this data set, we identify knowledge gaps in genetic research relating to geographic areas and species. Furthermore, we highlight future study priorities for the conservation of aquatic mammals in South America.

METHODS

We reviewed studies published in peer-reviewed journals in the last two decades, between 1993 and 2010, in which genetic approaches were applied to conservation-related issues involving natural populations of 25 species of aquatic mammals (Fig. 2) in South America (Table 1). The species included in these studies comprise just 34% of species occurring in South America ($n = 70$; Fig. 3). Most of the studies are related to population structure, phylogeography, gene flow and dispersal movements. In addition, recent findings relate to evolutionarily significant units (ESUs) and management units (MUs), forensics research and its role in conservation policy, and invasive and non-invasive methods of sampling. The results are divided into a summary of research in conservation genetics (according to species, order, suborder and family), sampling methods for genetic analyses and forensics.

RESULTS

Conservation genetics approaches

Order Cetartiodactyla, suborder Mysticeti, family Balaenopteridae

Megaptera novaeangliae. The humpback whale *Megaptera novaeangliae* is found throughout the world's oceans, from the tropics where it breeds during winter, to

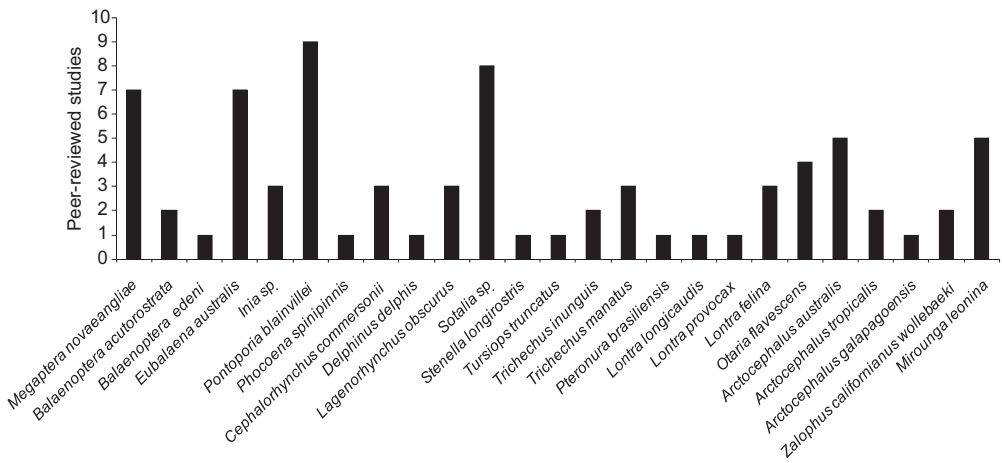


Fig. 2. Numbers of peer-reviewed papers on aquatic mammals in South America published between 1993 and 2010.

Table 1. Extant aquatic mammal species found in South America that have been the subject of genetic research, their IUCN status, and the number of published studies on the genetics of each species. Also shown, for each taxon, is the total number of species found in South America and the number which have been the subject of genetic research

Taxon	Number of species*	Species	IUCN category	Peer-reviewed papers published 1993–2010
Cetaceans	52 (11)	<i>Megaptera novaeangliae</i>	LC	7
		<i>Balaenoptera acutorostrata</i>	LC	2
		<i>Balaenoptera edeni</i>	DD	1
		<i>Eubalaena australis</i>	LC	7
		<i>Inia</i> sp.	DD	3
		<i>Pontoporia blainvillei</i>	VU	9
		<i>Phocoena spinipinnis</i>	DD	1
		<i>Cephalorhynchus commersonii</i>	DD	3
		<i>Delphinus delphis</i>	LC	1
		<i>Lagenorhynchus obscurus</i>	DD	3
		<i>Sotalia</i> sp.	DD	8
		<i>Stenella longirostris</i>	DD	1
		<i>Tursiops truncatus</i>	LC	1
		Sirenians	2 (2)	<i>Trichechus inunguis</i>
<i>Trichechus manatus</i>	VU			3
Mustelids	4 (4)	<i>Pteronura brasiliensis</i>	EN	1
		<i>Lontra longicaudis</i>	DD	1
		<i>Lontra provocax</i>	VU	1
		<i>Lontra felina</i>	EN	3
Pinnipeds	12 (6)	<i>Otaria flavescens</i>	LC	4
		<i>Arctocephalus australis</i>	LC	5
		<i>Arctocephalus tropicalis</i>	LC	2
		<i>Arctocephalus galapagoensis</i>	EN	1
		<i>Zalophus californianus wollebaeki</i>	EN	2
		<i>Mirounga leonina</i>	LC	5

Categories (Anonymous 2010): DD, data deficient; EN, endangered; VU, vulnerable; LC, least concern.

*Total species present in South America and, in parentheses, the number of species that have been subject to genetic research.

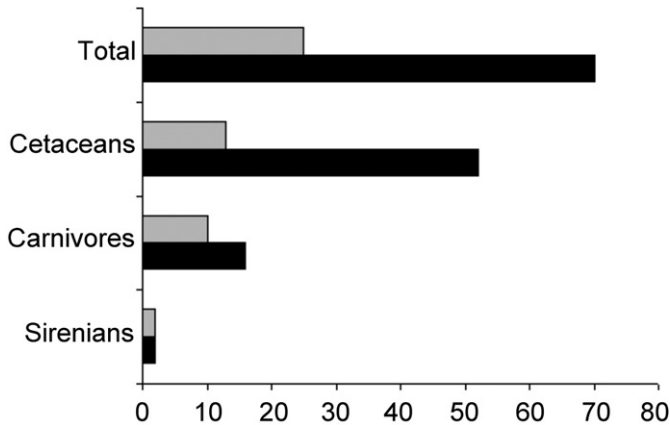


Fig. 3. Numbers of species of aquatic mammals (in total, and broken down into cetaceans, carnivores and sirenians) found in South America (black bars) and numbers of species about which genetic research has been published between 1993 and 2010 (grey bars).

high latitudes where it feeds during the summer. Two breeding stocks were found in South America, the southwestern Atlantic (Brazilian) stock and the southeastern Pacific (Colombian) stock. In the southern hemisphere, humpback whales were severely exploited by commercial whaling during the 19th and 20th centuries, but most populations are now undergoing significant recoveries (see Rosenbaum et al. 2009). Among the large whales, the humpback whale is one of the best studied species; the focus of research has been mostly on population structure and phylogeography. Baker et al. (1993) collected skin samples by biopsy darting from humpback whales in six seasonal habitats representing three stocks and four regions: groups IV (Western Australia), V western component (Eastern Australia), V eastern component (New Zealand and Tonga) and VI (the Antarctic Peninsula and Gorgona Island, Colombia, South America). A variable section of the mitochondrial DNA (mtDNA) control region was amplified from 84 individuals, distinguishing a total of 48 unique haplotypes. Phylogenetic reconstructions suggested that these haplotypes form three clades, corresponding to those previously described in a worldwide survey of humpback whale mtDNA variation (Gambell 1976). Recently, Rosenbaum et al. (2009) assessed population structure of humpback whales using samples collected from whales at 14 sampling sites within all breeding stocks, including the southwestern and southeastern Atlantic, the southwestern Indian Ocean and northern Indian Ocean (breeding stocks A, B, C and X, respectively). The results suggested significant population structure among all ocean basins; the southwestern and northern Indian Ocean stocks were most differentiated from each other. These genetic results supported the current management designations proposed by the International Whaling Commission of breeding stocks as four strongly structured populations (Anonymous 2007).

Olavarria et al. (2007) analysed the population structure of humpback whales in the South Pacific and eastern Indian oceans. The analysis of 1112 mtDNA sequences from the control region revealed 115 haplotypes identified by 71 variable sites. Significant differences at both haplotype and nucleotide level among all breeding grounds were found ($F_{st} = 0.033$, $\Phi_{st} = 0.022$, $P < 0.001$). Caballero et al. (2001) and

Medrano-González et al. (2002) demonstrated a migratory link between the population that feeds around the Antarctic Peninsula and that which breeds along the Pacific coast of Colombia and Ecuador (stock G).

Engel et al. (2008) studied the mtDNA sequence diversity of the southwestern Atlantic (Brazilian) breeding stock of humpback whales, and found high levels of diversity with no sign of any recent genetic bottleneck. Comparison between the Brazilian and Colombian breeding populations and the Antarctic Peninsula feeding population showed no genetic differentiation between the populations from Colombia and the Antarctic Peninsula. In contrast, these populations were genetically distinct from the Brazilian population. This is likely to be a result of the migratory connection between populations off Colombia and those of the Antarctic Peninsula. Engel et al. (2008) also suggested that the feeding ground for the Brazilian population is likely to be the South Georgia area, as indicated by recent photo identification (Stevick et al. 2006) and satellite tag data (Zerbini et al. 2006), which showed that two whales sampled near South Georgia Island had mtDNA haplotypes identical to the haplotypes previously found exclusively in the Brazilian breeding ground (Engel et al. 2008). The authors also suggested the existence of a new southern hemisphere clade represented by five haplotypes from the Brazilian coast found only in very low frequencies in other South Pacific breeding grounds, with the exception of the coast of Colombia, suggesting that this clade is geographically widespread in the southern hemisphere.

More recently, Cypriano-Souza et al. (2010) found no genetic differentiation between humpback whales from the two sub-regions of the entire southwest Atlantic area (Abrolhos Bank and Praia do Forte, both on the Brazilian coast) using nine microsatellite loci and mtDNA data. The microsatellite data also corroborated the high level of genetic diversity found with the mtDNA sequences. The data obtained provided no evidence of kinship associations within social groups. Finally, a female humpback whale sampled off the South Georgia Islands showed a putative parent – offspring relationship with a female off Abrolhos Bank (Brazil), supporting the migratory link between these two areas (Cypriano-Souza et al. 2010).

Balaenoptera acutorostrata. The common minke whale *Balaenoptera acutorostrata* is widely distributed throughout the world's oceans, is abundant (population size is likely to be >100000) and is listed as 'least concern' by the International Union for Conservation of Nature (IUCN; Reilly et al. 2008). Minke whales have been recorded off most of the South Atlantic coast of South America and in the Beagle Channel (Chile and Argentina; Reilly et al. 2008). Pastene et al. (2007) speculated that elevated ocean-surface temperatures may facilitate allopatry among pelagic populations due to reductions in upwelling and fragmentation of feeding areas, which may eventually lead to speciation. They tested this hypothesis by studying mtDNA sequences of two closely related species of baleen whales, the Antarctic minke whale *Balaenoptera bonaerensis* and common minke whale *B. acutorostrata*, collected from whales sampled in four different ocean basins (including samples from Brazil in the Atlantic basin). Their results suggested that the two species diverged in the southern hemisphere less than 5 million years ago (Ma), facilitated by the elevated ocean temperatures in the period that disrupted the continuous belt of upwelling maintained by the Antarctic Circumpolar Current. In addition, they suggested that the current populations of *B. acutorostrata* diverged some 1.5Ma, when global temperatures had

decreased, presumably coinciding with the re-establishment of the polar – equatorial temperature gradient that ultimately drives upwelling (Pastene et al. 2007). This hypothesis should be tested by comparative analyses in other pelagic species.

Pastene et al. (2009) analysed mtDNA control region sequences to investigate possible migratory links between common minke whales in two ocean basins: western South Atlantic and western South Pacific (WSP). The results consistently grouped all haplotypes but one, in two separate clades. South and North Atlantic haplotypes were more closely related to each other than either was to haplotypes from the WSP. The migration rate between the two ocean basins was estimated to be close to zero. Nevertheless, there is genetic evidence for migratory links among populations in Brazil, Chilean Patagonia and the Antarctic Peninsula, and between populations in low-latitude and Antarctic waters of the WSP. The results suggest that there are multiple populations of common minke whales in the southern hemisphere, which may have conservation as well as taxonomic implications.

Balaenoptera edeni. Bryde's whales *Balaenoptera edeni* differ from other typical baleen whale species because they are restricted to tropical and warm temperate waters in major oceans; frequent transequatorial movement has been suggested for the species. Kanda et al. (2007) tested this hypothesis by analysing genetic variation at 17 microsatellite loci and mtDNA control region sequences in 472 individuals obtained from the western North Pacific, South Pacific and eastern Indian Ocean. Both nuclear and mtDNA markers displayed similar population structure, indicating a lack of sex-specific philopatry. The authors observed low mtDNA sequence divergence among populations and a lack of concordance between geographic and phylogenetic position of mtDNA haplotypes, suggesting recent separation of populations rather than frequent transequatorial and inter-oceanic movement. Thus, they concluded that current gene flow between Bryde's whale populations is low and that effective management actions should treat them as separate entities.

Order Cetartiodactyla, suborder Mysticeti, family Balaenidae

Eubalaena australis. The southern right whale *Eubalaena australis* was once widely distributed in the southern hemisphere ocean basins but was driven to near extinction due to whaling during the 19th century. Southern right whales calve during the winter months in two main grounds in the Atlantic coast: the southern Brazilian Coast (–27°30'S–30°00'S) and Peninsula Valdés in Argentina (42°30'S; 63°30'W; Anonymous 1986, 2001), and along the Chilean coast in the Pacific (Aguayo-Lobo et al. 1992). Although the taxonomy of the right whales has been confusing, genetic studies corroborated the distinction between the southern and northern right whales (Baker et al. 1999, Rosenbaum et al. 2000), and more recently, Gaines et al. (2005) supported the three species hypothesis: that besides the southern species, there are also two northern species, *Eubalaena glacialis* and *Eubalaena japonica*, which are among the most endangered mammals.

Patenaude et al. (2007) published the most comprehensive genetic study of the southern right whale. They studied mtDNA variation in four calving grounds (Argentina, South Africa, Western Australia and the New Zealand subantarctic) and two feeding grounds (South Georgia and south of Western Australia). They found two maternal clades that differed significantly in frequency between the oceans. They also found that whales from the four calving grounds showed significant overall differentiation ($F_{st} = 0.0159$, $\Phi_{st} = 0.238$, $P < 0.001$). Measures of pairwise

differentiation showed that whales from the Argentina calving ground are significantly different from those from the three other winter grounds, but are not different from those from South Africa ($F_{st} = 0.009$, $\Phi_{st} = 0.221$, $P < 0.001$). These results suggest very restricted gene flow between populations in the oceans and in most of the calving grounds, corroborating the hypothesis of high maternal site fidelity for the southern species.

Valenzuela et al. (2009) found that genetic and isotopic signatures, analysed together, indicate maternally directed site fidelity to diverse summer feeding grounds for female right whales calving at Península Valdés, Argentina. Isotopic values from a broad range of skin samples are more similar than expected among individuals sharing the same mtDNA haplotype. This pattern indicates that calves learn summer feeding locations from their mothers, and that the timescale of culturally inherited site fidelity to feeding grounds is at least several generations.

The southern Brazilian population of the southern right whale has been surveyed for histocompatibility complex (MHC) expression. Heinzemann et al. (2009) was able to observe the DQB gene expression in skin of this species using reverse transcription polymerase chain reaction. A total of four alleles were found (Euau-DQB*6-9), and the observed dN/dS ratio of 2.77 ($P = 0.03$) suggests that this gene is under balancing selection pressure.

Order Cetartiodactyla, suborder Odontoceti, family Platanistidae

Inia sp. The Amazon river dolphin *Inia* sp. is widely distributed in many rivers in the Amazon and Orinoco basins, and the most recognized classification considers only one species with three subspecies (Rice 1998): *Inia geoffrensis boliviensis* for the system of Bolivian rivers, *I. g. geoffrensis* for the Amazonian basin rivers and *I. g. humboldtiana* for the Orinoco basin (Best & Da Silva 1989a, b).

In the first genetic study of this complex, Banguera-Hinestroza et al. (2002) collected 96 skin biopsies from different populations of Amazon river dolphin throughout its geographical range, and analysed the genetic variation of the three proposed subspecies of *Inia* based on sequences of mtDNA control region and cytochrome *b* gene. Phylogenetic reconstructions presented a topology with one of the clades consisting of the haplotypes belonging to the Bolivian populations and the other clade consisting of the populations of the Colombian Amazon and the Orinoco basin. Banguera-Hinestroza et al. (2002) also found that the haplotypes from the Orinoco basin and the Colombian–Brazilian Amazon were strikingly related. They proposed at least two extant evolutionarily units, which could reach species status: *I. boliviensis* in Bolivia and *I. geoffrensis* in the Orinoco and Amazon rivers.

Martínez-Agüero et al. (2006) reported the first major MHC DQB1 sequences for *I. g. geoffrensis* and *I. g. boliviensis*, which were found to be different but closely related. Although these results are preliminary, the polymorphism within the genus *Inia* could indicate that similar pathogenic pressures act upon river dolphins in different Amazon rivers. More data of this kind could give important insights into understanding the different selective pressures affecting the diverse *Inia* populations throughout their distribution range.

Pontoporia blainvillei. The franciscana dolphin *Pontoporia blainvillei* is an endemic species of the southwestern Atlantic, ranging from Espírito Santo (18°25'S–30°42'W), Brazil (Siciliano 1994) to Península Valdés (42°35'S–64°48'W), Argentina (Crespo et al. 1998). This species is particularly vulnerable to anthropogenic activities because its

distribution is restricted to shallow waters (<30m) within 55km of the shore (Pinedo et al. 1989). Mortality is mainly due to incidental catches in coastal gillnets (e.g. Praderi et al. 1989, Anonymous 2000); this makes the franciscana one of the most threatened small cetacean species in the southwestern Atlantic Ocean (Secchi et al. 2003).

Most studies on the franciscana have been focused on population structure and its bearing on conservation strategies. The first studies, based mainly on differences in skull morphometrics (Pinedo 1991, Higa et al. 2002, Ramos et al. 2002), parasite loads (Aznar et al. 1995, Andrade et al. 1997, 2000) and limited mtDNA control region data (Secchi et al. 1998) suggested two distinct management stocks: one to the north and the other to the south of Santa Catarina State, southern Brazil. Secchi et al. (2003) reviewed many of these previous studies (e.g. on distribution, contaminant and parasite loads and mtDNA) and suggested splitting the prior two management stocks into four Franciscana Management Areas (FMAs), as follows: FMA I: coastal waters of Espírito Santo and Rio de Janeiro; FMA II: coastal waters from São Paulo to Santa Catarina states; FMA III: coastal waters of Rio Grande do Sul and Uruguay; FMA IV: coastal waters of Argentina.

Mendez et al. (2008) conducted a more detailed study of the population structure of the franciscana dolphin using a denser sampling in FMA IV (Argentinian waters) and comparing these with most of the published mtDNA control region sequences from the rest of the distribution [including sequences from Uruguay and Argentina, Lázaro et al. (2004)]. The results support the current scheme of larger recognized FMAs, but they also found significant genetic divisions at the regional level ($\Phi_{st} = 0.05692$, $P < 0.05$), identifying at least two recognizable populations within FMA IV, from samples obtained in San Clemente and Claromec , Argentina.

Mendez et al. (2010) presented the first assessment combining the analysis of mtDNA and 12 microsatellite loci for 275 franciscanas from Argentina. The incorporation of more informative microsatellite data supports a finer-scale subdivision. They found two genetically isolated populations of franciscana within Argentina and a genetically separate population in northern Buenos Aires. Mendez et al. (2010) proposed that FMA IV should be updated to distinguish areas in which distinct populations are found. In addition, they used a combination of demographic and genetic data to show that pairs of franciscana dolphins entangled in fishing gear are often reproductive pairs or mother–offspring pairs. Therefore, the impacts of by-catch on cetacean populations in general may have more consequences at the population level than previously considered.

Initial studies of gene expression in the franciscana may be promising in describing the immune system in this species. Heinzemann et al. (2009) have described the DQB gene expression in skin of one specimen using reverse transcription polymerase chain reaction and have isolated a single allele (Pobl-DQB*1) for the species. Sampling more individuals may provide valuable insights into conservation and immune system.

Order Cetartiodactyla, suborder Odontoceti, family Phocoenidae

Phocoena spinipinnis. Little is known about the biology of Burmeister's porpoise *Phocoena spinipinnis*, an endemic cetacean from South American waters that has high mortality levels due to fisheries. In the only published study on population structure, Rosa et al. (2005) used mtDNA control region sequences and 11 microsatellite loci to assess genetic differentiation among 118 Burmeister's porpoises from Peruvian, Chilean and Argentine waters. *F*-statistics and Bayesian clustering analyses

indicated a major population differentiation along the South American Pacific coast, separating Peruvian from both Chilean ($F_{st} = 0.239$, $P < 0.0001$) and Argentine individuals ($F_{st} = 0.274$, $P < 0.0001$). This population boundary separating Peruvian from other populations is consistent with population structure found in other sympatrically occurring marine mammals such as the dusky dolphin *Lagenorhynchus obscurus* and the South American fur seal *Arctocephalus australis* (see data below).

Order Cetartiodactyla, suborder Odontoceti, family Delphinidae

Cephalorhynchus commersonii. Commerson's dolphins *Cephalorhynchus commersonii* are found in shallow waters along the southeastern coast of South America (40°S–56°S), including in the central and eastern Strait of Magellan and waters around the Falkland (Malvinas) Islands (Goodall et al. 1988, 1994). An isolated population in the Kerguelen Islands in the Indian Ocean (about 8000 km away from the South American populations) differs in morphology, pigmentation and genetic data (Robineau 1984) and has been proposed as a new subspecies *C. c. kerguelensis* (Robineau et al. 2007). Consequently, the populations of Commerson's dolphin endemic to South America should become the subspecies *C. c. commersonii*.

Moderate levels of incidental exploitation have been documented for this species (Goodall & Cameron 1980, Goodall et al. 1988, 1994), but the impact of this by-catch is unknown due to a lack of fundamental knowledge of the genetic structure of populations.

Pimper et al. (2010), using the skin, teeth and bones of 275 Commerson's dolphins from off the Atlantic Tierra del Fuego coast, detected significant population structuring over relatively small geographical distances (330 km of shoreline) from mtDNA control region sequences ($\Phi_{st} = 0.059$, $P < 0.01$). They proposed that the areas should be considered as independent management units (MUs). The use of bone and tooth samples as a source of DNA (Pimper et al. 2009) was an effective approach as it enabled the researchers to analyse a large number of individuals in the region and to examine areas for which only museum specimens were available.

Delphinus sp. In the southern hemisphere, the range of the common dolphin *Delphinus* sp. extends to roughly 40°S (Bastida & Rodríguez 2003). In the southwestern Atlantic Ocean, its taxonomic status is unclear; two distinct morphotypes, long-beaked and short-beaked, have been considered different species named *D. capensis* and *D. delphis*, respectively (Heyning & Perrin 1994). Natoli et al. (2006) conducted the only molecular study (mtDNA and nine microsatellite loci) of *Delphinus* species from various locations worldwide, although only samples from Argentina were used to represent the entire southwestern Atlantic Ocean. Natoli et al. (2006) labelled all the samples from Argentina as *D. delphis*, without distinguishing between morphotypes. The microsatellite results, although not very strong, suggest that the Argentine populations are most similar to the western North Atlantic populations. The existing *Delphinus* taxonomy (which is defined by beak length) was not supported, and results suggested that population structure and speciation in these taxa may be related to local founding events and subsequent adaptation of some coastal populations, originating from relatively panmictic oceanic populations (Natoli et al. 2006). Moreover, Tavares et al. (2010) demonstrated from skull measurements that short-beaked common dolphins *D. delphis* and long-beaked common dolphins *D. capensis* both occur in the southwestern Atlantic Ocean.

Lagenorhynchus obscurus. The dusky dolphin *Lagenorhynchus obscurus* is distributed along the Atlantic and Pacific temperate coastal regions of South America, New Zealand and South Africa. Cassens et al. (2003, 2005) investigated its phylogeography and dispersal patterns using nuclear and mtDNA genes from individuals from Peru, Argentina, southwest Africa and New Zealand. They found that dusky dolphin mtDNA haplotypes could be separated into two major haplogroups: (i) the Peruvian individuals and (ii) the remaining populations, suggesting a low rate of recent female dispersal between Peru and other populations as well as differential dispersal behavior along the South American coast and throughout the Atlantic. They proposed that the eastern South Pacific dusky dolphins should be considered as a separate MU.

Harlin-Cognato et al. (2007) studied the same populations and markers in order to test the west-wind drift hypothesis, which suggests an eastward dispersal via a unidirectional, linear route with the temperate west-wind drift ocean current present during the Plio-Pleistocene, and compared their results with the phylogeographic pattern of anchovy (Engraulidae), the main prey of dusky dolphins. Their results supported significant genetic differences among all regions (cytochrome *b* $\Phi_{st} = 0.49$, $P < 0.001$; control region $\Phi_{st} = 0.74$, $P < 0.001$) and high mtDNA diversity in all regions except Peru, as well as significant genetic differences among all regions, with few shared haplotypes. They found no support for the west-wind drift hypothesis and suggested a Pacific or Indian Ocean origin for the dusky dolphin, with a relatively early and continued isolation of the Peruvian population. They also suggested that the dispersal of the dusky dolphin into the Atlantic was correlated with the history of anchovy populations, including multiple migrations from New Zealand to South Africa.

Sotalia sp. The genus *Sotalia* is distributed along the Caribbean and Atlantic coasts of Central and South America, and in the Amazon River and most of its tributaries. Its taxonomy is confusing; there are two main proposals: (i) a single species, *Sotalia fluviatilis*, within which the marine and riverine populations are separate ecotypes (Borobia 1989); and (ii) two species, *S. fluviatilis* (riverine) and *Sotalia guianensis* (coastal or marine; Monteiro-Filho et al. 2002); for reviews, see Caballero et al. (2007, 2008).

Cunha et al. (2005) published the first study of the taxon, addressing the status of the two ecotypes using molecular markers. The authors analysed mtDNA sequences and found significant differences in population structure between marine and riverine individuals, supporting their separation into two species. This proposal was further corroborated by Caballero et al. (2007), who expanded this study with more markers (10 nuclear introns and three mtDNA regions) and more individuals. Caballero et al. (2008) investigated the phylogenetic placement of *Sotalia* using a large data set including two mtDNA genes, six autosomal and four Y chromosome introns, providing a total of 5196bp for each taxon (17 delphinid species). The results showed that *Sotalia* falls within a clade containing other members of Delphininae, exclusive of *Steno*. However, they could not resolve with confidence the sister-taxa relationship between *Sotalia* and *Sousa*, which was supported only in some analyses.

Caballero and Baker (2009) used mtDNA markers and nuclear autosomal introns to document the only known hybridization event between a male *S. guianensis* and a female bottlenose dolphin *Tursiops truncatus*, in captivity at Oceanario Islas del Rosario (Colombia). As expected, the mtDNA haplotype of the hybrid corresponded to the maternal species, *T. truncatus*. The hybrid was a heterozygote at three out of the five nuclear autosomal introns. The occurrence of this hybrid calf shows a

potential for hybridization in the wild along the coast of South America where the species are sympatric. The recent development of 12 polymorphic microsatellite loci for *Sotalia* by Cunha and Watts (2007) will allow more detailed studies on the population genetics, which is crucial for conservation of both species.

Stenella longirostris. The spinner dolphin *Stenella longirostris* lives in deep waters of tropical and sub-tropical seas and is commonly observed in Fernando de Noronha, northeastern Brazil (Perrin 2002). Although no conservation genetic studies have yet been published for this species, the development of eight polymorphic microsatellites by Farro et al. (2008) should facilitate future studies of population structure and gene flow.

Tursiops truncatus. The bottlenose dolphin *Tursiops truncatus* is a social species with a wide distribution in cold temperate to tropical waters, as well as inshore and offshore areas. In the only published study of South America populations to date, analysis of 331bp of mtDNA control region allowed the assessment of phylogenetic relationships between offshore–inshore populations from Chile and Peru (Sanino et al. 2005). Molecular results combined with morphological and parasite data (Van Waerebeek et al. 1990) showed that the Chilean and Peruvian inshore stocks should be each managed as distinct reproductive units. However, both offshore populations were part of a single wide-ranging population named ‘Peru–Chile offshore stock’. Moreover, the Peruvian inshore population should be considered an ESU and should be managed separately (Sanino et al. 2005). Sampling of more individuals may provide valuable insight into the taxonomic status of the genus *Tursiops* in South America.

Order Sirenia, family Trichechidae

Two species of manatees occur in South America: the marine West Indian manatee *Trichechus manatus* and the Amazonian manatee *Trichechus inunguis*, which is endemic to the Amazon River Basin. The two species have a zone of parapatry at the mouth of the Amazon River. Both species are listed as vulnerable by IUCN, and are critically endangered in several countries despite legal protection.

Trichechus inunguis. Variability of mtDNA in the Amazonian manatee has been quantified throughout the Amazon basin (Cantanhede et al. 2005, Vianna et al. 2006); haplotype diversity is high, but nucleotide diversity is low and there is an absence of geographic structuring. Vianna et al. (2006) suggested that low nucleotide diversity could be attributed to an ancient bottleneck followed by a recent population expansion, and may not be related to anthropogenic effects.

Trichechus manatus. García-Rodríguez et al. (1998) studied the phylogeography of the marine West Indian manatee using 86 mtDNA control region sequences from populations in Puerto Rico, the Dominican Republic, Mexico, Colombia, Venezuela, Guyana and Brazil. Low levels of genetic diversity within Florida and Brazilian samples might be explained by recent colonization into high latitudes or bottleneck effects. Three distinctive mtDNA lineages were observed in the phylogeographic reconstruction of *T. manatus*, corresponding to: (i) Florida and the West Indies; (ii) the Gulf of Mexico to the Caribbean rivers of South America; and (iii) the northeast Atlantic coast of South America. These results suggested strong population separations despite the manatee’s ability to move along continental margins. These lineages were not concordant with previous subspecies designations. Vianna et al.

(2006) conducted a much broader study of 200 samples from throughout the geographic range of *T. manatus* (Brazil to Florida), and found similar population structure. In addition, they found that the nucleotide diversity of the West Indian manatee ($\pi = 3.86\%$) is much higher than that of the Amazonian manatee ($\pi = 0.54\%$). A further complication for conservation strategies is the existence of hybrids (revealed by mtDNA, microsatellites and cytogenetic analyses) between the two species, both at their zone of overlap at the mouth of the Amazon River and extending at least to the Guyanas (Vianna et al. 2006).

Order Carnivora, family Mustelidae

Although molecular genetics studies have been recently conducted on all four species of South American otters, all were based only on mtDNA diversity and had limited sample sizes and distribution. Nevertheless, such studies have already greatly increased our understanding of the evolutionary history, taxonomy and conservation strategies of this group.

Pteronura brasiliensis. The giant otter *Pteronura brasiliensis* is the largest freshwater aquatic carnivore in South America, inhabits wetlands and river systems in forest habitats, and is classified as endangered by the IUCN. Its distribution originally ranged across north-central South America, but it is much reduced today. Two subspecies have been described, one in the northern part of the Amazon and Orinoco River Basins and another in the southern part of the Paraná and Paraguay River Basins (Harris 1968). Garcia et al. (2007) studied mtDNA in 30 individuals, and showed moderate intra- and inter-population diversity, with some geographic structuring. The mean nucleotide distance between the northern and southern populations is relatively low (0.9%); a single haplotype is shared. The clear geographic differences between populations, even if not large, suggest low gene flow between them, which is a significant concern for the conservation of this threatened species.

Lontra longicaudis. The Neotropical otter *Lontra longicaudis* is a widely distributed species, occurring from northern Argentina to Mexico. It is one of the least known otter species and its conservation status is 'data deficient', though there are important threats in several parts of its range. Trinca et al. (2007) studied the mtDNA control region sequence variability of samples from 24 individuals collected in southern and southeastern Brazil. The sequence analysis revealed a high level of haplotype diversity but low nucleotide variability. No significant genetic differentiation was observed between the regions, suggesting a recent origin with high gene flow between southern and southeastern populations.

Lontra provocax. The southern river otter *Lontra provocax* is endemic to Patagonia and is listed as endangered by the IUCN. Centrón et al. (2008) have conducted the only genetic study of this species, analysing mtDNA from 150 scat samples in the Argentine Patagonia. They found significant differences between the southern and northern Patagonian populations ($F_{ST} = 0.15$, $P = 0.018$), suggesting the occurrence of two distinct stocks in Argentina. A more comprehensive genetic comparison between the Chilean and the Argentine populations of southern Patagonia is required to identify potential genetic divisions and to design a common conservation strategy.

Lontra felina. The marine otter *Lontra felina* occurs along the Pacific coast of South America from 6°S to 56°S in Peru, Chile and Argentina, but its distribution is

disjunctive (Larivière 1998). Valqui et al. (2010) found 11 mtDNA haplotypes in 37 scat samples along the entire coast of Peru. Based on the spatial distribution and home range of marine otters, Valqui et al. (2010) assumed that their data set represented at least 24 individuals, yielding surprisingly high genetic variability ($h = 0.86$, $P = 0.0117$). They did not find evidence for genetic substructuring, isolation by distance or a population bottleneck. Vianna et al. (2010) found a strong population structure ($\Phi_{st} = 0.83$, $P < 0.0001$) and a significant pattern of isolation by distance across a much wider geographical distribution ($13^{\circ}53'S$ to $43^{\circ}36'S$). They also found two main geographic clades in the mtDNA phylogeny: a Peruvian and a Chilean one, corresponding to two ESUs in agreement with a previous proposal of two subspecies: *L. felina peruviensis* and *L. f. felina*, respectively. These studies present important genetic information for the establishment of reserves, potential future expansion and recolonization or translocations.

Order Carnivora, family Otariidae

Otaria flavescens. The South American sea lion *Otaria flavescens* occurs in the Atlantic Ocean from southern Brazil to Cape Horn (including the Falkland Islands), and in the Pacific Ocean from Cape Horn to Peru. In the southwestern Atlantic, it was heavily exploited from the 1920s to the 1960s (Godoy 1963). Most populations were reduced to <10% of their original numbers, and population recovery did not begin in Argentina until the early 1990s, after several decades of stagnation (Crespo & Pedraza 1991, Reyes et al. 1999, Schiavini et al. 2004). Szapkievich et al. (1999) conducted the first genetic study on the species, analysing 10 protein loci in 70 South American sea lion pups from two rookeries 1300km apart (Isla de Lobos, Uruguay and Peninsula Valdés, Argentina). They found only a small genetic distance between the rookeries, suggesting that they belong to the same population in which gene flow is currently occurring. However, allozymes are not as sensitive as other molecular markers. Túnez et al. (2007) studied the population structure of this species by analysing mtDNA from a few colonies along the Atlantic coast and comparing their results with five sequences previously published from Peruvian populations (Wynen et al. 2001). They found no shared haplotypes between the Atlantic and Peruvian colonies, which suggests the existence of different ESUs in each ocean basin. Moreover, the colonies from Uruguay and Patagonia presented significant differences in haplotype frequencies ($\Phi_{st} = 0.95$; $P < 0.00001$), which corresponded to different genetic stocks. Túnez et al. (2010), studying the mtDNA of five north-central Patagonian breeding colonies, found small but significant genetic differences ($F_{st} = 0.093$, $P < 0.05$) within north-central breeding colonies from Argentine Patagonia, mainly related to Monte Loayza and Punta Norte, the southernmost and northernmost breeding colonies of the species in Chubut Province, respectively. They also detected signs of a genetic bottleneck approximately 64000 years ago, followed by a demographic expansion in the southernmost colonies, which they related to the Late Pleistocene glaciations.

Artico et al. (2010) analysed 56 specimens collected from the southern Brazilian coast and described seven novel haplotypes of mtDNA control region for the species.

Arctocephalus australis. The South American fur seal *Arctocephalus australis* is one of the most widely distributed South American otariid species, occurring along both the Atlantic and the Pacific coasts of South America (Repenning et al. 1971, Vaz-Ferreira 1982). Based on size differences in the skulls of animals from the Falkland

Islands and from the South American coast, King (1954) proposed three subspecies: *A. australis* on the Falkland Islands, *A. a. galapagoensis* on the Galápagos Islands and *A. a. gracilis* on the remaining coast of South America. Later Repenning et al. (1971) attributed species status to *A. galapagoensis* and emphasized the need for additional studies on *A. australis*.

Túnez et al. (2007) compared the mtDNA of South American fur seals from colonies along the coasts of Argentina and Uruguay with five published sequences from Peru (Wynen et al. 2001). As in the South American sea lion, fur seals from the colonies in the Atlantic and the Pacific oceans did not share haplotypes. Recently, Oliveira et al. (2008) conducted extensive genetic analyses (using seven microsatellite loci) and morphometric analyses to determine the level of differentiation between the same populations of South American fur seal (but with much larger sample sizes), and discussed these results in the light of some ESU concepts. The Pacific (Peruvian) and Atlantic (Uruguayan) populations differed significantly in the size and shape of the skull and in their allele frequency distributions (G -test, d.f. = 16, $P < 0.001$; corresponding R_{st} value = 0.136, $P < 0.05$). More than 96% of the specimens could be assigned correctly to their original population based on their genotypes. This degree of differentiation for both genetic and morphological traits suggests complete and possibly prolonged isolation; consequently the Pacific and Atlantic populations of South American fur seals should be considered distinct ESUs and should be managed separately, according to their own life histories and particular conservation issues (Oliveira et al. 2006, 2008). Furthermore, Oliveira et al. (2009a), using the same seven microsatellite loci, found that the Peruvian population suffered a genetic bottleneck in the last century, probably due to a combination of *El Niño* events (ENSO) and hunting activity.

Arctocephalus tropicalis. The subantarctic fur seal *Arctocephalus tropicalis* suffered severe population reductions and local extinctions due to commercial exploitation. After sealing, pronounced population expansions and recolonization of historical sites, and probable colonization of new breeding sites occurred (Wynen et al. 2001), and the species was found outside its range in South America, Angola, New Zealand, Australia, South Africa and on several islands (for a review, see Bester & Reisinger 2010). Ferreira et al. (2008) analysed mtDNA control region sequences from vagrant subantarctic fur seals found on the Brazilian coast and from animals from the main breeding colonies. Five new haplotypes were found in the vagrant individuals, which were mostly from Gough Island (the closest breeding site to the Brazilian coast), although they also came from other breeding colonies, such as Crozet Island (approx. 16500km away). Hence, the occurrence of vagrant individuals with haplotypes from geographically distant localities is an indication of the multiple origins of individuals found along the Brazilian coast, and corroborates the great dispersal ability of this species.

Arctocephalus galapagoensis. The Galápagos fur seal *Arctocephalus galapagoensis* is endemic to the Galápagos Islands, but there are a few records of vagrant individuals from the coast of South and Central America (Félix et al. 2001), which highlight the need for research on the genetic drift and dispersal of this species. During the past decade, 10 Galápagos fur seals have been reported along the Ecuador coast; five individuals were identified by their external appearance and also by mtDNA analysis, which allowed a more precise identification of the vagrants by

their haplotypes (Félix et al. 2001). These long distance displacements of the species occur usually during or immediately after ENSO events, and thus are probably a response to low prey availability, which forces Galápagos fur seals to explore alternative feeding grounds (Chiluiza et al. 1998, Félix et al. 2001).

Zalophus californianus wollebaeki. The California, Galápagos and Japanese sea lions were until recently considered to be geographically isolated subspecies (*Z. californianus californianus*, *Z. c. wollebaeki* and *Z. c. japonicus*) occupying widely separated regions of the Pacific. The Japanese sea lion is now considered extinct, and recent discoveries of substantial morphological and behavioural differences between the California and Galápagos sea lions have led to their reclassification as separate species (Heath 2002). This status was widely corroborated by Wolf et al. (2007) in a molecular study of mtDNA, 25 microsatellite loci and 13 unlinked single nucleotide polymorphisms.

Recently, Pörschmann et al. (2010) examined the reproductive success of approximately 300 male Galápagos sea lions *Z. wollebaeki*, and assigned paternity using 22 microsatellite loci. They found that female mate choice was driven by the length of time males spend on the breeding colony, rather than by the males' dominance status, suggesting that for this species, dominance hierarchy is not a major determinant of reproductive success.

Order Carnivora, family Phocidae

Mirounga leonina. Like many mammals, the southern elephant seal *Mirounga leonina* shows greater population structure for mtDNA than for nuclear DNA (nDNA) markers (for a review, see Hoelzel et al. 2001). Slade et al. (1998) assayed mtDNA and nDNA variation in the three main populations in the South Atlantic, South Indian and South Pacific Oceans, and in a smaller continental population in South America. Population structure was strong and not consistent with isolation by distance. Geographic structure appears to be dominated by historical processes rather than by contemporary gene flow.

Hoelzel et al. (2001) also compared genetic (both nDNA and mtDNA) and morphometric data between two putative populations of southern elephant seals: the Argentine mainland population and the South Georgia Island population, 2400km apart. They found pronounced differentiation at the mtDNA control region that was distinct from the pattern of variation seen among island rookeries. Some morphometric characters and seven of the ten nDNA markers also showed differentiation between the island and mainland sites. Diversity of nuclear markers was high in both populations, but mtDNA diversity was low in the mainland population, suggesting a founder event and little subsequent immigration of females. Fabiani et al. (2003) compared mtDNA haplotypes from 57 seals of Antarctic circumpolar distribution with published sequences (Hoelzel et al. 1993, Slade et al. 1998), and found strong evidence for male-mediated genetic dispersal over a geographic range of about 8000km. This indicates current gene flow between populations that show fixed differences and reciprocal monophyly for mtDNA markers, and significant differentiation for some nuclear markers (ESUs; Moritz 1994a, b). Finally, Fabiani et al. (2003) suggested that significant gene flow exists between distant populations, illustrating the potential homogenizing effect that even rare dispersal events can have in species with polygamous mating systems.

Invasive and non-invasive sampling methods for genetic analysis

The collection of genetic material from free-ranging animals, particularly semi-aquatic and entirely aquatic mammals, can be challenging. Remote biopsy systems have become valuable research tools (e.g. Whitehead et al. 1990). Nevertheless, each procedure involves some level of intrusion or disturbance, and so efforts have been made to devise systems that minimize impact on individuals. Invasive methods, such as the use of crossbows and rifles, provided biological samples with enough DNA for a multiple genetic markers approach. Non-invasive sampling, which is fortunately now common practice, reduces danger and stress to both animals and biologists and increases researchers' ability to obtain the sample sizes necessary to perform multi-marker studies (Swanson et al. 2006). Perhaps the most valuable impact of non-invasive sampling has been the increased ability to sample rare or elusive species (e.g. Valqui et al. 2010). However, non-invasive sampling in aquatic or semi-aquatic environments remains challenging.

In this section, we review six important contributions to invasive and non-invasive sampling methods, as used in South American aquatic mammals: fur seal skin samples (Gemmell & Majluf 1997), skin biopsies from southern right whales (Oliveira et al. 2009b), faeces from the West Indian manatee (Muschett et al. 2009) and from the South American marine otter (Valqui et al. 2010), DNA extracted from formalin fixed specimens (Rodriguez et al. 2002) and skin biopsies from *Tursiops* spp. (Krützen et al. 2002).

The first description of the use of a remote biopsy system to study pinniped biology in South America was by Gemmell and Majluf (1997). In order to avoid the risk associated with restraint in many species, they developed a projectile biopsy instrument to collect tissue samples of South American fur seals in Punta San Juan, Peru. Gemmell and Majluf (1997) implemented a crossbow-launched biopsy system for sampling territorial males in a population of *A. australis* for the first time. This biopsy sampling device allowed the selective non-lethal sampling of fresh, uncontaminated tissue suitable for genetic and toxicological analyses of specimens from adults.

Skin biopsies from cetaceans are of use for many biological studies, but are especially useful for sex determination of some free-ranging cetaceans, in which there is often no distinct external sexual dimorphism. Using a crossbow as a biopsy device, Oliveira et al. (2009b) collected 21 biopsies from live calves of southern right whales, between 1998 and 2002, along the coast of southern Brazil. Biopsy samples provided sufficient DNA for genetic determination of gender using ZFX and ZFY genes (Palsbøll et al. 1992). The calculated sex ratio was two females: one male, which is similar to most species of baleen whales.

Muschett et al. (2009) proposed the collection of faeces of the West Indian manatee as a source of DNA, which proved to be a completely non-invasive method of sampling. Faecal samples yielded enough high-quality DNA for satisfactory amplification (Tringali et al. 2008). Given the highly endangered status of the manatee, any information gathered could enhance the long-term conservation of the species.

Valqui et al. (2010) used scats from marine otters collected from the population along the Pacific coast of Peru. Partial mtDNA control region sequences (265bp) were successfully amplified and analysed in 37 out of 87 samples. They presented the first genetic data for this endangered species, and highlighted the significance of the Peruvian gene pool for the establishment of reserves, potential future expansion and recolonization or translocations.

Rodriguez et al. (2002) demonstrated that it is possible to extract DNA from formalin-preserved samples obtained from museum collections, using samples from museum specimens of franciscanas. Formalin is the most acceptable fluid for soft tissue preservation, and is by far the most widely used in collections. This method is particularly important as it allows the utilization of samples not originally preserved for genetic studies. Museum and laboratory collections usually include fixed tissues of rarely available, severely declining or nearly extinct species [such as beaked whales (Ziphiidae family), monk seals *Monachus* spp. or river dolphins], collected over a wide temporal and spatial scale, where sample collection is difficult and costly.

Finally, Krützen et al. (2002) evaluated the success of a biopsy system for *Tursiops* spp. in genetic analyses. They collected samples from different areas, including from specimens from Patos Lagoon on the Brazilian coast. Approximately 95% of the samples were sufficient for microsatellite and control region analyses as well as for genetic sexing.

Forensics

With few exceptions, the forensic genetics of aquatic mammals in South America has received little attention until recently. All of the published studies to date are related to the illegal trade of body parts of Amazonian dolphins in Brazil, where cetaceans have been protected from commercial whaling since 1986 (Portaria no. N-11 de 21/fev./1986 and Lei no. 7.643 de 18/dez/1987). Despite this protection, the trade of 'love charms' (dehydrated or preserved genitalia sold as aphrodisiacs) from Amazonian dolphins represents a serious threat to the survival of the species (Sholl et al. 2008). Previously, Best and Da Silva (1989a, b) tentatively identified the Amazonian river dolphin *I. geoffrensis* as the species from which samples were frequently traded in two major public markets in the Amazonian region, the 'Ver-o-Peso' of Belém (Pará, Brazil) and the Municipal Market of Manaus (Amazonas, Brazil). However, the two other dolphin species found in the mouth of the Amazon River, *S. fluviatilis* (riverine species) and *S. guianensis* (estuarine and/or marine species), may also be sold as Amazonian river dolphins.

Gravena et al. (2008) and Sholl et al. (2008) used molecular genetics to investigate the taxonomic status of samples of 'love charms' purchased in the two Amazonian markets. The complete cytochrome *b* gene and the control region of each sample were PCR-amplified, and their sequences were compared with the GenBank sequences from *I. geoffrensis*, *S. fluviatilis* and *S. guianensis*. Both groups of researchers found that all samples belonged to the marine species *S. guianensis*. These findings contradict the conclusion of Best and Da Silva (1989a, b) that samples traded in the public markets were from *I. geoffrensis*, as reported by local traders. The marine species *S. guianensis* is probably under higher harvest pressure than the Amazonian river dolphin and *S. fluviatilis*. Efforts should therefore be made to monitor populations of *S. guianensis*, in particular because the species is also incidentally captured in gill nets set off the Marajó Bay and the Amapá state coast (Brazil), a region of intensive fishing activities.

Molecular markers were also used as forensic tools for the molecular sexing of cetacean species that show no sexual dimorphism and are illegally traded in Amazon River markets. Cunha and Solé-Cava (2007) conducted molecular sexing on 46 Amazonian river dolphins (36 *S. guianensis* and 10 *S. fluviatilis*) using the Zfx/Zfy (Bérubé & Palsbøll 1996) and Sry (Palsbøll et al. 1992) regions. They showed that both regions

can be used for sexing skin biopsies, carcasses of stranded animals and mummified samples from genitals obtained from the local market 'Ver-o-Peso' (Belém, Brazil). The sex of all dolphins could be identified, and expected patterns were reproduced exactly.

Tzika et al. (2010) analysed sequences of mtDNA cytochrome *b* gene and five microsatellite loci from 182 meat samples of unidentified small cetaceans collected at three Peruvian markets. The authors identified *L. obscurus*, *P. spinipinnis*, *T. truncatus*, *D. delphis* and *D. capensis*, suggesting that by-catch mortality and illegal trade of cetacean meat still persist in this country. Furthermore, current mitigation measures such as penalizing indirect takes of small cetaceans in Peru have made Peruvian fishermen reluctant to report by-catch, resulting in increased deception rather than an elimination of the threat to small cetacean species.

DISCUSSION: FUTURE STUDY PRIORITIES

Marine and freshwater mammals face an uncertain fate in our rapidly changing world. Despite human fascination with these species and protective legislation in many countries, conservation efforts have achieved mixed results to date: some species have experienced a degree of recovery following centuries of exploitation, whereas others have perished or are on the brink of extinction (Reynolds et al. 2009). Although South American countries are rich in freshwater and marine mammal biodiversity, most aquatic mammal species are listed as data deficient, vulnerable or endangered by the IUCN, and are exposed to habitat degradation, commercial exploitation, and other unfavourable interactions with humans. Since genetic variability is key for the species' evolutionary potential and for their ability to evolve to cope with environmental change, there is no doubt that knowledge about molecular diversity is a prerequisite for their conservation, especially during the current scenario of global climate change (Frankham et al. 2002).

In this review of the published genetic studies of South American aquatic mammals, we now identify knowledge gaps and research priorities for species and geographical areas and suggest guidelines for the conservation of these species in this continent.

Although there are many more genetic studies of cetaceans ($n = 47$) than of aquatic carnivores ($n = 25$; Fig. 3), this probably reflects relative species richness in South America (cetaceans = 52, pinnipeds = 12 and mustelids = 4) rather than differential efforts according to the taxa. For the 47 papers on cetaceans, 31 were focused on just four taxa: *Megaptera novaengliae*, *Eubalaena australis*, *Pontoporia blainvillei* and *Sotalia* sp., and most of them were about population structure based on mtDNA sequences. Consequently there is still much to learn about conservation genetics for these and other cetacean taxa.

No research on baleen whales has investigated the effective population size or gene diversity before and after human harvesting, or analysed the species' demography, both of which are crucial information for identifying MUs. Also, most of the studies are focused on mtDNA, so studies of biparental loci should also be conducted to evaluate correctly the degree of recent gene flow between feeding and calving grounds, as well as to identify local populations. Although a few small cetacean species have been well studied, there are still knowledge gaps and conservation actions to implement. For example, *Sotalia* sp. is one of the most studied species, but there remains a need for an evaluation of the existence of sympatric zones between

marine and riverine species along the Amazon River, since the marine species *S. guianensis* has been found at the mouth of the Amazon River (Pará; Cunha et al. 2005). Much research has been focused on clarifying the taxonomic status of *Inia*, but there is a lack of basic genetic population information for the species of the genus. Endemic species like *C. commersonii* and *P. spinipinnis* need special attention because they are listed as data deficient by the IUCN, there is little genetic information available, and their distribution is restricted to a small area. Even for widely distributed species such as *Tursiops truncatus* and *Lagenorhynchus* sp., which also suffer multiple impacts from human activities, not enough genetic information is published for South America. The taxonomic status remains unresolved for the South American populations of the genus *Delphinus*, which urgently needs phylogenetic and population structure studies, due to incidental captures and the impact of tourism. Natoli et al. (2006) conducted the only molecular study on these species at a global scale, but they only included samples from Argentina to represent the southwestern Atlantic Ocean.

Therefore, we strongly recommend increased sampling effort for the species with little or no genetic information as well as the development of new studies with nuclear genes in order to understand the evolutionary history of all cetacean species in South America. We also recommend phylogeographic studies to define MUs and ESUs for small cetacean populations, in order to improve their management and conservation under continuing human impact, especially for species along the Pacific coast.

As for cetaceans, the 25 publications on South American aquatic carnivores are primarily focused on *Arctocephalus australis*, *Otaria flavescens* and *Mirounga leonina*, all of which are classed as of least concern by the IUCN. However, *O. flavescens* urgently needs a comprehensive phylogeographic study (including populations from Pacific and Atlantic oceans), using both molecular markers to analyse historical and current gene flow as well as potential genetic bottlenecks. Similarly, studies of *A. australis* have focused on the Uruguayan and Peruvian populations, but no data have been published for populations on the Argentine coast, nor for the identification of migratory links between all three populations. Moreover, there is insufficient genetic information for other species such as *A. philippii*, *A. galapagoensis* and *Z. c. wollebaeki*. Studies of these endemic pinnipeds must be made a priority due to their restricted distribution around islands, decreasing population trends and their status as near threatened or endangered species.

Although genetic studies have been published for all South American mustelids, they still require more comprehensive genetic studies using nuclear markers in order to identify potential genetic divisions and gene flow, which is essential information for designing an appropriate conservation strategy in the species' geographical range. The sirenian species are also well studied, but more population structure studies using nDNA are needed to understand historical barriers to gene flow and to identify any occurrence of interspecific hybridization.

It is important to note that most of the South American pinnipeds and cetaceans occur along the coast of seven countries, and migration patterns are driven by environmental features, not by geopolitical borders. However, there is no information about migratory links or gene flow for most of these species. Moreover, there are no integrated or international management plans among these countries in order to protect the migratory species. The exception is the franciscana, the only species with internationally established MUs for the coast of Brazil, Argentina and

Uruguay (Secchi et al. 2003). In particular, baleen whales (e.g. southern right whale and humpback whale) that have breeding areas along the South American coast and feeding grounds in Antarctic and subantarctic waters need special multi-country agreements for their management and conservation. Furthermore, small cetacean species which are also subjected to illegal trade or incidental catch (e.g. *Inia* sp., *Sotalia* sp., and *Phocoena* sp.) need more comprehensive genetic studies in order to identify clear genetic population subdivisions, to assist in determining the origin of illegal dolphin products (meat and aphrodisiacs), and to design a common conservation strategy to preserve species continuity.

Pinniped populations in South America (e.g. fur seals and sea lions) have distinct ESUs in the Pacific coast (Peruvian and Chilean populations) and the Atlantic coast (Argentine, Uruguayan and Brazilian populations). Therefore, future management plans for these species must be shared by different countries and should simultaneously focus on local conservation problems, which is a challenging goal for international management policy. In addition, the continent of South America is surrounded by two ocean basins: the southeast Pacific and southwest Atlantic oceans, which have different important evolutionary and environmental pressures. The southeast Pacific Ocean has high levels of productivity and suffers frequent and cyclic *El Niño* events (Glantz 1996), which influence the entire ecosystem and local species, causing mass mortality events of marine mammals due to starvation (Trillmich & Ono 1991). In contrast, the extension of the continental shelf in the southwestern Atlantic coast has allowed for the development of a great diversity of mesoscale fronts which help to maintain a more stable and predictable upwelling system (Acha et al. 2004), that clearly influences the habitat and the diversity of aquatic mammals in this ocean basin. The environmental features of local habitat have the potential to isolate populations by assortative mating and differentiation by drift. In this context, population structure and local adaptation as well as phylogeography studies (with both mtDNA and nuclear genes) are critical for the development of effective management plans for all aquatic mammals in South America.

Moreover, most of the South American aquatic mammal species were historically exploited by commercial sealers and whalers in the 18th and 19th centuries, and most of their populations were substantially reduced in the early 1900s (Reeves et al. 1992, Wynen et al. 2000). Historical samples should be analysed, to allow demographic studies to be conducted, in order to estimate effective population size and detect potential genetic bottlenecks due to loss of genetic diversity. This research will be especially important for the severely hunted species such as *Eubalaena australis*, *Megaptera novaengliae*, *Otaria flavescens* and *Arctocephalus* spp., as well as for the species most often captured incidentally such as *Trichechus* spp., *Pontoporia blainvillei*, *P. spinipinnis*, *Sotalia* spp. *C. commersonii* and *L. obscurus*, in order to evaluate the impacts of human activities on their natural populations.

In terms of geographic priorities related to genetics research in South America, populations of the Pacific coast are probably the least studied and the most threatened, due to unknown levels of incidental catches (Van Waerebeek & Reyes 1994, Majluf et al. 2002) and demographic bottlenecks caused by recurrent *El Niño* events (Oliveira et al. 2009a). Among all the Pacific countries, the Peruvian populations of marine mammals seem to be the most vulnerable because of competition with the massive anchovy fishery for prey species (Van Waerebeek & Reyes 1994). Peruvian populations also suffer most directly from the effects of *El Niño* (Barber & Chavez

1983, Trillmich & Ono 1991) and face increasing illegal poaching (Tzika et al. 2010). Another area of concern for conservation genetics is the Galápagos Islands, mainly its pinniped populations, because of the endemic nature of the species found there. Colombian populations of aquatic mammals also need more genetic studies, mainly focused on endangered species, such as the manatees from the Amazonian and Caribbean basins.

We believe that all studies suggested here will provide critical information to wildlife managers and policy makers. Unfortunately, due to socio-economic and political difficulties, scientific research and financial support for conservation in these countries are insufficient. This in turn limits environmental awareness, education, and commitment to conservation (Vidal 1993). Thus, conservation genetics research is an essential tool for a comprehensive approach, not only to increase our knowledge of the genetic history of the species but to support more realistic conservation strategies and policies for South American aquatic mammal species.

We hope that our review inspires additional research and encourages collaboration among South American researchers, especially because most of the published papers to date have been supported and conducted by researchers from outside the South American region. More studies are needed to evaluate the relative power of monitoring genetic diversity. These studies will help to determine when it is more effective to monitor abundance or effective population size in order to establish more realistic measures for the management of these species. Ultimately, new studies are essential for the viability of local populations, and even for species' survival, as well for the success of future international and integrated conservation plans for South American aquatic mammals.

ACKNOWLEDGEMENTS

We thank all the researchers who shared information about their studies on conservation genetics of aquatic mammals in South America. We are also grateful to the participants of the MARMAM e-mail group, which is an important communication tool for marine mammal scientists. We also thank Susana Caballero, Alana Phillips and one anonymous referee for comments and suggestions on this manuscript. Support for this research was provided by *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (MCT/CNPq 14/2010-479199/2010-8), *Fundação de Amparo à Pesquisa do Estado de São Paulo* (FAPESP), which provided a post-doctoral fellowship to Larissa Rosa de Oliveira (FAPESP 07/58728-9) and by the National Research Council of Argentina (CENPAT-CONICET), which provided a PhD Scholarship to Rocío Loizaga de Castro. This paper is GEMARS contribution no. 34.

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Submitted 27 July 2010; returned for revision 6 January 2011; revision accepted 23 June 2011

Editor: KH