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Research paper

Romeo and Juliet: a forbidden love story? A review of hybridization in keystone, aquatic megafauna

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Abstract

Romeo and Juliet: a forbidden love story? A review of hybridization in keystone, aquatic megafauna. Hybridization, understood here as the sexual reproduction between individuals of different species, is relatively common in riverine, estuarine, and marine environments. Investigating hybridization in wild populations of aquatic megafauna species provides important insight into their biology, evolution, and conservation. Here, we conducted an extensive and systematic review of published reports of hybrids in keystone, aquatic megafauna, aiming to provide a clear summary of state-of-the-art and hybridization trends in this group. We selected 129 journal articles reporting 80 hybrids in aquatic megafauna. We included mammals (40.3 %), turtles (33.3 %), crocodilians (17.8 %), and elasmobranchs (8.5 %) that are widely distributed in oceans and continental waters. Our results showed a clear increase in reports of hybrids involving aquatic megafauna in recent years, possibly reflecting the improvement in molecular techniques. However, this increase could also be a consequence of translocation of organisms and habitat modification by humans, and may have a critical impact on conservation, particularly regarding already depleted populations. Hybridization has directly or indirectly facilitated the extinction of many species, but it has also played a crucial role in the evolution and adaptation of many others. To determine whether hybridization is a natural effect or a collateral effect of anthropic pressures we need to understand its implications on the conservation of aquatic megafauna.

Key words: Hybrids, Interbreeding, Aquatic fauna, Key species, Conservation

Resumen

Romeo y Julieta: ¿una historia de amor prohibido? Revisión de la hibridación en megafauna acuática clave. La hibridación, entendida aquí como la reproducción sexual entre individuos de diferentes especies, es relativamente común en ambientes fluviales, estuarinos y marinos. El estudio de la hibridación en poblaciones silvestres de especies de megafauna acuática aporta importantes conocimientos sobre su biología, evolución y conservación. Aquí, llevamos a cabo una revisión extensa y sistemática de los informes publicados sobre híbridos en megafauna acuática clave, con el objetivo de proporcionar un resumen claro de la situación actual y las tendencias de la hibridación en este grupo. Seleccionamos 129 artículos de revistas que informan sobre la detección de 80 híbridos en megafauna acuática entre los que se incluyen mamíferos acuáticos (40,3 %), tortugas (33,3 %), cocodrilos (17,8 %) y elasmobranquios (8,5 %) que estaban ampliamente distribuidos en océanos y aguas continentales. Nuestros resultados muestran un claro aumento de reportes híbridos en megafauna acuática durante los últimos años, lo cual puede ser un reflejo de los avances en las técnicas moleculares. Sin embargo, esto también puede ser una consecuencia de la translocación de organismos y la modificación del hábitat por parte de los seres humanos y puede tener un impacto crítico en la conservación, especialmente de las poblaciones que ya están empobrecidas. La hibridación ha facilitado directa o indirectamente la extinción de muchas especies, pero también ha desempeñado un papel crucial en la evolución y adaptación de muchas otras. Es necesario determinar si la hibridación en este grupo es natural o un efecto colateral de las presiones antrópicas para comprender sus implicaciones en la conservación de la megafauna acuática.

Palabras clave: Híbridos, Mestizaje, Fauna acuática, Especies clave, Conservación

Introduction

Hybridization is defined as the interbreeding of individuals from different lineages (Grant and Grant 1992). Populations may show five recognized hybridization levels regardless of the environment in which they occur (Mayr 2013): (1) infrequent interbreeding of sympatric species which results in hybrid offspring that are unable, for ecological, physiological and/or behavioral reasons, to backcross to one or both of the parental species; (2) frequent or occasional interbreeding of sympatric species resulting in the production of at least partially fertile offspring, some of which are able to backcross to one or both parental species; (3) this level occurs when two previously geographically isolated populations did not achieve complete reproductive isolation, leading to the formation of a secondary contact zone where partial interbreeding occurs; (4) extensive interbreeding, resulting from the complete breakdown of reproductive isolation between sympatric species, producing a hybrid swarm in which the complete range of parental phenotypic traits may be observed; and (5) hybrid speciation: interspecific hybridization generates a new species which is reproductively isolated from its parental species. Typically, reproductive isolating barriers among the parental species may limit hybridization. There are two types of prezygotic barriers: premating and post-mating isolating barriers. The former stops gamete transfer between species and includes mechanisms such as behavioral, ecological, mechanical, and mating system isolation. The latter occurs after gametes have been exchanged between organisms but before fertilization, a stage known as post-mating pre-fertilization barriers. These barriers include various strategies, such as copulatory behavioural isolation and gametic isolation (Coyne and Orr 2004), and conspecific sperm precedence, where sperm from a conspecific male is more successful at fertilization. Other mechanisms include hybrid unviability, where hybrids do not survive (Mendelson et al 2007), and genetic incompatibilities that hinder successful reproduction (Ferree and Barbash 2009, Gibeaux et al 2018). Morphological clues of hybridization can be expressed in three ways (Gardner 1997): (1) the hybrid can be morphologically intermediate between the parental types for each character; (2) it can possess one suite of characters typical of one parent, and simultaneously another suite typical of the other parent; or (3) it can present higher values of a particular trait fitness, a concept known as 'hybrid vigor' or heterosis (East 1936, Duvick 2001). or lower fitness traits (Muhlfeld et al 2009) compared to both parents. Interactions between parental genomes can lead to either additive (i.e. the contribution of genes from each parent sum together) or non-additive (e.g. over or under-dominance) patterns of gene expression (Bouvet et al 2016). Both additive and non-additive effects can affect the offspring's phenotype (de Almeida Filho et al 2019).

Although natural hybridization is a well-described phenomenon in terrestrial environments and is not uncommon in aquatic habitats, it is sometimes assessed only through morphological criteria (Gardner 1997). In aquatic environments, hybrid zones -regions where genetically distinct populations meet, mate, and produce hybrids- tend to be larger due to the continuous nature of the habitat and the potential for extensive gene flow (Barton and Hewitt 1985, Espregueira Themudo et al 2012). In contrast, terrestrial areas experience more frequent habitat fragmentation, which restricts the size of these zones (Barton and Hewitt 1985). In some cases, hybrid zones can evolve into swarms, that is, collections of individuals with mixed ancestry, resulting from extensive interbreeding between genetically distinct parental types, and accompanied by introgression (Gardner 1997). Documented cases of natural marine hybridization involve commercially important species, such as a variety of fishes, clams, mussels, and crabs (Gardner 1997).

The term 'megafauna' has been widely applied in ecological and paleontological research. It is simply defined as the subset of largest species in a community or an ecosystem (Moleón et al 2020). Megafaunal species have disproportionately large effects on the structure and functioning of ecosystems and play a critical role as shapers of the environment (e.g. Guldemond and Van Aarde 2008, Pimiento et al 2020). Here, we used the concept of 'keystone megafauna' (Moleón et al 2020) to integrate the ecological function and functional traits of the selected species along with its relative body size and biomass. Aquatic keystone megafauna include extant species of mammals, ray-finned fish, cartilaginous fish, amphibians, birds, and reptiles. The detailed study of hybrid cases within a particular megafauna taxa can give us insight into the evolutionary history of species by documenting the viability and fitness of their offspring, and analyzing the contribution of markers from the parental species and the permeability of the isolation barriers to gene flow (Arnold 1992). For these reasons, it is important to analyze all cases of hybridization documented within a particular taxa in detail and to investigate the viability and fitness of hybrids from different species in different conditions and environments.

Here we review the reported hybridization cases in freshwater and marine keystone megafauna, specifically mammals, reptiles and elasmobranchs, in order to investigate the potential spatial-temporal and inter-taxa variations in hybridization and to discuss potential consequences on the persistence and conservation of these taxa.

Methods

We conducted a systematic review of the literature up until December 2023 that reported hybridization cases in aquatic megafauna species, including aquatic and semi-aquatic mammals (cetaceans, sirenians, ursids, otters, and pinnipeds), reptiles (crocodilians and turtles) and elasmobranchs (sharks and rays). Hybridization has been defined as "the successful mating between individuals from two genetically different lineages that can be either interspecific (i.e., between different species), intraspecific (i.e., between divergent populations of the same species), or involve subspecies" (Chan et al 2019). However, in this study we only consider hybrids as the

Table 1. Resume of hybridization cases in freshwater and marine megafauna reported in published literature by December 2023: NA, number of articles; NSI, number of species/subspecies involved; TH, total of hybrids; ES, only occurring *ex situ*; IS, only occurring *in situ;* Both, occurring ex situ and in situ; MF, based only on morphological features; MT, based on molecular techniques

Tabla 1. *Resumen de los casos de hibridación en especies de megafauna de aguas dulces y marinas señalados en la bibliografía en diciembre de 2023: NA, número de artículos; NSI, número de especies o subespecies; TH, total de híbridos; ES, solo* ex situ; *IS, solo* in situ; *Both, tanto* ex situ *como* in situ; *MF, basado únicamente en características morfológicas; MT, basado en técnicas moleculares.*

Group	NA	NSI	TH	ES	IS	Both	MF	MT
Aquatic mammals	52	46	30	5	23	2	9	21
Crocodilians	23	9	7	3	3	1	-	7
Turtles	43	41	33	2	31	-	1	32
Sharks and rays	11	20	10	-	10	-	-	10
Total	129	116	80	10	67	3	10	70

product of successful interbreeding between species or between subspecies (either naturally occurring or anthropogenic) (Mallet et al 2007).

The selected species were considered 'megafauna' not only based on their size but also within their ecological context (Moleón et al 2020), i.e. if they are considered among the largest animals in the area they inhabit. Birds, amphibians and ray-finned fishes were not considered in this review due to the high number of species we would have to include. Peer-reviewed studies included were identified by keyword searches in several engines: Google Scholar, SpringerLink, JSTOR, Science Direct, Wiley Online Library and PubMed. Keywords searched were 'hybridization', and 'hybridisation' in combination with 'marine mammals', 'aquatic mammals', 'polar bear', otter', 'pinnipeds', 'sirenians', 'cetaceans', 'crocodilians', 'turtles', 'sharks', 'rays'. We also performed hand searches of other relevant journals and screened reference lists of primary articles found from initial searches. We differentiated the studies demonstrating hybridization through molecular analysis from those based exclusively on morphological features. The information was organized in databases, compiling the following associated information: taxa, species, source, year of publication, and country. We also included information regarding the situation in which the hybridization occurred, specifying whether this was natural (*in situ*) or under human care (*ex situ*).

Results

We found 129 journal articles (1974-2023) reporting hybridization in aquatic mammals (52 articles, 40.3 %), turtles (43 articles, 33.3 %), crocodilians (23 articles, 17.8 %), and elasmobranchs (11 articles, 8.5 %) (table 1). We summarized 80 different hybrids involving 116 species and subspecies, most of which were aquatic mammals (*n* = 46) and turtles (*n* = 41). In the literature we also found the description of seven hybrids of crocodilians and 10 descriptions of elasmobranchs. From the total of hybrids, 12.5 % (*n* = 10: nine in aquatic mammals and one in turtles) were described based only on the description of morphological features, and 87.5 % (*n* = 70) were confirmed by molecular methods, including mitochondrial and nuclear DNA, barcoding, microsatellite analysis, karyotypes analysis, and genomics. We also compiled 13 cases of hybridization that occurred in captivity (*ex situ*): these involved aquatic mammals (*n* = 7), crocodilians (*n* = 4), and turtles (*n* = 2).

Hybrids of aquatic megafauna were widely distributed (fig. 1), with presence in all the oceans and continents. However, the geographic distribution also depended on the taxonomic group. For example, cetacean hybrids were reported mostly from the USA; pinniped hybrids from Uruguay, and ursid hybrids for Canada, while sirenian hybrids were found only in Brazil, Guyana and French Guiana. Hybrids of turtles have been reported in multiple countries, but most often in Brazil, the USA and China, whereas crocodilian hybrids have been reported in Mexico and Belize. Elasmobranch hybrids were predominantly found in the USA and Italy.

Aquatic mammals

Fifty-two articles from 1974 to 2023 reported hybridization in aquatic mammals (table 2), including species of cetaceans (*n* = 29), pinnipeds (*n* = 11), ursids (*n* = 2), sirenians (*n* = 2), and mustelids (*n* = 2). The majority (*n* = 44) are reports of natural hybridization, but we also found eight articles reporting *ex situ* hybrids in marine mammals; involving captive Bottlenose dolphins (*Tursiops truncatus*): *T. truncatus* x *Delphinus capensis* (Zornetzer and Duffield 2003), *T. truncatus* x *Grampus griseus* (Sezaki et al 1984, Zhang et al 2014), *T. truncatus* x *Pseudorca crassidens* (Nishiwaki and Tobayama 1982), *T. truncatus* x *Sotalia guianensis* (Caballero and Baker 2010), *T. truncatus* x *Steno bredanensis* (Dohl et al 1974), and *T. truncatus* x *T. aduncus* (Gridley et al 2018), genus *Tursiops* is one of the best studied of all the Cetacea with a minimum of two species widely recognised. Common bottlenose dolphins (*T. truncatus* and seals *Phoca largha* x *Halichoerus grypus* (Liu et al 2023). Thirteen hybridization reports (12 hybrids) were based only on

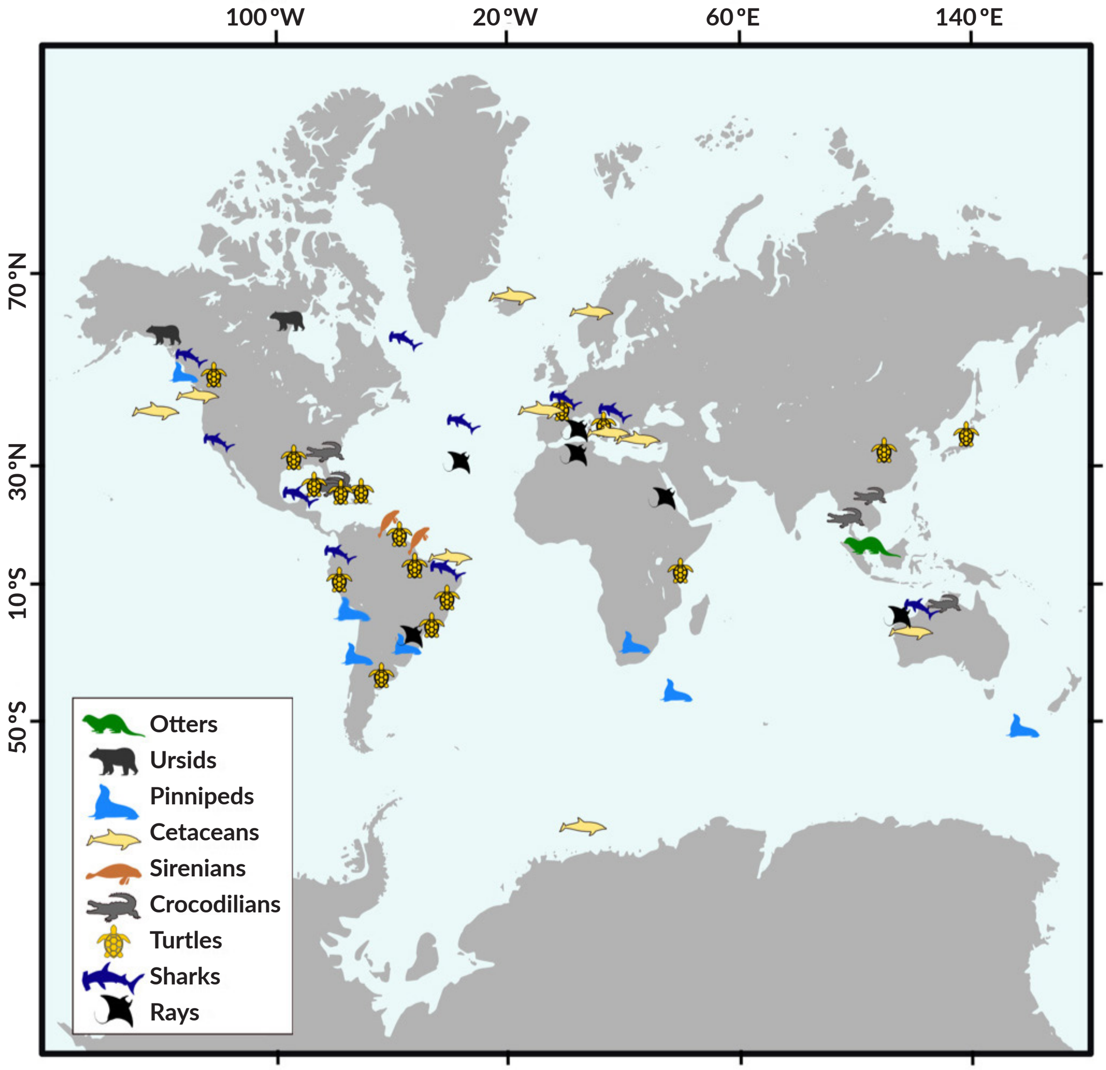

Fig. 1. Global distribution of hybridization cases in aquatic megafauna species. Cases described for individuals *ex situ* or under human care are not included.

Fig. 1. *Distribución mundial de los casos de hibridación en especies de megafauna acuática. No se incluyen los casos descritos de ejemplares* ex situ *o al cuidado de los seres humanos.*

morphological characteristics: *Zalophus californianus* x *Otaria flavescens* (Brunner 2002), *Stenella longirostris* x *Stenella attenuata* x *Stenella clymene* (Silva et al 2005), *Lagenorhynchus obscurus* x *Delphinus capensis* (Reyes 1996), *Lagenorhynchus obscurus* x *Lissodelphis peronii* (Yadzi 2002), *T. truncatus* x *Delphinus delphis* (Espada et al 2019), *T. truncatus* x *D. capensis* (Zornetzer and Duffield 2003), *T. truncatus* x *G. griseus* (Hodgins et al 2014, Van Geel et al 2022), *T. truncatus* x *Pseudorca crassidens* (Nishiwaki and Tobayama 1982), *T. truncatus* x *Stenella frontalis* (Herzingm et al 2003), *T. truncatus* x *Steno bredanensis* (Dohl et al 1974), *Phocoenoides dalli* x *Phocoena phocoena* (Baird et al 1998); and *Delphinapterus leucas* x *Monodon monoceros* (Heide-Jørgensen and Reeves 1993). Thirty-nine articles from 1984 to 2023 confirmed hybridization in aquatic mammals by molecular analysis.

We found one case of natural hybridization between otters *Lutrogale perspicillata* x *Aonyx cinereus* reported for Singapore (Moretti et al 2017). The pinniped group showed most cases of natural hybridization in the Otariidae family: *Arctocephalus australis* x *Arctocephalus galapagoensis* (Lopes et al 2023), *Arctocephalus australis* x *Otaria flavescens* (Franco-Trecu et al 2016, Franco-Trecu 2021), *Arctocephalus gazella* x *A. tropicalis* x *A. forsteri* (Lancaster et al 2006, 2007, Goldsworthy et al 2009), and *Arctocephalus gazella* x *Arctocephalus tropicalis* (Kingston and Gwilliam 2007, Maboko et al 2007). One case of natural hybridization in the Phocidae family is also reported: *Pagophilus groenlandicus* x *Cystophora cristata* (Kovacs et al 1997). Cases of hybridization involving polar and grizzly bears *Ursus maritimus* x *U. arctos* have also been reported (Edwards et al 2011, Pongracz et al 2017).

Table 2. Hybrids reported between species of freshwater and marine mammals. *based only on morphological differences, [c], under human care. Species abbreviations: *Aoc, Aonyx cinereus; Ar, Arctocephalus australis; Arf, Arctocephalus forsteri; Argal, Arctocephalus galapagoensis; Argaz, Arctocephalus gazella; Art, Arctocephalus tropicalis; Baa, Balaenoptera acutorostrata; Bab, B. bonaerensis; Bam, B. musculus; Bamb, B. musculus brevicauda; Bami, B. musculus intermedia; Bap, B. physalus; Cyc, Cystophora cristata; Grg, Grampus griseus; Inb, Inia boliviensis; Ing, I. geoffrensis; Dec, Delphinus capensis; Ded, Delphinus delphis; Del, Delphinapterus leucas; Hag, Halichoerus grypus; Lao, Lagenorhynchus obscurus; Lip, Lissodelphis peronii; Lup, Lutrogale perspicillata; Mom, Monodon monoceros; Orh, Orcaella heinsohni; Otf, Otaria flavescens (previously known as Otaria byronia); Pag, Pagophilus groenlandicus; Phl, Phoca larga; Php, Phocoena Phocoena; Phd, Phoconoides dalli; Psc, Pseudorca crassidens; Soc, Sousa chinensis; Sog, Sotalia guianensis; Sta, Stenella attenuate; Stf, Stenella frontalis; Stcl, Stenella clymene; Stco, Stenella coeruleoalba; Stl, Stenella longisrostris; Stb, Steno bredanensis; Tri, Trichechus inunguis; Trm, Trichechus manatus; Tua, Tursiops aduncus; Tut, Tursiops truncatus; Ura, Ursus arctos; Urm, U. maritimus; Zac, Zalophus californianus*. [Source: 1, Moretti et al (2017); 2, Lopes et al (2023); 3, Franco-Trecu (2021); 4, Franco-Trecu et al (2016); 5, Lancaster et al (2006); 6, Lancaster et al (2007); 7, Goldsworthy et al (2009); 8, Kingston and Gwilliam (2007); 9, Maboko et al (2007); 10, Brunner (2002); 11, Kovacs et al (1997); 12, Liu et al (2023); 13, Edwards et al (2011); 14, Pongracz et al (2017); 15, Glover et al (2013); 16, Árnason et al (1991); 17, Spilliaert et al (1991); 18, Árnason and Gullberg (1993); 19, Bérubé and Aguilar (1998); 20, Pampoulie et al (2021); 21, Jefferson et al (2021); 22, Fioravanti et al (2022); 23, Attard et al (2012); 24, Reyes (1996); 25, Zornetzer and Duffield (2003); 26, Antoniou et al (2018); 27, Espada et al (2019); 28, Sezaki et al (1984); 29, Hodgins et al (2014); 30, Zhang et al (2014), 31, Van Geel et al (2022); 32, Yadzi (2002); 33, Brown et al (2014); 34, Nishiwaki and Tobayama (1982); 35, Caballero and Baker (2010); 36, Silva et al (2005); 37, Amaral et al (2014); 38, Herzingm et al (2003); 39, Dohl et al (1974); 40, Gridley et al (2018); 41, Inamori et al (2021); 42, Gravena et al (2015), 43, Heide-Jørgensen and Reeves (1993); 44, Skovrind et al (2019); 45, Baird et al. (1998); 46, Crossman et al. (2014); 47, Willis et al (2004); 48, Vianna et al (2006); 49, Lima et al (2019); 50, Luna et al (2021); 51, de Oliveira et al (2022); 52, Noronha et al (2022)].

Tabla 2. *Híbridos reportados entre especies de mamíferos de aguas dulces y marinas: * basado únicamente en las diferencias morfológicas; [c] al cuidado de los seres humanos. (Para las abreviaturas del nombre de las especies y de las fuentes bibliográficas, véase arriba).*

Order	Family	Sp 1	Sp 2	Sp 3	Region	Source
Carnivora						
	Mustelidae	*Aci*	*Lup*		Singapore	1
	Otariidae	*Ara*	*Argal*		Chile, Peru	2
	Otariidae	*Ara*	*Otf*		Uruguay	3, 4
	Otariidae	*Arf*	*Argaz*	*Art*	Australia	5-7
	Otariidae	*Argaz*	*Art*		South Africa, France	8, 9
	Otariidae	*Otf*	*Zac*		Argentina, Peru, Chile, Uruguay, Mexico, USA	10*
	Phocidae	*Cyc*	*Pag*		Canada	11
	Phocidae	*Hag*	*Phl*		China	12[c]
	Ursidae	*Ura*	*Urm*		USA, Canada	13, 14
Cetacea						
	Balaenopteridae	*Baa*	*Bab*		North Atlantic	15
	Balaenopteridae	*Bam*	*Bap*		Iceland, Spain, Italy	16-22
	Balaenopteridae	*Bamb*	*Bami*		Antarctica	23
	Delphinidae	*Dec*	*Lao*		Peru	24*
	Delphinidae	*Dec*	*Tut*		USA	25*[c]
	Delphinidae	*Ded*	*Stco*		Greece	26
	Delphinidae	*Ded*	*Tut*		Spain	27*
	Delphinidae	*Grg*	*Tut*		Scothland, Japan, China	28[c], 29*, 30[c], 31*
	Delphinidae	*Lao*	*Lip*		Argentina	32*
	Delphinidae	*Orh*	*Soc*		Australia	33
	Delphinidae	*Psc*	*Tut*		Japan	34*[c]
	Delphinidae	*Sog*	*Tut*		Colombia	35c
	Delphinidae	*Sta*	*Stcl*	*Stl*	Brazil	36*
	Delphinidae	*Stco*	*Stl*		Atlantic, Pacific and Indian oceans	37
	Delphinidae	*Stf*	*Tut*		Bahamas	38*
	Delphinidae	*Stb*	*Tut*		USA	39*[c]
	Delphinidae	*Tua*	*Tut*		South Africa, Japan	40[c], 41
	Iniidae	*Inb*	*Ing*		Brazil	42
	Monodontidae	*Del*	*Mom*		Greenland	43*,44
	Phocoenidae	*Phd*	*Php*		Canada	45*-47
Sirenia						
	Trichechidae	*Tri*	*Trm*		Brazil, Guiana, French Guiana	48-52

Natural hybridization cases in the family Balaenopteridae, confirmed by molecular methods, have involved species of the genus *Balaenoptera*: between blue whale and fin whale *Balaenoptera musculus* x *B. physalus* (Árnason et al 1991, Spilliaert et al 1991, Árnason and Gullberg 1993, Bérubé and Aguilar 1998, Jefferson et al 2021, Pampoulie et al 2021, Fioravanti et al 2022); Antarctic minke whale and common minke whale (*B. bonaerensis* x *B. acutorostrata*, Glover et al 2013) and Southern Hemisphere blue whale subspecies (*B. m. intermedia* x *B. m. brevicauda*, Attard et al 2012). Regarding the family Delphinidae, the following wild hybrids have been confirmed using molecular techniques: *Tursiops aduncus* x *Tursiops truncatus* (Inamori et al 2021), *Orcaella heinsohni* x *Sousa chinensis* (Brown et al 2014), *Stenella coerueloalba* x *Stenella longirostris* (Amaral et al 2014), and *Stenella coeruleoalba* x *Delphinus delphis* (Antoniou et al 2018). For the family Iniidae, only one hybrid has been reported: *Inia boliviensis* x *I. geoffrensis* (Gravena et al 2015). We also found confirmed hybrids among members of the family Phocoenidae; *Phocoena phocoena* x *Phocoenoides dalli* (Baird et al 1998, Willis et al 2004, Crossman et al 2014); and between a beluga and a narwhal (family Monodontidae); *Delphinapterus leucas* x *Monodon monoceros* (Skovrind et al 2019). Regarding the order Sirenia (Family Trichechidae), five articles document natural cases of interspecific cross between Antillean and Amazonian manatees (*Trichechus manatus* x *Trichechus inunguis*), confirmed by molecular methods (Vianna et al 2006, Lima et al 2019, Luna et al 2021, de Oliveira et al 2022, Noronha et al 2022).

According to the IUCN Red List of Threatened Species, fourteen (30.4%) of aquatic mammals on our list are considered threatened, that is, they are classified as Vulnerable (VU), Endangered (EN) or Critically Endangered (CR). The population trend is unknown for most of the aquatic mammals involved in hybridization (52.2 %), but 19.6 % of the species show a decreasing population trend, 19.6 % have an increasing population trend, and 6.5 % are classified as stable (See supplementary material).

Crocodilians

Twenty-three articles, published between 2002 and 2023, documented hybridization in nine species of crocodilians (table 3). Most of these reports (*n* = 10) indicated hybrids between wild *Crocodylus acutus* and *C. moreletii* (Ray et al 2004, Cedeño-Vázquez et al 2008, Rodriguez et al 2008, Machkour-M'Rabet et al 2009, Hekkala et al 2015, Pacheco-Sierra et al 2016, 2018, Platt et al 2021, Villegas et al 2022, Suarez-Atilano et al 2023), and occurred in coastal Mexico and Belize. Four publications reporting the hybrid *C. acutus* x *C. rhombifer* were found, in Cuba, USA, and Mexico (Weaver et al 2008, Rodriguez et al 2011, Milián-García et al 2011, 2015). Two other publications reported the existence of *C. mindorensis* x *C. porosus* hybrids in the wild and under human care in the Philippines (Tabora et al 2012, Hinlo et al 2014). We found five articles reporting hybridization between *C. porosus* x *C. siamensis* both *in situ* (Chawananikun et al 1999, Panthum et al 2023) and *ex situ* (Fitzsimmons et al 2002, Lapbenjakul et al 2017, Wei et al 2022, Panthum et al 2023). We also found hybrids only reported in captivity, these being *C. niloticus* x *C. porosus* and *C. niloticus* x *C. siamensis* in Cambodia (Wei et al 2022), and *Osteolaemus tetraspis* x *O. sp. nov.* cf. *tetraspis* in Africa (Schmidt et al 2015, Shirley et al 2015).

According to the IUCN Red List of Threatened Species, 33.3 % of the crocodilian species involved in hybridization events are considered of Least Concern (LC) status, 33.5 % belong to the Critically Endangered (CE) species status, 22.2 % are classified as Vulnerable (VU) and the remaining 11.1 % have not been assessed. While 22.2 % of the species have a stable population trend, 44.4 % have an unspecified population trend. Only one species (*Crocodylus acutus*) has an increasing population trend, whereas two species (*C. mindorensis* and *C. siamensis*) present a decreasing population trend (See supplementary material).

Turtles

From the publications consulted, 43 (1983 to 2023) reported hybridization in turtles (table 4), totaling 33 hybrids in this group, 41 involving turtle species. One hybrid was described based only on morphological features: *Cuora mouhotii obsti* x *Cuora picturata* in Vietnam (Struijk 2016), while the rest were confirmed through molecular techniques. Two hybrids occurred *ex situ* and involved turtles breeds: *Mauremys reevesii* x *Sacalia quadriocellata* (Buskirk et al 2005) and *M. sinensis* x *Cyclemys oldhamii* (Schilde et al 2004). Thirty-one hybrid turtles were documented in wild environments, and involved members of the families Emydidae (*n* = 11), Chelonidae (*n* = 9), Geoemydidae (*n* = 9), and Kinosternidae (*n* = 2. The hybrid reported most often was that occurring between hawksbill and loggerhead sea turtles (*Eretmochelys imbricata* x *Caretta caretta*), found extensively in Brazil (Conceição et al 1990, Karl et al 1995, Vilaça et al 2012, Proietti et al 2014, Soares et al 2017, Arantes et al 2020a, 2020b, Brito et al 2020), but also reported from Argentina (Prosdocimi et al 2014) and the US (Witzell and Schmid 2003. Another relatively common hybrid was *E. imbricata* x *Chelonia mydas*, which was reported from the in the South East Pacific, Surinam and Costa Rica (Wood et al 1983, Karl et al 1995, Seminoff et al 2003, Kelez et al 2016, Restrepo et al 2022). Additionally, nuclear markers revealed a triple hybrid among hawksbill, loggerhead and green turtles (*E. imbricata* x *Caretta caretta* x *Chelonia mydas*) on the Brazilian coast (Vilaça et al 2012) a high frequency of interspecific sea turtle hybrids has been previously recorded in a nesting site along a short stretch of the Brazilian coast. Mitochondrial DNA data indicated that as much as 43 % of the females identified as *Eretmochelys imbricata* are hybrids in this area (Bahia State of Brazil).

According to the IUCN Red List of Threatened Species, most of the turtle species involved in natural hybridization (58.5 %) are threatened to extinction (Critically Endangered = 7. Endangered = 8, and Vulnerable = 9), whereas 31.7 % are considered in one of the non-threatened categories (Near threatened = 7, Least Concern = 6. For the rest of the species (9.7 %) the conservation status is still unknown or the data are deficient. None of the population of turtle species

Table 3. Hybrids reported between species of crocodilians (Order Crocodylia): [c] under human care. Species abbreviations: *Cra, Crocodylus acutus; Crm, Crocodylus moreletii; Crmi, Crocodylus mindorensis; Crn, Crocodylus niloticus; Crp, Crocodylus porosus; Crr, Crocodylus rhombifer; Crs, Crocodylus siamensis; Ost, Osteolaemus tetraspis; Oscft, O.* sp. nov. cf. *tetraspis.* [Sources: 1, Ray et al (2004); 2, Cedeño-Vázquez et al (2008); 3, Rodriguez et al (2008); 4, Machkour-M'Rabet et al (2009); 5, Hekkala et al (2015); 6, Pacheco-Sierra et al (2016); 7, Pacheco-Sierra et al (2018); 8, Platt et al (2021); 9, Villegas et al (2022); 10, Suarez-Atilano et al (2023); 11, Weaver et al (2008); 12, Milián-García et al (2011); 13, Rodriguez et al (2011); 14, Milián-García et al (2015); 15, Tabora et al (2012); 16, Hinlo et al (2014); 17, Wei et al (2022); 18, Fitzsimmons et al (2002); 19, Chawananikun et al (1999; 20, Lapbenjakul et al (2017); 21, Panthum et al (2023); 22, Schmidt et al (2015); 23, Shirley et al (2015)].

Tabla 3. Híbridos reportados entre especies de cocodrilos (orden Crocodylia): [c] al cuidado de los seres humanos. (Para las abreviaturas del nombre de las especies y de las fuentes bibliográficas, véase arriba).

Family	Sp 1	Sp 2	Region	Source
Crocodylidae	*Cra*	*Crm*	Belize, Mexico	1-10
	Cra	*Crr*	Cuba, USA	11-14
	Crmi	*Crp*	Philippines	15-16
	Crn	*Crp*	Cambodia	17[c]
	Crn	*Crs*	Cambodia	17[c]
	Crp	*Crs*	Australia, Cambodia, Thailand	17[c], 18[c], 19[c], 20[c], 21
	Oscft	*Ost*	Africa	22[c], 23[c]

involved in hybridization is increasing, while 46.3% show a decrease in their numbers, and only three species show a stable population. The population trend for 46.3% of the species is unknown (See supplementary material.

Elasmobranchs

Eleven studies from 2012 to 2023 confirmed hybridization in elasmobranchs through molecular methods, all of them occurring *in situ* (table 5). Six shark hybridization cases have been reported, four of which involved species of the Order Carcharhiniformes: *Carcharhinus galapagensis* x *C. obscurus* in Ecuador and Mexico (Pazmiño et al 2019), *C. tilstoni* x *C. limbatus* along the Australian coast (Morgan et al 2012). One of the reports, with samples collected in the USA, corresponds to the Sphyrnidae family (*Sphyrna lewini* x *S. gilbert*, Barker et al 2019). As well, we found reports of hybrids involving species of the Triakidae family (*Mustelus mustelus* x *M.s punctulatus*), specifically in two embryos in Italy (Marino et al 2015). Other study (Walter et al 2017) reports the occurrence of hybridization between *Somniosus pacificus* x *S. microcephalus*, two sharks of the Squaliformes order, in Canada and the USA. Recently, hybridization among sawsharks (Family Pristiophoridae) was confirmed and involves the species *Pristiophorus cirratus* and *Pristiophorus nudipinnis* (Nevatte et al 2023). Hybrids in marine rays have been reported in Sudan: *Manta alfredi* x *M. birostris* (Walter et al 2017), in Algeria and Italy: *Raja montagui* x *R. polystigma*, (Frodella et al 2016), and in Australia: *Trygonorrhina dumerilii* x *T. fasciata* (Donnellan et al 2015); whereas hybrids in freshwater rays have been reported in the Parana River, Brazil: *Potamotrygon motoro* x *P. falkneri* (Cruz et al 2014).

According to the IUCN Red List of Threatened Species, 35% of the shark and ray species involved in hybridization are in a threatened category (Critically Endangered, Endangered or Vulnerable), while for 20% of the species (n = 4), the conservation status is still unknown due to deficient data. From the elasmobranch involved in hybrids, none have a population trend that is considered to be increasing. *Raja montagui*, *Carcharhinus tilstoni, Pristiophorus cirratus, Pristiophorus nudipinnis, and Trygonorrhina dumerilii* (25%) have a current population trend considered stable, while for *Manta alfredi*, *Manta birostris*, *C. obscurus*, *Sphyrna lewini*, *Mustelus mustelus*, *Mustelus punctulatus*, and *Somniosus microcephalus* (35%) the population trend is decreasing. For *Potamotrygon motoro*, *P. falkneri*, *R. polystigma*, *C. galapagensis*, *C. limbatus*, *Sphyrna gilberti* and *Somniosus pacificus, and Trygonorrhina fasciata* (40%), the current population trend is unknown.

Discussion

The phenomenon of hybridization occurs in aquatic megafauna worldwide. One of the earliest discoveries of marine hybridization was reported in whales *Balaenoptera musculus* x *B. physalus* (Cocks 1887). Reports of hybridization in aquatic megafauna apparently show a tendency to increase, although this could be due to a variety of reasons, such as the development and availability of novelty methodologies capable of reliably detecting these cases (fig. 2), together with an increased number of specialists in the different taxa able to identify hybrids from all over the world. However, in some species, it could be related to a decreasing population trend or an increased overlap between distribution areas of species, due, for example, to a shift in species' range related to climate change (Muhlfeld et al 2014).

Table 4. Hybrids reported between species of turtles (Order Testudines): * based only on morphological differences; [c] under human care. Species abbreviations: *Cac, Caretta caretta; Chm, Chelonia mydas; Chp, Chrysemys picta; Chpb, Chrysemys picta belli; Cumo, Cuora mouhotii obsti; Cup, Cuora picturata; Cut, Cuora trifasciata; Cya, Cyclemys atripons; Cyo, Cyclemys oldhamii; Emo, Emys orbicularis; Emog, Emys orbicularis galloitalica; Emoo, Emys orbicularis orbicularis; Emt, Emys trinacris; Eri, Eretmochelys imbricata; Grg, Graptemys geographica; Grp, G. pseudogeographica; Grb, G. barbouri; Gre, G. ernsti; Lek, Lepidochelys kempii; Leo, L. olivácea; Maa, Mauremys cf. Annamensis; Maj, M. japónica; Mam, M. mutica; Mar, M. reevesii; Mas, M. sinensis; Psa, Pseudemys alabamensis; Psc, P. concinna; Saq, Sacalia quadriocellata; Std, Sternotherus depressus; Stp, Stemotherus peltifer; Tec, Terrapene carolina; Tecc, Terrapene carolina carolina; Tecm, Terrapene carolina major; Temt, Terrapene mexicana triunguis; Teo, Terrapene ornata; Trdeco, Trachemys decorata; Trdecu, Trachemys decusata; Tre, Trachemys emolli; Trt, Trachemys terrapen; Trs, Trachemys stejnegeri; Trv, Trachemys venusta*. [Sources: 1, Karl et al (1995); 2, James et al (2004); 3, Shamblin et al (2018); 4, Vilaça et al (2012); 5, Machado et al (2023); 6 Conceição et al (1990); 7, Witzell and Schmid (2003); 8, Lara-Ruiz et al (2006); 9, Proietti et al (2014); 10, Prosdocimi et al (2014); 11, Soares et al (2017); 12, Arantes et al (2020); 13, Arantes et al (2020); 14, Brito et al (2020); 15, Soares et al (2018); 16, Almeida et al (2023); 17, Vilaça et al (2023); 18, Reis et al (2010); 19, Soares et al (2021); 20, Wood et al (1983); 21, Seminoff et al (2003); 22, Anyembe and Van De Geer (2015); 23, Kelez et al (2016); 24, Restrepo et al (2022); 25, Jensen et al (2014); 26, Godwin et al (2014); 27, Mitchell et al (2016); 28, Moreno et al (2022); 29, Cureton et al (2011); 30, Martin et al (2020); 31, Parham et al (2013); 32, Struijk (2016); 33, Stuart and Parham (2007); 34, Vamberger et al (2017); 35, Schilde et al (2004); 36, Suzuki et al (2013); 37, Ueno et al (2021); 38, Fujii et al (2014); 39, Fong and Chen (2010); 40, Buskirk et al (2005); 41, Scott et al (2019); 42, Vamberger et al (2015); 43, Raemy et al (2017)].

***Tabla 4**. Híbridos reportados entre especies de tortugas (orden Testudines): * basado únicamente en diferencias morfológicas; [c] al cuidado de los seres humanos. (Para las abreviaturas del nombre de las especies y las fuentes bibliográficas, véase arriba).*

Family	Sp1	Sp2	Sp3	Region	Sources
Chelonidae	*Cac*	*Chm*		Canada, USA	1-3
	Cac	*Chm*	*Eri*	Brazil	4, 5
	Cac	*Eri*		Brazil, Argentina, USA	1, 4, 6-14
	Cac	*Eri*	*Leo*	Brazil	15-17
	Cac	*Lek*		USA	8
	Cac	*Leo*		Brazil	4, 18, 19
	Chm	*Eri*		Costa Rica, Kenya, Mexico, Peru,	1, 20, 21, 22*,
				Southeast Pacific, Suriname	23, 24*
	Eri	*Lek*		Brazil	6
	Eri	*Leo*		Brazil	4, 14
Emydidae	*Chp*	*Chpb*		Canada	25
	Grb	*Gre*		USA	26
	Grg	*Grp*		USA	27
	Psa	*Psc*		USA	28
	Tec	*Teo*		USA	29
	Tecc	*Tecm*		USA	30
	Tecc	*Temt*		USA	30
	Tecm	*Temt*		USA	30
	Trdeco	*Trs*		Hispaniola	31
	Trdecu	*Trt*		Jamaica	31
	Tre	*Trv*		Central America	31
Geoemydidae	*Cumo*	*Cup*		Vietnam	32*
	Cut	*Mas*		China	33
	Cut	*Saq*		China	33
	Cya	*Cyo*		Cambodia	34
	Cyo	*Mas*		Unknown	35c
	Maa	*Mas*		China	33
	Maj	*Mar*		Japan	36, 37*
	Mam	*Mar*		Japan	38
	Mar	*Mas*		China	39
	Mar	*Saq*		USA	40c
	Std	*Stp*		USA	41
Kinosternidae	*Emo*	*Emt*		Italy	42
	Emog	*Emoo*		France	43

Table 5. Hybrids reported in sharks and rays (Class Chondrichthyes): *Cag, Carcharhinus galapagensis; Cal, C. Limbatus; Cao, C. Obscurus; Cat, C. Tilstoni; Maa, Manta alfredi; Mab, Manta birostris; Mum, Mustelus mustelus; Mup, Mustelus punctulatus; Pof, Potamotrygon falkneri; Pom, Potamotrygon motoro; Prc, Pristiophorus cirratus; Prn, Pristiophorus nudipinnis; Ram, Raja montagui; Rap, R. Polystigma; Som, Somniosus microcephalus; Sop, Somniosus pacificus; Spg, Sphyrna gilberti; Spl, Sphyrna lewini; Trd, Trygonorrhina dumerilii; Trf, T. fasciata*. [Sources: 1, Pazmiño et al (2019); 2, Morgan et al (2012); 3, Barker et al (2019); 4, Marino et al (2015); 5, Walter et al (2014); 6, Cruz et al (2014); 7, Cruz et al (2017); 8, Nevatte et al (2023); 9, Frodella et al (2016); 10, Donnellan et al (2015); 11, Walter et al (2017)].

***Tabla 5**. Híbridos reportados en tiburones y rayas (clase Chondrichthyes). (Para las abreviaturas del nombre de las especies y las fuentes bibliográficas, véase arriba).*

Order						
	Family	Sp 1	Sp 2	Region	Country	Source
Carcharhiniformes						
	Carcharhinidae	*Cag*	*Cao*	Indo-Pacific Ocean	Ecuador, Mexico, France (Clipperton Island)	1
		Cal	*Cat*	Australia	Australia	2
	Sphyrnidae	*Spg*	*Spl*	Northwest Atlantic	USA	3
	Triakidae	*Mum*	*Mup*	Northern Adriatic Sea	Italy	4
Myliobatiformes						
	Myliobatidae	*Maa*	*Mab*	Red Sea	Sudan	5
	Potamotrygonidae	*Pof*	*Pom*	Paraná River	Brazil	6, 7
Pristiophoriformes						
	Pristiophoridae	*Prc*	*Prn*	Australia	Australia	8
Rajiformes						
	Rajidae	*Ram*	*Rap*	Western and Central Mediterranean Sea	Algeria and Italy	9
Rhinopristiformes						
	Trygonorhinidae	*Trd*	*Trf*	Adelaida	Australia	10
Squaliformes						
	Somniosidae	*Som*	*Sop*	North Atlantic	Canada, USA	11

Based on the number of reports found here, turtles apparently showed considerable rates of hybridization, with especially high numbers of cases in sea turtles along the coast of Brazil. In this area, previous studies on loggerhead/hawksbill hybrids suggested no negative effect of hybridization on the reproductive output of the hybrids (Soares et al 2017). Neither did hybridization show consequences on fitness using hatching rate as a proxy (Soares et al 2018). Both male and female hybrid males and females were fertile and produced viable offspring, and there was no evidence of hybrid breakdown (Soares et al 2018). However, recent research has evidenced an association between hybridization between hawksbill and loggerhead turtles and low reproductive success, representing a threat to sea turtle conservation (Arantes et al 2020a). Also, hybrid offspring of sea turtles has shown high mortality, with increased susceptibility to lung infection (Karl et al 1995). These cases match the decline in sea turtle populations during the last century, and the probable secondary contact between previously isolated populations led by habitat destruction, propitiating these high hybridization rates (Arantes et al 2020b).

In the case of crocodilians, natural hybridization is relatively common and plays an important role in the evolution and speciation of this group. However, anthropogenic factors can also promote hybridization between species, posing important conservation problems (Pacheco-Sierra and Amavet 2021). In some Asian countries *Crocodylus siamensis* has been intentionally crossed with *C. porosus* and *C. rhombifer* under human care to obtain hybrids that grow faster and have superior leather quality, giving them a higher commercial value than parental species (Thorbjarnarson 1999, Fitzsimmons et al 2002). In this group, introgression is specially of high concern, since hybrids are exceptionally similar in morphology to the parental species (Lapbenjakul et al 2017), which can cause problems when reintroducing captive individuals aiming to recover wild populations of critically endangered species (Fitzsimmons et al 2002, Tabora et al 2012, Hinlo et al 2014, Chattopadhyay et al 2019). Considering natural hybridization, studies have mainly been conducted on the admixture of the vulnerable *C. acutus* and *C. moreletii* and *C. rhombifer*. Although *C. acutus* presents the wider distribution range of all New World crocodilians and shows an increasing trend in its population size, natural hybridization with

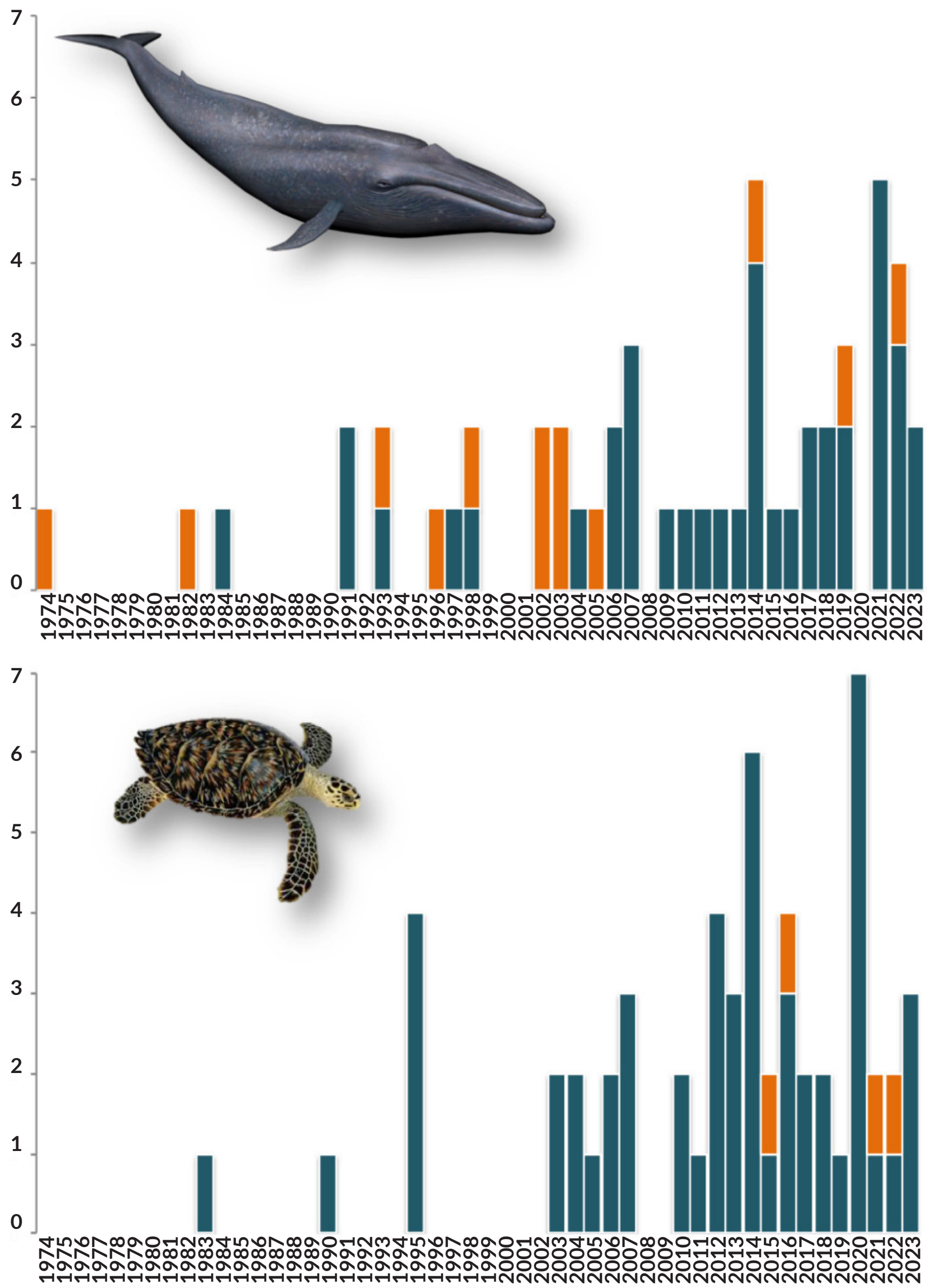

Fig. 2A. Number of articles reporting hybrids in aquatic mammals and turtles until 2023. (Reports based only on morphological descriptions are indicated in orange).

Fig. 2A. *Número de artículos en los que se reportan híbridos en mamíferos acuáticos y en tortugas hasta 2023. Los informes basados únicamente en las descripciones morfológicas se indican en color naranja.*

sympatric species could affect its populations in some regions. For example, coastal crocodile populations from Belize to the state of Tamaulipas (Mexico) consist mainly of hybrid individuals, with only two genetically pure populations of *C. acutus* remaining on islands in the Mexican Caribbean and three pure populations of *C. moreletii* in isolated lagoons in the states of Tabasco and San Luis Potosí, leading to significant conservation and taxonomic implications (Machkour-M'Rabet et al 2009, Pacheco-Sierra et al 2016, 2018). Furthermore, new potential hybridization processes with introduced species could threaten *C. acutus* recovery in other areas (Rochford et al 2016, Serrano-Gómez et al 2016, Metzger III et al 2020). Considering the importance of

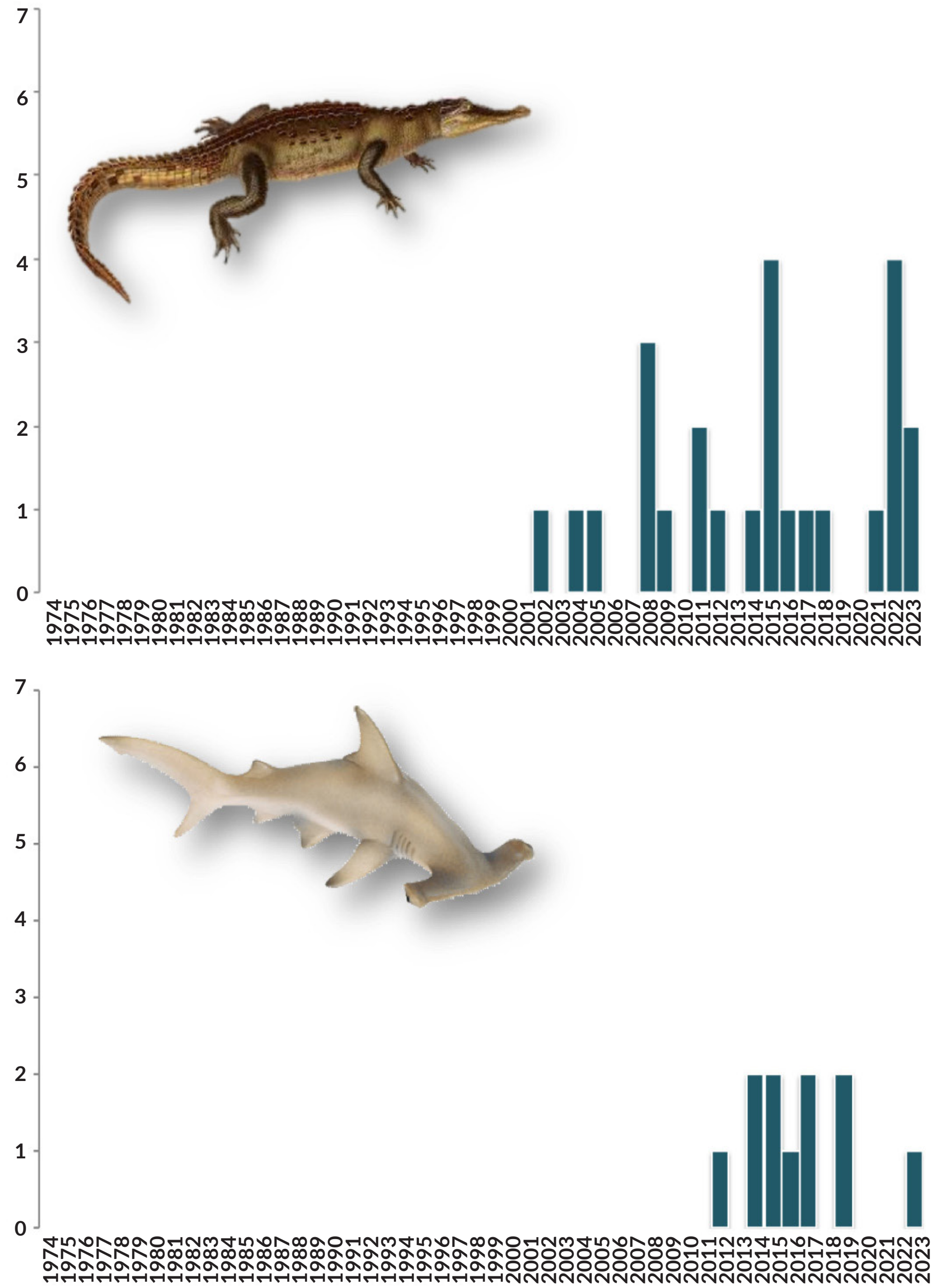

Fig. 2B. Number of articles reporting hybrids in crocodilians, and elasmobranchs until 2023. (Reports based only on morphological descriptions are indicated in orange).

***Fig. 2B**. Número de artículos en los que se reportan híbridos en cocodrilos y en elasmobranquios hasta 2023. (Los informes basados únicamente en las descripciones morfológicas se indican en color naranja).*

hybridization for evolution, speciation, and conservation of crocodilians, more studies should be conducted on natural admixtures between species of this group because many species occur sympatrically, especially in Alligatoridae and Gavialidae families, as studies to date have exclusively involved species from the Crocodylidae family.

Marine populations are characterized by high levels of genetic similarity over very large distances. This is usually attributed to high levels of gene flow (that result from the dispersal potential of the organisms), reducing the frequency in which hybridization can occur (Gardner 1997). Although genetic divergence between marine populations is presumed to be slow

(Gardner 1997), this is not the case for some cetacean populations in lesser numbers which show high levels of genetic divergence, even in sympatric populations, such as *Orcinus orca* (Foote et al 2016) and *Tursiops truncatus* worldwide (Hoelzel et al 1998, Natoli et al 2004, Louis et al 2014). Divergence within the Delphinidae seems to be driven by ecological and habitat specialization, followed by genetic divergence (Ford et al 1998, Natoli et al 2005, Louis et al 2014, Foote et al 2019). Delphinids also show complex dynamics of population divergence and admixture throughout their evolutionary history (Foote et al 2019). All these traits could be promoting hybridization to the point of forming new species as is the case for *Stenella clymene* arising from the parental species *S. coerueloalba* and *S. longirostris* (Amaral et al 2014). In marine mammals, a hybridization event of *Pseudorca crassidens* x *Tursiops truncatus gilli* had a negative outcome, with the observation of abortive fetuses, and acute-pneumonia in a calf specimen that survived for a few months (Nishiwaki and Tobayama 1982). This offspring was likely unviable because the species involved are not closely related, the former being a member of the Globicephalinae subfamily and the latter a member of the Delphininae, having been separated in the late Miocene between 11.6 and 5-3 Mya (Vilstrup et al 2011).

The reports of hybridization in elasmobranchs are very recent but could potentially influence the populations in the long-term because elasmobranchs are currently considered among the most endangered vertebrate groups in the world (Carlson et al 2019). It is difficult to predict whether, as reported due to extensive interbreeding and hybrid fertility, individuals are likely to have a hybrid ancestry within a few generations (i.e. swarm model Morgan et al 2012) or whether hybrid viability could be reduced as there is no evidence of adult hybrids in their findings (Marino et al 2015). Further studies are required to delve into the species hybridization of this group.

Many species of aquatic megafauna have undergone large declines in population and geographic range, mainly due to human-related factors, and some are on the verge of extinction (Ripple et al 2019). Such impacts are caused by a variety of sources, such as overfishing (Dulvy et al 2021), bycatch (Larsen et al 2021), habitat destruction (Arantes et al 2020b), invasive species (Vilizzi et al 2021), and illegal trade (Tulloch et al 2018, Asbury et al 2021). Hybridization may impact populations of rare species much more strongly than species with an abundant population, and its consequences may depend on whether populations are growing or contracting, or whether they are local or invasive (Currat et al 2008), indicating plausible habitat disturbance, range expansion, or both (Abbott et al 2013). However, the outcomes of hybridization are often difficult to predict regardless of the demographics of the paternal species. Furthermore, hybridization may limit the distribution of a species if the hybrid is less fit than its parental species, or it may promote speciation through better adaptation of the offspring to new environments (Barton and Hewitt 1985). Risks associated with hybridization include (Chan et al 2019): (a) the likelihood of outbreeding depression; and (b) the loss of parental species due to genetic admixture. The main conservation issues that could be expected regarding these cases are misclassification of individuals (Lapbenjakul et al 2017), low reproduction, and low survival rates (Nishiwaki and Tobayama 1982, Karl et al 1995, Marino et al 2015, Lapbenjakul et al 2017), with the concomitant extinction of the species (Allendorf et al 2001) exacerbating the current anthropogenic pressure on aquatic megafauna (e.g. Field et al 2009; Zucoloto et al 2021).

Nevertheless, hybrids very often occur in aquatic ecosystems and do not always have negative ecological or genetic consequences (Piett et al 2015). Hybridization is in many cases a mechanism that facilitates adaptation and speciation, and it has become increasingly evident that it plays a key role in the evolution of many taxa, sometimes resulting in an entirely new plant or animal species (Chapman and Burke 2007). With the global decline in the biodiversity of aquatic megafauna, further research is needed to determine whether hybridization in a particular taxon has negative impacts on its conservation, or if, on the other hand, it has a potential role in maintaining and preserving biodiversity.

References

Abbott R, Albach D, Ansell S, Arntzen JW, Baird SJ, Bierne, N, Boughman J, Brelsford A, Buerkle CA, Buggs R 2013. Hybridization and speciation. *Journal of Evolutionary Biology* 26(2), 229-246. DOI: 10.1111/j.1420-9101.2012.02599.x

Allendorf FW, Leary RF, Spruell P, Wenburg JK 2001. The problems with hybrids: setting conservation guidelines. *Trends in Ecology and Evolution* 16(11), 613-622. DOI: 10.1016/S0169-5347(01)02290-X

Almeida JPFA, Marques OKL, Mott T, Santos RG, 2023. Hybridization and genetic characterization of sea turtles in Alagoas, northeastern Brazil. *Marine Biology* 170(2), 14. DOI: 10.1007/s00227-022-04168-y

Amaral AR, Lovewell G, Coelho MM, Amato G, Rosenbaum HC, 2014. Hybrid speciation in a marine mammal: the Clymene dolphin (*Stenella clymene*. *Plos One* 9(1), e83645. DOI: 10.1371/journal.pone.0083645

Antoniou A, Frantzis A, Alexiadou P, Paschou N, Poulakakis N, 2018. Evidence of introgressive hybridization between *Stenella coeruleoalba* and *Delphinus delphis* in the Greek Seas. *Molecular Phylogenetics and Evolution* 129, 325-337. DOI: 10.1016/j.ympev.2018.09.007

Anyembe D, Van De Geer C, 2015. The first photo-documented hybrid of a green turtle, *Chelonia mydas*, and a hawksbill turtle, *Eretmochelys imbricata*, in East Africa. *African Sea Turtle Newsletter* 3, 42-47.

Arantes LS, Ferreira LCL, Maximilian D, Marinho RFFP, Mazzoni CJ, Santos FR, 2020a. Genomic evidence of recent hybridization between sea turtles at Abrolhos Archipelago and its association to low reproductive output. *Scientific Reports* 10(1), 1-13. DOI: 10.1038/s41598-020-69613-8

Arantes LS, Vilaça ST, Mazzoni CJ, Santos FR, 2020b. New genetic insights about hybridization and population structure of hawksbill and loggerhead turtles from Brazil. *Journal of Heredity* 111(5), 444-456. DOI: 10.1093/jhered/esaa024

Árnason Ú, Gullberg A, 1993. Comparison between the complete mtDNA sequences of the blue and the fin whale, two species that can hybridize in nature. *Journal of Molecular Evolution* 37(4), 312-322. DOI: 10.1007/BF00178861

Árnason Ú, Spilliaert R, Pálsdottir A, Árnason A, 1991. Molecular identification of hybrids between the two largest whale species, the blue whale (*Balaenoptera musculus*) and the fin whale (*B. physalus*. *Hereditas* 115(2), 183-189. DOI: 10.1111/j.1601-5223.1991.tb03554.x

Arnold ML, 1992. Natural hybridization as an evolutionary process. *Annual Review of Ecology and Systematics* 23(1), 237-261. DOI: 10.1146/annurev.es.23.110192.001321

Asbury T, Bennett R, Price A, da Silva C, Bürgener M, Klein J, Maduna S, Sidat N, Fernando S, Bester-van der Merwe A, 2021. Application of DNA mini-barcoding reveals illegal trade in endangered shark products in southern Africa. *African Journal of Marine Science* 43(4), 511-520. DOI: 10.2989/1814232X.2021.1996459

Attard CR, Beheregaray LB, Jenner KCS, Gill PC, Jenner MN, Morrice MG, Robertson KM, Möller LM, 2012. Hybridization of Southern

Hemisphere blue whale subspecies and a sympatric area off Antarctica: impacts of whaling or climate change? *Molecular Ecology* 21(23), 5715-5727. DOI: 10.1111/mec.12025
Baird RW, Willis PM, Guenther TJ, Wilson PJ, White BN, 1998. An intergeneric hybrid in the family Phocoenidae. *Canadian Journal of Zoology* 76(1), 198-204. DOI: 10.1139/z97-175a
Barker AM, Adams DH, Driggers III WB, Frazier BS, Portnoy DS, 2019. Hybridization between sympatric hammerhead sharks in the western North Atlantic Ocean. *Biology Letters* 15(4), 20190004. DOI: 10.1098/rsbl.2019.0004
Barton NH, Hewitt GM, 1985. Analysis of hybrid zones. *Annual Review of Ecology and Systematics* 16(1), 113-148. DOI: 10.1146/annurev.es.16.110185.000553
Bérubé M, Aguilar A, 1998. A new hybrid between a blue whale, *Balaenoptera musculus*, and a fin whale, *B. physalus*: frequency and implications of hybridization. *Marine Mammal Science* 14(1), 82-98. DOI: 10.1111/j.1748-7692.1998.tb00692.x
Bouvet J-M, Makouanzi G, Cros D, Vigneron P, 2016. Modeling additive and non-additive effects in a hybrid population using genome-wide genotyping: prediction accuracy implications. *Heredity* 116(2), 146-157. DOI: 10.1038/hdy.2015.78
Brito C, Vilaça ST, Lacerda AL, Maggioni R, Marcovaldi MÂ, Vélez-Rubio G, Proietti MC, 2020. Combined use of mitochondrial and nuclear genetic markers further reveal immature marine turtle hybrids along the South Western Atlantic. *Genetics and Molecular Biology* 43. DOI: 10.1590/1678-4685-GMB-2019-0098
Brown AM, Kopps AM, Allen SJ, Bejder L, Littleford-Colquhoun B, Parra GJ, Cagnazzi D, Thiele D, Palmer C, Frere CH, 2014. Population differentiation and hybridisation of Australian snubfin (*Orcaella heinsohni*) and Indo-Pacific humpback (*Sousa chinensis*) dolphins in north-western Australia. *Plos One* 9(7), e101427. DOI: 10.1371/journal.pone.0101427
Brunner S, 2002. A probable hybrid sea lion-*Zalophus californianus* × *Otaria byronia*. *Journal of Mammalogy* 83(1), 135-144. DOI: 10.1644/1545-1542(2002)083<0135:APHSLZ>2.0.CO;2
Buskirk JR, Parham JF, Feldman CR, 2005. On the hybridisation between two distantly related Asian turtles (Testudines: Sacalia x Mauremys. *Salamandra* 41(1/2), 21.
Caballero S, Baker C, 2010. Captive-born intergeneric hybrid of a Guiana and bottlenose dolphin: *Sotalia guianensis* × *Tursiops truncatus*. *Zoo Biology* 29(5), 647-657. DOI: 10.1002/zoo.20299
Carlson JK, Heupel MR, Young CN, Cramp JE, Simpfendorfer CA, 2019. Are we ready for elasmobranch conservation success? *Environmental Conservation* 46(4), 264-266. DOI: 10.1017/S0376892919000225
Cedeño-Vázquez JR, Rodriguez D, Calmé S, Ross JP, Densmore LD, Thorbjarnarson JB, 2008. Hybridization between *Crocodylus acutus* and *Crocodylus moreletii* in the Yucatan Peninsula: I. Evidence from mitochondrial DNA and morphology. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* 309(10), 661-673. DOI: 10.1002/jez.473
Chan WY, Hoffmann AA, van Oppen MJ, 2019. Hybridization as a conservation management tool. *Conservation Letters* 12(5), e12652. DOI: 10.1111/conl.12652
Chapman MA, Burke JM, 2007. Genetic divergence and hybrid speciation. *Evolution: International Journal of Organic Evolution* 61(7), 1773-1780. DOI: 10.1111/j.1558-5646.2007.00134.x
Chattopadhyay B, Garg KM, Soo YJ, Low GW, Frechette JL, Rheindt FE, 2019. Conservation genomics in the fight to help the recovery of the critically endangered Siamese crocodile *Crocodylus siamensis*. *Molecular Ecology* 28(5), 936-950. DOI: 10.1111/mec.15023
Chawananikun W, Suwatthana D, Koyakun W, Watthanodon S, Sukkhai C, 1999. Karyotypes of freshwater crocodiles (*Crocodylus siamensis*), salt water crocodiles (*Crocodylus porosus*) and the interspecific hybrids by conventional and banding techniques (Research abstracts of universities' lecturer in Thailand during 1997-1999. Office of the Permanent Secretary, Bangkok (Thailand): 464-465. Bureau of Higher Education Standards, Bangkok, Thailand.
Cocks A, 1887. The fin whale fishery of 1886 on the Lapland coast. *Zoologist* 11, 207-222.
Conceição MB de, Sabaj JAL, Marins LFF, Marcovaldi MAAGD, 1990. Electrophoretic characterization of a hybrid between *Eretmochelys imbricata* and *Caretta caretta* (Cheloniidae. *Comparative Biochemistry and Physiology* 97(2), 275-278.
Coyne JA, Orr HA, 2004. *Speciation*. Sinauer Associates, Sunderland, Massachusetts, USA..
Crossman CA, Barrett-Lennard LG, Taylor EB, 2014. Population structure and intergeneric hybridization in harbour porpoises *Phocoena phocoena* in British Columbia, Canada. *Endangered Species Research* 26(1), 1-12. DOI: 10.3354/esr00624
Cruz V, Vera M, Mendonça F, Pardo B, Martinez P, Oliveira C, Foresti F, 2014. First identification of interspecies hybridization in the freshwater stingrays *Potamotrygon motoro* and *P. falkneri* (Myliobatiformes, Potamotrygonidae. *Conservation Genetics* 16(1), 241-245. DOI: 10.1007/s10592-014-0642-8
Cruz VP, Vera M, Pardo BG, Taggart J, Martinez P, Oliveira C, Foresti F 2017. Identification and validation of single nucleotide polymorphisms as tools to detect hybridization and population structure in freshwater stingrays. *Molecular Ecology Resources* 17(3), 550-556. DOI: 10.1111/1755-0998.12564
Cureton JC, Buchman AB, Deaton R, Lutterschmidt WI, 2011. Molecular analysis of hybridization between the box turtles *Terrapene carolina* and *T. ornata*. *Copeia* 2011(2), 270-277. DOI: 10.1643/CG-10-066
Currat M, Ruedi M, Petit RJ, Excoffier L, 2008. The hidden side of invasions: massive introgression by local genes. *Evolution: International Journal of Organic Evolution* 62(8), 1908-1920. DOI: 10.1111/j.1558-5646.2008.00413.x
de Almeida Filho JE, Guimarães JFR, Fonsceca e Silva F, Vilela de Resende MD, Muñoz P KM, de Resende Júnior MFR, 2019. Genomic prediction of additive and non-additive effects using genetic markers and pedigrees. *G3: Genes, Genomes, Genetics* 9(8), 2739-2748. DOI: 10.1534/g3.119.201004
de Oliveira EH, Gomes AJ, Costa AF, Emin-Lima R, Bonvicino CR, Viana MC, Reis LM, Vidal MD, Cavalcanti MV, Attademo FL, 2022. Karyotypical confirmation of natural hybridization between two manatee species, *Trichechus manatus* and *Trichechus inunguis*. *Life* 12(5), 616. DOI: 10.3390/life12050616
Dohl TP, Norris KS, Kang I, 1974. A porpoise hybrid: *Tursiops* × *Steno*. *Journal of Mammalogy* 55(1), 217-221. DOI: 10.2307/1379276
Donnellan SC, Foster R, Junge C, Huveneers C, Rogers P, Kilian A, Bertozzi T, 2015. Fiddling with the proof: the magpie fiddler ray is a colour pattern variant of the common southern fiddler ray (Rhinobatidae: Trygonorrhina. *Zootaxa* 3981(3), 367-384. DOI: 10.11646/zootaxa.3981.3.3
Dulvy NK, Pacoureau N, Rigby CL, Pollom RA, Jabado RW, Ebert DA, Finucci B, Pollock CM, Cheok J, Derrick DH, 2021. Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology* 31(21), 4773-4787.e8. DOI: 10.1016/j.cub.2021.08.062
Duvick DN, 2001. Biotechnology in the 1930s: the development of hybrid maize. *Nature Reviews Genetics* 2(1), 69-74. DOI: 10.1038/35047587
East EM, 1936. Heterosis. *Genetics* 21(4), 375.
Edwards CJ, Suchard MA, Lemey P, Welch JJ, Barnes I, Fulton TL, Barnett R, O'Connell TC, Coxon P, Monaghan N, 2011. Ancient hybridization and an Irish origin for the modern polar bear matriline. *Current Biology* 21(15), 1251-1258. DOI: 10.1016/j.cub.2011.05.058
Espada R, Olaya-Ponzone L, Haasova L, Martín E, García-Gómez JC, 2019. Hybridization in the wild between *Tursiops truncatus* (Montagu 1821) and *Delphinus delphis* (Linnaeus 1758). *Plos One* 14(4), e0215020. DOI: 10.1371/journal.pone.0215020
Espregueira Themudo G, Nieman A, Arntzen J, 2012. Is dispersal guided by the environment? A comparison of interspecific gene flow estimates among differentiated regions of a newt hybrid zone. *Molecular Ecology* 21(21), 5324-5335. DOI: 10.1111/mec.12026
Ferree PM, Barbash DA, 2009. Species-specific heterochromatin prevents mitotic chromosome segregation to cause hybrid lethality in *Drosophila*. *Plos Biology* 7(10), e1000234. DOI: 10.1371/journal.pbio.1000234
Field IC, Meekan MG, Buckworth RC, Bradshaw CJ, 2009. Susceptibility of sharks, rays and chimaeras to global extinction. *Advances in Marine Biology* 56, 275-363. DOI: 10.1016/S0065-2881(09)56004-X
Fioravanti T, Maio N, Latini L, Splendiani A, Guarino F, Mezzasalma M, Petraccioli A, Cozzi B, Mazzariol S, Centelleghe C, 2022. Nothing is as it seems: Genetic analyses on stranded fin whales unveil the presence of a fin-blue whale hybrid in the Mediterranean Sea (Balaenopteridae. *The European Zoological Journal* 89(1), 590-600. DOI: 10.1080/24750263.2022.2063426
Fitzsimmons NN, Buchan JC, Lam PV, Polet G, Hung TT, Thang NQ, Gratten J, 2002. Identification of purebred *Crocodylus siamensis* for reintroduction in Vietnam. *Journal of Experimental Zoology 294*(4), 373-381. DOI: 10.1002/jez.10201
Fong JJ, Chen T-H, 2010. DNA evidence for the hybridization of wild turtles in Taiwan: possible genetic pollution from trade animals. *Conservation Genetics* 11(5), 2061-2066. DOI: 10.1007/s10592-010-0066-z
Foote AD, Martin MD, Louis M, Pacheco G, Robertson KM, Sinding MHS, Amaral AR, Baird RW, Baker CS, Ballance L, 2019. Killer whale genomes reveal a complex history of recurrent admixture and vicariance. *Molecular Ecology* 28(14), 3427-3444. DOI: 10.1111/mec.15099

Foote AD, Vijay N, Ávila-Arcos MC, Baird RW, Durban JW, Fumagalli M, Gibbs RA, Hanson MB, Korneliussen TS, Martin MD, 2016. Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. *Nature Communications* 7(1), 1-12. DOI: 10.1038/ncomms11693

Ford JK, Ellis GM, Barrett-Lennard LG, Morton AB, Palm RS, Balcomb III KC, 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology* 76(8), 1456-1471. DOI: 10.1139/z98-089

Franco-Trecu V, 2021. Intergeneric fertile hybridization in otariids. In: *Ethology and Behavioral Ecology of Otariids and the Odobenid*, 243-247 (C Campagna, R Harcourt, Eds). Springer. DOI: 10.1007/978-3-030-59184-7

Franco-Trecu V, Abud C, Feijoo M, Kloetzer G, Casacuberta M, Costa-Urrutia P, 2016. Sex beyond species: the first genetically analyzed case of intergeneric fertile hybridization in pinnipeds. *Evolution and Development* 18(2), 127-136. DOI: 10.1111/ede.12183

Frodella N, Cannas R, Velonà A, Carbonara P, Farrell ED, Fiorentino F, Follesa MC, Garofalo G, Hemida F, Mancusi C, 2016. Population connectivity and phylogeography of the Mediterranean endemic skate *Raja polystigma* and evidence of its hybridization with the parapatric sibling *R. montagui*. *Marine Ecology Progress Series* 554, 99-113. DOI: 10.3354/meps11799

Fujii R, Ota H, Toda M, 2014. Genetic and morphological assessments of hybridization between two non-native geoemydid turtles, *Mauremys reevesii* and *Mauremys mutica*, in northcentral Japan. *Chelonian Conservation and Biology* 13(2), 191-201. DOI: 10.2744/CCB-1067.1

Gardner J, 1997. Hybridization in the sea. *Advances in Marine Biology* 31, 1-78. DOI: 10.1016/S0065-2881(08)60221-7

Gibeaux R, Acker R, Kitaoka M, Georgiou G, van Kruijsbergen I, Ford B, Marcotte EM, Nomura DK, Kwon T, Veenstra GJC, 2018. Paternal chromosome loss and metabolic crisis contribute to hybrid inviability in *Xenopus*. *Nature* 553(7688), 337-341. DOI: 10.1038/nature25188

Glover KA, Kanda N, Haug T, Pastene LA, Øien N, Seliussen BB, Sørvik AG, Skaug HJ, 2013. Hybrids between common and Antarctic minke whales are fertile and can back-cross. *Bmc Genetics* 14(1), 1-11. DOI: 10.1186/1471-2156-14-25

Godwin JC, Lovich JE, Ennen JR, Kreiser BR, Folt B, Lechowicz C, 2014. Hybridization of two megacephalic map turtles (Testudines: Emydidae: Graptemys) in the Choctawhatchee River drainage of Alabama and Florida. *Copeia* 2014(4), 725-742. DOI: 10.1643/CH-13-132

Goldsworthy SD, McKenzie J, Page B, Lancaster ML, Shaughnessy PD, Wynen LP, Robinson SA, Peters KJ, Baylis AM, McIntosh RR, 2009. Fur seals at Macquarie Island: post-sealing colonisation, trends in abundance and hybridisation of three species. *Polar Biology* 32(10), 1473-1486. DOI: 10.1007/s00300-009-0645-y

Grant PR, Grant BR, 1992. Hybridization of Bird Species. *Science* 256(5054), 193-197. DOI: 10.1126/science.256.5054.193

Gravena W, Da Silva VM, Da Silva MN, Farias IP, Hrbek T, 2015. Living between rapids: genetic structure and hybridization in botos (Cetacea: Iniidae: *Inia* spp.) of the Madeira River, Brazil. *Biological Journal of the Linnean Society* 114(4), 764-777. DOI: 10.1111/bij.12463

Gridley T, Elwen SH, Harris G, Moore D, Hoelzel A, Lampen F, 2018. Hybridization in bottlenose dolphins - A case study of *Tursiops aduncus* × *T. truncatus* hybrids and successful backcross hybridization events. *Plos One* 13(9), e0201722. DOI: 10.1371/journal.pone.0201722

Guldemond R, Van Aarde R, 2008. A meta-analysis of the impact of African elephants on savanna vegetation. *The Journal of Wildlife Management* 72(4), 892-899. DOI: 10.2193/2007-072

Heide-Jørgensen MP, Reeves RR, 1993. Description of an anomalous monodontid skull from west Greenland: a possible hybrid? *Marine Mammal Science* 9(3), 258-268. DOI: 10.1111/j.1748-7692.1993.tb00454.x

Hekkala ER, Platt SG, Thorbjarnarson JB, Rainwater TR, Tessler M, Cunningham SW, Twomey C, Amato G, 2015. Integrating molecular, phenotypic and environmental data to elucidate patterns of crocodile hybridization in Belize. *Royal Society Open Science* 2(9), 150409. DOI: 10.1098/rsos.150409

Herzingm DL, Moewe K, Brunnickl BJ, 2003. Interspecies interactions between Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals* 29(3), 335-334.

Hinlo MRP, Tabora JA, Bailey CA, Trewick S, Rebong G, Weerd M, Pomares CC, Engberg SE, Brenneman RA, Louis Jr E, 2014. Population genetics implications for the conservation of the Philippine Crocodile *Crocodylus mindorensis* Schmidt, 1935 (Crocodylia: Crocodylidae. *Journal of Threatened Taxa* 6(3), 5513-5533. DOI: 1011609/JoTT.o3384.5513-33

Hodgins NK, Dolman SJ, Weir CR, 2014. Potential hybridism between free-ranging Risso's dolphins (*Grampus griseus*) and bottlenose dolphins (*Tursiops truncatus*) off north-east Lewis (Hebrides, UK. *Marine Biodiversity Records*, 7. DOI: 10.1017/S175526721400089X

Hoelzel AR, Potter CW, Best PB, 1998. Genetic differentiation between parapatric 'nearshore'and 'offshore'populations of the bottlenose dolphin. *Proceedings of the Royal Society B* 265(1402), 1177-1183. DOI: 10.1098/rspb.1998.0416

Inamori D, Kita YF, Funasaka N, 2021. External morphological and molecular evidence of natural intrageneric hybridization between common and Indo-Pacific bottlenose dolphins (*Tursiops truncatus* × *T. aduncus*) from Japanese waters. *Mammal Study* 47(2), 133-140. DOI: 10.1371/journal.pone.0201722

James MC, Martin K, Dutton PH, 2004. Hybridization between a green turtle, *Chelonia mydas*, and loggerhead turtle, *Caretta caretta*, and the first record of a green turtle in Atlantic Canada. *The Canadian Field-Naturalist* 118(4), 579-582. DOI: 10.22621/cfn.v118i4.59

Jefferson TA, Palacios DM, Calambokidis J, Baker CS, Hayslip CE, Jones PA, Lagerquist B, Jørgensen M, Schulman-JanigerA, 2021. Sightings and satellite tracking of a Blue/Fin Whale hybrid in its wintering and summering ranges in the Eastern North Pacific. *Advances in Oceanography and Marine Biology* 2(4), 1-9. DOI: 10.1121/1.2799905

Jensen EL, Govindarajulu P, Madsen J, Russello MA, 2014. Extirpation by introgression? Genetic evidence reveals hybridization between introduced *Chrysemys picta* and endangered western painted turtles (*C. p. bellii*) in British Columbia. *Herpetological Conservation and Biology* 9(2), 342-353. Available online at: http://www.herpconbio.org/Volume_9/Issue_2/Jensen_etal_2014.pdf

Karl S, Bowen B, Avise J, 1995. Hybridization among the ancient mariners: characterization of marine turtle hybrids with molecular genetic assays. *Journal of Heredity* 86(4), 262-268. DOI: 10.1093/oxfordjournals.jhered.a111579

Kelez S, Velez-Zuazo X, Pacheco AS, 2016. First record of hybridization between green *Chelonia mydas* and hawksbill *Eretmochelys imbricata* sea turtles in the Southeast Pacific. *PeerJ* 4, e1712. DOI: 10.7717/peerj.1712

Kingston J, Gwilliam J, 2007. Hybridization between two sympatrically breeding species of fur seal at Iles Crozet revealed by genetic analysis. *Conservation Genetics* 8(5), 1133-1145. DOI: 10.1007/s10592-006-9269-8

Kovacs KM, Lydersen C, Hammill MO, White BN, Wilson PJ, Malik, S, 1997. A harp seal × hooded seal hybrid. *Marine Mammal Science* 13(3), 460-468. DOI: 0.1111/j.1748-7692.1997.tb00652.x

Lancaster M, Bradshaw C, Goldsworthy S, Sunnucks P, 2007. Lower reproductive success in hybrid fur seal males indicates fitness costs to hybridization. *Molecular Ecology* 16(15), 3187-3197. DOI: 10.1111/j.1365-294X.2007.03339.x

Lancaster M, Gemmell NJ, Negro S, Goldsworthy S, Sunnucks P, 2006. Ménage à trois on Macquarie Island: hybridization among three species of fur seal (*Arctocephalus* spp.) following historical population extinction. *Molecular Ecology* 15(12), 3681-3692. DOI: 10.1111/j.1365-294X.2006.03041.x

Lapbenjakul S, Thapana W, Twilprawat P, Muangmai N, Kanchanaketu T, Temsiripong Y, Unajak S, Peyachoknagul S, Srikulnath K, 2017. High genetic diversity and demographic history of captive Siamese and Saltwater crocodiles suggest the first step toward the establishment of a breeding and reintroduction program in Thailand. *Plos One* 12(9), e0184526. DOI: 10.1371/journal.pone.0184526

Lara-Ruiz P, Lopez G, Santos F, Soares L, 2006. Extensive hybridization in hawksbill turtles (*Eretmochelys imbricata*) nesting in Brazil revealed by mtDNA analyses. *Conservation Genetics* 7(5), 773-781. DOI: 10.1007/s10592-005-9102-9

Larsen F, Kindt-Larsen L, Sørensen TK, Glemarec G, 2021. *Bycatch of marine mammals and seabirds: Occurrence and mitigation*. DTU Aqua. *DTU Aqua-rapport* No. 389-2021. Available online at: https://www.aqua.dtu.dk/-/media/institutter/aqua/publikationer/rapporter-352-400/389-2021-bycatch-of-marine-mammals-and-seabirds.pdf

Lima CS, Magalhaes RF, Marmontel M, Meirelles AC, Carvalho VL, Lavergne A, Thoisy BD, Santos FR, 2019. A hybrid swarm of manatees along the Guianas coastline, a peculiar environment under the influence of the Amazon River plume. *Anais da Academia Brasileira de Ciencias* 26, 91. DOI: 10.1590/0001-3765201920190325

Liu D, Zhang P, Wang Y, Lu Z, Deng W, Li S, 2023. Hybrids between Gray seals (*Halichoerus grypus*) and Spotted seals (*Phoca largha*): A case of xeno-breeding preference in pinnipeds. *Aquatic Mammals* 49(6), 550-560. DOI: 10.1578/AM.49.6.2023.550

Lopes F, Oliveira LR, Beux Y, Kessler A, Cárdenas-Alayza S, Majluf P, Páez-Rosas D, Chaves J, Crespo E, Brownell Jr RL, 2023. Genomic evidence for homoploid hybrid speciation in a marine mammal apex predator. *Science Advances* 9(18), eadf6601. DOI: 10.1126/

sciadv.adf6601
Louis M, Fontaine MC, Spitz J, Schlund E, Dabin W, Deaville R, Caurant F, Cherel Y, Guinet C, Simon-Bouhet B, 2014. Ecological opportunities and specializations shaped genetic divergence in a highly mobile marine top predator. *Proceedings of the Royal Society B* 281(1795), 20141558. DOI: 10.1098/rspb.2014.1558
Louis, M., Viricel, A., Lucas, T., Peltier, H., Alfonsi, E., Berrow, S., Brownlow, A., Covelo, P., Dabin, W., Deaville, R, 2014. Habitat-driven population structure of bottlenose dolphins, *Tursiops truncatus*, in the North-East Atlantic. *Molecular Ecology* 23(4), 857-874. DOI: 10.1111/mec.12653
Luna FdO, Beaver CE, Nourisson C, Bonde RK, Attademo FL, Miranda AV, Torres-Florez JP, de Sousa GP, Passavante JZ, Hunter ME, 2021. Genetic connectivity of the west Indian manatee in the southern range and limited evidence of hybridization with Amazonian manatees. *Frontiers in Marine Science* 7, 574455. DOI: 10.3389/fmars.2020.574455
Maboko, V., Bastos, A., Maswime, T., Hoelzel, R., Wynen, L., Bester, M, 2007. Diversity and hybridisation estimates in Antarctic and Subantarctic fur seals from Marion Island based on mitochondrial and microsatellite DNA markers. *ARESSA THEME III: Biodiversity: Responses to Earth System Variability (Posters).* http://hdl.handle.net/123456789/27840
Machado, C. R. D., Azambuja, M., Domit, C., da Fonseca, G. F., Glugoski, L., Gazolla, C. B., de Almeida, R. B., Pucci, M. B., Pires, T. T., Nogaroto, V., Vicari, M. R, 2023. Integrating morphological, molecular and cytogenetic data for F2 sea turtle hybrids diagnosis revealed balanced chromosomal sets. *Journal of Evolutionary Biology* 36(11), 1595-1608. DOI: 10.1111/jeb.14236
Machkour-M'Rabet, S., Hénaut, Y., Charruau, P., Gevrey, M., Winterton, P., Legal, L, 2009. Between introgression events and fragmentation, islands are the last refuge for the American crocodile in Caribbean Mexico. *Marine Biology* 156(6), 1321-1333. DOI: 10.1007/s00227-009-1174-5
Mallet, J., Beltrán, M., Neukirchen, W., Linares, M, 2007. Natural hybridization in heliconiine butterflies: the species boundary as a continuum. *BMC Evolutionary Biology* 7(1), 1-16. DOI: 10.1186/1471-2148-7-28
Marino, I. A., Riginella, E., Gristina, M., Rasotto, M. B., Zane, L., Mazzoldi, C, 2015. Multiple paternity and hybridization in two smooth-hound sharks. *Scientific Reports* 5(1), 1-11. DOI: 10.1038/srep12919
Martin, B. T., Douglas, M. R., Chafin, T. K., Placyk Jr, J. S., Birkhead, R. D., Phillips, C. A., Douglas, M. E, 2020. Contrasting signatures of introgression in North American box turtle (*Terrapene* spp.) contact zones. *Molecular Ecology* 29(21), 4186-4202. DOI: 10.1111/mec.15622
Mayr, E, 2013. *Animal Species and Evolution*. Harvard University Press.
Mendelson, T. C., Imhoff, V. E., Venditti, J. J, 2007. The accumulation of reproductive barriers during speciation: postmating barriers in two behaviorally isolated species of darters (Percidae: Etheostoma. *Evolution* 61(11), 2596-2606. DOI: 10.1111/j.1558-5646.2007.00220.x
Metzger III, E. F., Rochford, M. R., Lawrence, A. M., Mazzotti, F. J, 2020. Morelet's Crocodile, *Crocodylus moreletii* (Duméril and Bibron 1851) (Crocodylidae), another nonnative crocodilian species introduced to Florida, USA. *Reptiles and Amphibians* 26(3), 259-260. DOI: 10.17161/randa.v26i3.14433
Milián-García Y, Ramos-Targarona R, Pérez-Fleitas E, Sosa-Rodríguez G, Guerra-Manchena L, Alonso-Tabet M, Espinosa-López G, Russello M, 2015. Genetic evidence of hybridization between the critically endangered Cuban crocodile and the American crocodile: implications for population history and in situ/ex situ conservation. *Heredity* 114(3), 272-280. DOI: 10.1038/hdy.2014.96
Milián-García Y, Venegas-Anaya M, Frias-Soler R, Crawford AJ, Ramos-Targarona R, Rodríguez-Soberón R, Alonso-Tabet M, Thorbjarnarson J, Sanjur OI, Espinosa-López G, 2011. Evolutionary history of Cuban crocodiles *Crocodylus rhombifer* and *Crocodylus acutus* inferred from multilocus markers. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* 315(6), 358-375. DOI: 10.1002/jez.683
Mitchell SM, Muehlbauer LK, Freedberg S, 2016. Nuclear introgression without mitochondrial introgression in two turtle species exhibiting sex-specific trophic differentiation. *Ecology and Evolution* 6(10), 3280-3288. DOI: 10.1002/ece3.2087
Moleón M, Sánchez-Zapata JA, Donázar JA, Revilla E, Martín-López B, Gutierrez-Canovas C, Getz WM, Morales-Reyes Z, Campos-Arceiz A, Crowder LB, 2020. Rethinking megafauna. *Proceedings of the Royal Society B* 287(1922), 20192643. DOI: 10.1098/rspb.2019.2643
Moreno N, Heaton A, Bruening K, Milligan E, Nelson D, Glaberman S, Chiari Y, 2022. Hybridization and low genetic diversity in the endangered Alabama red-bellied turtle (*Pseudemys alabamensis*. *Ecology and Evolution* 12(6), e8964. DOI: 10.1002/ece3.8964
Moretti B, Al-Sheikhly OF, Guerrini M, Theng M, Gupta BK, Haba MK, Khan WA, Khan AA, Barbanera F, 2017. Phylogeography of the smooth-coated otter (*Lutrogale perspicillata*): distinct evolutionary lineages and hybridization with the Asian small-clawed otter (*Aonyx cinereus*. *Scientific Reports* 7(1), 1-13. DOI: 10.1038/srep41611
Morgan JA, Harry AV, Welch DJ, Street R, White J, Geraghty PT, Macbeth WG, Tobin A, Simpfendorfer CA, Ovenden JR, 2012. Detection of interspecies hybridisation in Chondrichthyes: hybrids and hybrid offspring between Australian (*Carcharhinus tilstoni*) and common (*C. limbatus*) blacktip shark found in an Australian fishery. *Conservation Genetics* 13(2), 455-463. DOI: 10.1007/s10592-011-0298-6
Muhlfeld CC, Kalinowski ST, McMahon TE, Taper ML, Painter S, Leary RF, Allendorf FW, 2009. Hybridization rapidly reduces fitness of a native trout in the wild. *Biology Letters* 5(3), 328-331. DOI: 10.1098/rsbl.2009.0033
Muhlfeld CC, Kovach RP, Jones LA, Al-Chokhachy R, Boyer MC, Leary RF, Lowe WH, Luikart G, Allendorf FW, 2014. Invasive hybridization in a threatened species is accelerated by climate change. *Nature Climate Change* 4(7), 620-624. DOI: 10.1038/nclimate2252
Natoli A, Birkun A, Aguilar A, Lopez A, Hoelzel AR, 2005. Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*. *Proceedings of the Royal Society B* 272(1569), 1217-1226. DOI: 10.1098/rspb.2005.3076
Natoli A, Peddemors VM, Rus Hoelzel A, 2004. Population structure and speciation in the genus *Tursiops* based on microsatellite and mitochondrial DNA analyses. *Journal of Evolutionary Biology* 17(2), 363-375. DOI: 10.1046/j.1420-9101.2003.00672.x
Nevatte RJ, Williamson JE, Gillings MR, 2023. First evidence of multiple paternity and hybridisation in Australian sawsharks. *Marine and Freshwater Research* 74(7), 586-600. DOI: 10.1071/MF22234
Nishiwaki M, Tobayama T, 1982. Morphological study on the hybrid between *Tursiops* and *Pseudorca*. *Scientific Reports of the Whales Research Institute* 34, 109-121.
Noronha RC, Almeida BR, Chagas MC, Tavares FS, Cardoso AL, Bastos CE, Silva NK, Klautau AG, Luna FO, Attademo FL, 2022. Karyotypes of manatees: new insights into hybrid formation (*Trichechus inunguis* × *Trichechus m. manatus*) in the Amazon estuary. *Genes* 13(7), 1263. DOI: 10.3390/genes13071263
Pacheco-Sierra G, Amavet PS, 2021. Hybridization and speciation among New-world crocodilian species. In: *Conservation Genetics of New World Crocodilians:* 171-183 (R BArban Zucoloto P S Amavet, L M Verdade I P Farias Eds). Springer. DOI: 10.1007/978-3-030-56383-7_7
Pacheco-Sierra G, Vázquez-Domínguez E, Pérez-Alquicira J, Suárez-Atilano M, Domínguez-Laso J, 2018. Ancestral hybridization yields evolutionary distinct hybrids lineages and species boundaries in crocodiles, posing unique conservation conundrums. *Frontiers in Ecology and Evolution*, 138. DOI: 10.3389/fevo.2018.00138
Pacheco-Sierra G, Gompert Z, Domínguez-Laso J, Vázquez-Domínguez E, 2016. Genetic and morphological evidence of a geographically widespread hybrid zone between two crocodile species, *Crocodylus acutus* and *Crocodylus moreletii*. *Molecular Ecology* 25(14), 3484-3498. DOI: 10.1111/mec.13694
Pampoulie C, Gíslason D, Ólafsdóttir G, Chosson V, Halldórsson SD, Mariani S, Elvarsson BÞ, Rasmussen MH, Iversen MR, Daníelsdóttir AK, 2021. Evidence of unidirectional hybridization and second-generation adult hybrid between the two largest animals on Earth, the fin and blue whales. *Evolutionary Applications* 14(2), 314-321. DOI: 10.1111/eva.13091
Panthum T, Ariyaraphong N, Wongloet W, Wattanadilokchatkun P, Laopichienpong N, Rasoarahona R, Singchat W, Ahmad SF, Kraichak E, Muangmai N, Duengkae P, Fukuda Y, Banks S, Temsiripong Y, Ezaz T, Srikulnath K, 2023. Preserving pure siamese crocodile populations: a comprehensive approach using multi-genetic tools. *Biology* 12(11), 1428. DOI: 10.3390/biology12111428
Parham JF, Papenfuss TJ, Dijk PPV, Wilson BS, Marte C, Schettino LR, Brian Simison W, 2013. Genetic introgression and hybridization in Antillean freshwater turtles (*Trachemys*) revealed by coalescent analyses of mitochondrial and cloned nuclear markers. *Molecular Phylogenetics and Evolution* 67(1), 176-187. DOI: 10.1016/j.ympev.2013.01.004
Pazmiño DA, van Herderden L, Simpfendorfer CA, Junge C, Donnellan SC, Hoyos-Padilla EM, Duffy CA, Huveneers C, Gillanders BM, Butcher PA, 2019. Introgressive hybridisation between two widespread sharks in the east Pacific region. *Molecular Phylogenetics and Evolution* 136, 119-127. DOI: 10.1016/j.ympev.2019.04.013
Piett S, Hager HA, Gerrard C, 2015. Characteristics for evaluating the conservation value of species hybrids. *Biodiversity and Conservation*

24(8), 1931-1955. DOI: 10.1007/s10531-015-0919-3

Pimiento C, Leprieur F, Silvestro D, Lefcheck J, Albouy C, Rasher D, Davis M, Svenning J-C, Griffin J, 2020. Functional diversity of marine megafauna in the Anthropocene. *Science Advances* 6(16), eaay7650. DOI: 10.1126/sciadv.aay7650

Platt SG, Rainwater TR, McMurry ST, 2021. Fauna associated with the nests of *Crocodylus moreletii* and *Crocodylus moreletii* × *acutus* in Belize. *Journal of Natural History* 55(3-4), 133-149. DOI: 10.1080/00222933.2021.1895350

Pongracz JD, Paetkau D, Branigan M, Richardson E, 2017. Recent hybridization between a polar bear and grizzly bears in the Canadian Arctic. *Arctic* 151-160. DOI: 10.14430/arctic4643

Proietti MC, Reisser J, Marins LF, Marcovaldi MA, Soares LS, Monteiro DS, Wijeratne S, Pattiaratchi C, Secchi ER, 2014. Hawksbill × loggerhead sea turtle hybrids at Bahia, Brazil: where do their offspring go? *PeerJ* 2, e255. DOI: 10.7717/peerj.255

Prosdocimi L, Bruno I, Diaz L, Carman VG, Albareda DA, Remis MI, 2014. Southernmost reports of the hawksbill sea turtle, *Eretmochelys imbricata*, in temperate waters of Argentina and evidence of a hybrid origin supported by mitochondrial DNA analysis. *Herpetological Review* 45, 1-5.

Raemy M, Fritz U, Cheylan M, Ursenbacher S, 2017. Hybridisation between turtle subspecies: a case study with the European pond turtle (*Emys orbicularis*. *Conservation Genetics* 18(2), 287-296. DOI: 10.1007/s10592-016-0901-y

Ray DA, Dever JA, Platt SG, Rainwater TR, Finger AG, McMurry ST, Batzer MA, Barr B, Stafford PJ, McKnight J, 2004. Low levels of nucleotide diversity in *Crocodylus moreletii* and evidence of hybridization with *C. acutus*. *Conservation Genetics* 5(4), 449-462. DOI: 10.1023/B:COGE.0000041024.96928.fe

Reis EC, Soares L, Lôbo-Hajdu G, 2010. Evidence of olive ridley mitochondrial genome introgression into loggerhead turtle rookeries of Sergipe, Brazil. *Conservation Genetics* 11(4), 1587-1591. DOI: 10.1007/s10592-009-9973-2

Restrepo J, Gutiérrez-Lince J, Valverde RA, 2022. Evaluation of putative hybrid hatchlings between Hawksbill Sea Turtle (*Eretmochelys imbricata*) and Green Sea Turtle (*Chelonia mydas*) in Tortuguero, Costa Rica. *Journal of Herpetology* 56(4), 514-520. DOI: 10.1670/21-017

Reyes JC, 1996. A possible case of hybridism in wild dolphins. *Marine Mammal Science* 12(2), 301-307. DOI: 10.1111/j.1748-7692.1996.tb00581.x

Ripple WJ, Wolf C, Newsome TM, Betts MG, Ceballos G, Courchamp F, Hayward MW, Van Valkenburgh B, Wallach AD, Worm B, 2019. Are we eating the world's megafauna to extinction? *Conservation Letters* 12(3), e12627. DOI: 10.1111/conl.12627

Rochford MR, Krysko KL, Mazzotti FJ, Shirley MH, Parry MW, Wasilewski JA, Beauchamp JS, Gillette CR, Metzger III EF, Squires MA, 2016. Molecular analyses confirming the introduction of Nile crocodiles, *Crocodylus niloticus* Laurenti 1768 (Crocodylidae), in southern Florida, with an assessment of potential for establishment, spread, and impacts. *Herpetological Conservation and Biology* 11(1), 80-89.

Rodriguez D, Cedeño-Vázquez JR, Forstner MR, Densmore III LD, 2008. Hybridization between *Crocodylus acutus* and *Crocodylus moreletii* in the Yucatan Peninsula: II. Evidence from microsatellites. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* 309(10), 674-686. DOI: 10.1002/jez.499

Rodriguez D, Forstner MR, Moler PE, Wasilewski JA, Cherkiss MS, Densmore III LD, 2011. Effect of human-mediated migration and hybridization on the recovery of the American crocodile in Florida (USA). *Conservation Genetics* 12(2), 449-459. DOI: 10.1007/s10592-010-0153-1

Schilde M, Barth D, Fritz U, 2004. An *Ocadia sinensis* x *Cyclemys shanensis* hybrid (Testudines: Geoemydidae. *Asiatic Herpetological Research* 10, 120-125.

Schmidt F, Franke F, Shirley M, Vliet K, Villanova V, 2015. The importance of genetic research in zoo breeding programmes for threatened species: the A frican dwarf crocodiles (genus *Osteolaemus*) as a case study. *International Zoo Yearbook* 49(1), 125-136. DOI: 10.1111/izy.12082

Scott PA, Glenn TC, Rissler LJ, 2019. Formation of a recent hybrid zone offers insight into the geographic puzzle and maintenance of species boundaries in musk turtles. *Molecular Ecology* 28(4), 761-771. DOI: 10.1111/mec.14983

Seminoff JA, Karl SA, Schwartz T, Resendiz A, 2003. Hybridization of the green turtle (*Chelonia mydas*) and hawksbill turtle (*Eretmochelys imbricata*) in the Pacific Ocean: indication of an absence of gender bias in the directionality of crosses. *Bulletin of Marine Science* 73(3), 643-652.

Serrano-Gómez SS, Guevara-Chumacero LM, Barriga-Sosa ID, Ullóa-Arvízu R, González-Guzmán S, Vázquez-Peláez CG, 2016. Low levels of genetic diversity in *Crocodylus acutus* in Oaxaca and Guerrero, Mexico, and molecular-morphological evidence of the presence of *C. moreletii*. *Biochemical Systematics and Ecology* 69, 51-59. DOI: 10.1016/j.bse.2016.08.005

Sezaki K, Hirosaki Y, Watabe S, Hashimoto K, 1984. Electrophoretic characters of the hybrids between two dolphins *Tursiops truncatus* and *Grampus griseus*. *Bulletin of the Japanese Society of Scientific Fisheries (Japan)* 50(10), 1771-1776. DOI: 10.2331/suisan.50.1771

Shamblin BM, Mansfield KL, Seney EE, Long CA, Bagley DA, Nairn CJ, 2018. Brazilian origin of a neritic juvenile hybrid Loggerhead x Green turtle foraging in Florida. *Marine Turtle Newsletter* 155, 4-7.

Shirley MH, Villanova VL, Vliet KA, Austin JD, 2015. Genetic barcoding facilitates captive and wild management of three cryptic African crocodile species complexes. *Animal Conservation* 18(4), 322-330. DOI: 10.1111/acv.12176

Silva JM, Silva FJ, Sazima I, 2005. Two presumed interspecific hybrids in the genus Stenella (Delphinidae) in the Tropical West Atlantic. *Aquatic Mammals* 31(4), 468. DOI: 10.1578/AM.31.4.2005.467

Skovrind M, Castruita JAS, Haile J, Treadaway EC, Gopalakrishnan S, Westbury MV, Heide-Jørgensen MP, Szpak P, Lorenzen ED, 2019. Hybridization between two high Arctic cetaceans confirmed by genomic analysis. *Scientific Reports* 9(1), 1-10. DOI: 10.1038/s41598-019-44038-0

Soares L, Bjorndal KA, Bolten AB, dei Marcovaldi MAG, Luz PB, Machado R, Lo R, McDaniel SF, Payton AC, Waltzek TB, Wayne ML, 2018. Effects of hybridization on sea turtle fitness. *Conservation Genetics* 19(6), 1311-1322. DOI: 10.1007/s10592-018-1101-8

Soares LS, Bjorndal KA, Bolten AB, Wayne ML, Castilhos JC, Weber MI, López-Mendilaharsu M, Marcovaldi MA, Vilaça ST, Naro-Maciel E, 2021. Reproductive output, foraging destinations, and isotopic niche of olive ridley and loggerhead sea turtles, and their hybrids, in Brazil. *Endangered Species Research* 44, 237-251. DOI: 10.3354/esr01095

Soares L, Bolten AB, Wayne ML, Vilaça ST, Santos FR, dei Marcovaldi MA, Bjorndal KA, 2017. Comparison of reproductive output of hybrid sea turtles and parental species. *Marine Biology* 164(1), 1-10. DOI: 10.1007/s00227-016-3035-3

Spilliaert R, Vikingsson G, Arnason U, Palsdottir A, Sigurjonsson J, Arnason A, 1991. Species hybridization between a female blue whale (*Balaenoptera musculus*) and a male fin whale (*B. physalus*): molecular and morphological documentation. *Journal of Heredity* 82(4), 269-274. DOI: 10.1093/oxfordjournals.jhered.a111085

Struijk R, 2016. A likely new natural hybrid form of "*Cuora serrata*" (*Cuora picturata* x *Cuora mouhotii obsti*) and its finding in the wild in Phu Yen province, Vietnam. *Herpetology Notes* 9, 73-80.

Stuart BL, Parham JF, 2007. Recent hybrid origin of three rare Chinese turtles. *Conservation Genetics* 8(1), 169-175. DOI: 10.1007/s10592-006-9159-0

Suarez-Atilano M, Pacheco-Sierra G, Kass JM, Paz A, Perez-Alquicira J, 2023. Genomic and environmental insights and conservation challenges for two hybridizing iconic crocodile species across Mexico: *Crocodylus acutus* and *C. moreletii*. *Animal Conservation*. DOI: 10.1111/acv.12907

Suzuki D, Yabe T, Hikida T, 2013. Hybridization between *Mauremys japonica* and *Mauremys reevesii* inferred by nuclear and mitochondrial DNA analyses. *Journal of Herpetology* 48(4), 445-454. DOI: 10.1670/11-320

Tabora JAG, Hinlo MRP, Bailey CA, Lei R, Pomares CC, Rebong G, Van Weerd M, Engberg SE, Brennemann R, Louis Jr E, 2012. Detection of *Crocodylus mindorensis* x *Crocodylus porosus* (Crocodylidae) hybrids in a Philippine crocodile systematics analysis. *Zootaxa* 3560(1), 1-31.

Thorbjarnarson J, 1999. Crocodile tears and skins: international trade, economic constraints, and limits to the sustainable use of crocodilians. *Conservation Biology* 13(3), 465-470.

Tulloch VJ, Plagányi ÉE, Matear R, Brown CJ, Richardson AJ, 2018. Ecosystem modelling to quantify the impact of historical whaling on Southern Hemisphere baleen whales. *Fish and Fisheries* 19(1), 117-137. DOI: 10.1111/faf.12241

Ueno S, Kamezaki N, Mine K, Suzuki D, Hosoya S, Kikuchi K, Okamoto K, Torii M, Kadowaki K, Okamoto K, Sano M, 2021. Reproductive ability of hybrids between Japanese pond turtle (*Mauremys japonica*) and Reeves' pond turtle (*Mauremys reevesii*. *Zoological Science* 39(2), 186-192, 187. DOI: 10.2108/zs210047

Vamberger M, Durkin L, Kim C, Handschuh M, Seng R, Fritz U, 2017. The leaf turtle population of Phnom Kulen National Park (northwestern Cambodia) has genetic and morphological signatures of hybridization. *Journal of Zoological Systematics and Evolutionary Research* 55(2), 167-174. DOI: 10.1111/jzs.12161

Vamberger M, Stuckas H, Sacco F, D'Angelo S, Arculeo M, Cheylan M, Corti C, Lo Valvo M, Marrone F, Wink M, Fritz U, 2015. Differences in gene flow in a twofold secondary contact zone of pond turtles in southern Italy (Testudines: Emydidae: *Emys orbicularis galloitalica*, *E. o. hellenica*, *E. trinacris*. *Zoologica Scripta* 44(3), 233-249. DOI: 10.1111/zsc.12102

Van Geel N, Marr T, Hastie GD, Wilson B, 2022. First reported observation of an apparent reproductive Bottlenose x Risso's dolphin hybrid. *Aquatic Conservation: Marine and Freshwater Ecosystems*. DOI: 10.1002/aqc.3872

Vianna JA, Bonde RK, Caballero S, Giraldo JP, Lima RP, Clark A, Marmontel M, Morales-Vela B, De Souza MJ, Parr L, Rodriguez-Lopez MA, Mignucci-Giannoni AA, Powell JA, Santos FR, 2006. Phylogeography, phylogeny and hybridization in trichechid sirenians: implications for manatee conservation. *Molecular Ecology* 15(2), 433-447. DOI: 10.1111/j.1365-294X.2005.02771.x

Vilaça ST, Maroso F, Lara P, de Thoisy B, Chevallier D, Arantes LS, Santos FR, Bertorelle G, Mazzoni CJ, 2023. Evidence of backcross inviability and mitochondrial DNA paternal leakage in sea turtle hybrids. *Molecular Ecology* 32(3), 628-643. DOI: 10.1111/mec.16773

Vilaça ST, Vargas SM, Lara-Ruiz P, Molfetti É, Reis EC, Lobo-Hajdu G, Soares LS, Santos FR, 2012. Nuclear markers reveal a complex introgression pattern among marine turtle species on the Brazilian coast. *Molecular Ecology* 21(17), 4300-4312. DOI: 10.1111/j.1365-294X.2012.05685.x

Vilizzi L, Copp GH, Hill JE, Adamovich B, Aislabie L, Akin D, Al-Faisal AJ, Almeida D, Azmai MA, Bakiu R, 2021. A global-scale screening of non-native aquatic organisms to identify potentially invasive species under current and future climate conditions. *Science of the total Environment* 788, 147868. DOI: 10.1016/j.scitotenv.2021.147868

Villegas A, Rojas-Santoyo A, Ulloa-Arvizu R, 2022. Population genetics and molecular identification of *Crocodylus acutus* and *C. moreletii* (Crocodilia: Crocodylidae) in captive and wildlife populations. *Revista de Biología Tropical* 70(1), 67-81. DOI: 10.15517/rev.biol.trop..v70i1.46962

Vilstrup JT, Ho SY, Foote AD, Morin PA, Kreb D, Krützen M, Parra GJ, Robertson KM, de Stephanis R, Verborgh P, 2011. Mitogenomic phylogenetic analyses of the Delphinidae with an emphasis on the Globicephalinae. *BMC Evolutionary Biology* 11, 1-10.

Walter R, Kessel ST, Alhasan N, Fisk AT, Heath DD, Chekchak T, Klaus R, Younis M, Hill G, Jones B, Braun CD, Berumen ML, DiBattista JD, Priest MA, Hussey NE, 2014. First record of living *Manta alfredi* × *Manta birostris* hybrid. *Marine Biodiversity* 44(1), 1-2. DOI: 10.1007/s12526-013-0183-2

Walter R, Roy D, Hussey NE, Stelbrink B, Kovacs KM, Lydersen C, McMeans BC, Svavarsson J, Kessel ST, Biton Porsmoguer S, 2017. Origins of the Greenland shark (*Somniosus microcephalus*): Impacts of ice-olation and introgression. *Ecology and Evolution* 7(19), 8113-8125. DOI: 10.1002/ece3.3325

Weaver JP, Rodriguez D, Venegas-Anaya M, Cedeño-Vázquez JR, Forstner MR, Densmore III LD, 2008. Genetic characterization of captive Cuban crocodiles (*Crocodylus rhombifer*) and evidence of hybridization with the American crocodile (*Crocodylus acutus*. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* 309(10), 649-660. DOI: 10.1002/jez.471

Wei W, Li T, Yao B, Fan G, Zhang H, Pan T, Lee P, Nie H, Yan P, Xu J, 2022. The reproductive characteristics of the first-generation hybrid derived from three introduced purebred crocodile species. *Current Herpetology* 41(1), 101-113. DOI: 10.5358/hsj.41.101

Willis PM, Crespi BJ, Dill LM, Baird RW, Hanson MB, 2004. Natural hybridization between Dall's porpoises (*Phocoenoides dalli*) and harbour porpoises (*Phocoena phocoena*. *Canadian Journal of Zoology* 82(5), 828-834. DOI: 10.1139/z04-059

Witzell W, Schmid JR, 2003. Multiple recaptures of a hybrid hawksbill-loggerhead turtle in the Ten Thousand Islands, Southwest Florida. *Herpetological Review* 34(4), 323.

Wood J, Wood F, Critchley K, 1983. Hybridization of *Chelonia mydas* and *Eretmochelys imbricata*. *Copeia* 1983(3), 839-842. DOI: 10.2307/1444361

Yadzi, P, 2002. A possible hybrid between the dusky dolphin (*Lagenorhynchus obscurus*) and the southern right whale dolphin (*Lissodelphis peronii*. *Aquatic Mammals*, *28*(2), 211-217.

Zhang P, Han J, Lu Z, Chen R, 2014. Molecular evidence of a captive-born intergeneric hybridization between Bottlenose and Risso's dolphins: *Tursiops truncatus* × *Grampus griseus*. *Aquatic Mammals* 40(1), 5. DOI: 10.1578/AM.40.1.2014.5

Zornetzer HR, Duffield DA, 2003. Captive-born bottlenose dolphin× common dolphin (*Tursiops truncatus* × *Delphinus capensis*) intergeneric hybrids. *Canadian Journal of Zoology* 81(10), 1755-1762. DOI: 10.1139/z03-150

Zucoloto RB, Amavet PS, Verdade LM, Farias IP, 2021. *Conservation genetics of New World crocodilians*. Springer.

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V Islas-Villanueva included important input from the conservation genetics perspective.
DN Castelblanco-Martínez, P Charruau, MP Blanco-Parra, CA Niño-Torres made significant contributions to the discussion of the results.
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Supplementary material

Annex 1. List of freshwater and marine megafauna species involved in natural or anthropogenic hybridization. The conservation status (CS) and population trends (PT) were consulted in the IUCN Red Data Book (https://www.iucnredlist.org).

Anexo 1. *Lista de especies de megafauna de aguas dulces y marinas que presentan hibridación natural o antropogénica. El estado de conservación (CS) y las tendencias de las poblaciones (PT) se consultaron en la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza (UICN) (https://www.iucnredlist.org/es/).*

Grupo	Order	Family	Species	CS	PT
Aquatic mammals	Carnivora	Mustelidae	*Aonyx cinereus*	VU	Decreasing
Aquatic mammals	Carnivora	Mustelidae	*Lutrogale perspicillata*	VU	Decreasing
Aquatic mammals	Carnivora	Otariidae	*Arctocephalus australis*	LC	Increasing
Aquatic mammals	Carnivora	Otariidae	*Arctocephalus forsteri*	LC	Increasing
Aquatic mammals	Carnivora	Otariidae	*Arctocephalus galapagoensis*	EN	Decreasing
Aquatic mammals	Carnivora	Otariidae	*Arctocephalus gazella*	LC	Decreasing
Aquatic mammals	Carnivora	Otariidae	*Arctocephalus tropicalis*	LC	Stable
Aquatic mammals	Carnivora	Otariidae	*Otaria flavescens*	LC	Stable
Aquatic mammals	Carnivora	Otariidae	*Zalophus californianus*	LC	Increasing
Aquatic mammals	Carnivora	Phocidae	*Cystophora cristata*	VU	Unknown
Aquatic mammals	Carnivora	Phocidae	*Halichoerus grypus*	LC	Increasing
Aquatic mammals	Carnivora	Phocidae	*Pagophilus groenlandicus*	LC	Increasing
Aquatic mammals	Carnivora	Phocidae	*Phoca largha*	LC	Unknown
Aquatic mammals	Carnivora	Ursidae	*Ursus arctos*	LC	Stable
Aquatic mammals	Carnivora	Ursidae	*Ursus maritimus*	VU	Unknown
Aquatic mammals	Cetacea	Balaenopteridae	*Balaenoptera acutorostrata*	LC	Unknown
Aquatic mammals	Cetacea	Balaenopteridae	*Balaenoptera bonaerensis*	NT	Unknown
Aquatic mammals	Cetacea	Balaenopteridae	*Balaenoptera musculus*	EN	Increasing
Aquatic mammals	Cetacea	Balaenopteridae	*Balaenoptera musculus brevicauda*	EN	Increasing
Aquatic mammals	Cetacea	Balaenopteridae	*Balaenoptera musculus intermedia*	EN	Increasing
Aquatic mammals	Cetacea	Balaenopteridae	*Balaenoptera physalus*	VU	Increasing
Aquatic mammals	Cetacea	Delphinidae	*Delphinus capensis*	LC	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Delphinus delphis*	LC	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Grampus griseus*	LC	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Lagenorhynchus obscurus*	LC	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Lissodelphis peronii*	LC	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Orcaella heinsohni*	VU	Decreasing
Aquatic mammals	Cetacea	Delphinidae	*Pseudorca crassidens*	NT	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Stenella attenuata*	LC	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Stenella clymene*	LC	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Stenella coeruleoalba*	LC	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Stenella frontalis*	LC	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Stenella longirostris*	LC	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Steno bredanensis*	LC	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Sotalia guianensis*	NT	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Sousa chinensis*	VU	Decreasing
Aquatic mammals	Cetacea	Delphinidae	*Tursiops aduncus*	NT	Unknown
Aquatic mammals	Cetacea	Delphinidae	*Tursiops truncatus*	LC	Unknown

Annex 1. (Cont).

Grupo	Order	Family	Species	CS	PT
Aquatic mammals	Cetacea	Iniidae	*Inia boliviensis*	--	Unknown
Aquatic mammals	Cetacea	Iniidae	*Inia geoffrensis*	EN	Decreasing
Aquatic mammals	Cetacea	Monodontidae	*Delphinapterus leucas*	LC	Unknown
Aquatic mammals	Cetacea	Monodontidae	*Monodon monoceros*	LC	Unknown
Aquatic mammals	Cetacea	Phocoenidae	*Phoconoides dalli*	LC	Unknown
Aquatic mammals	Cetacea	Phocoenidae	*Phocoena phocoena*	LC	Unknown
Aquatic mammals	Sirenia	Trichechidae	*Trichechus inunguis*	VU	Decreasing
Aquatic mammals	Sirenia	Trichechidae	*Trichechus manatus*	VU	Decreasing
Crocodiles	Crocodylia	Crocodylidae	*Crocodylus acutus*	VU	Increasing
Crocodiles	Crocodylia	Crocodylidae	*Crocodylus mindorensis*	CR	Decreasing
Crocodiles	Crocodylia	Crocodylidae	*Crocodylus moreletii*	LC	Stable
Crocodiles	Crocodylia	Crocodylidae	*Crocodylus niloticus*	S	Least concern
Crocodiles	Crocodylia	Crocodylidae	*Crocodylus porosus*	LC	Unspecified
Crocodiles	Crocodylia	Crocodylidae	*Crocodylus rhombifer*	CR	Unspecified
Crocodiles	Crocodylia	Crocodylidae	Crocodylus siamensis	CR	Decreasing
Crocodiles	Crocodylia	Crocodylidae	*Osteolaemus* sp. nov. *cf. tetraspis*	--	Unknown
Crocodiles	Crocodylia	Crocodylidae	*Osteolaemus tetraspis*	VU	Unspecified
Turtles	Testudines	Chelonidae	*Caretta caretta*	VU	Decreasing
Turtles	Testudines	Chelonidae	*Chelonia mydas*	EN	Decreasing
Turtles	Testudines	Chelonidae	*Eretmochelys imbricata*	CR	Decreasing
Turtles	Testudines	Chelonidae	*Lepidochelys kempii*	CR	Unknown
Turtles	Testudines	Chelonidae	*Lepidochelys olivacea*	VU	Decreasing
Turtles	Testudines	Emydidae	*Chrysemys picta*	LC	Stable
Turtles	Testudines	Emydidae	*Chrysemys picta belli*	LC	Stable
Turtles	Testudines	Emydidae	*Emys trinacris*	DD	Unspecified
Turtles	Testudines	Emydidae	*Emys orbicularis*	NT	Unspecified
Turtles	Testudines	Emydidae	*Emys orbicularis galloitalica*	NT	Unspecified
Turtles	Testudines	Emydidae	*Emys orbicularis orbicularis*	NT	Unspecified
Turtles	Testudines	Emydidae	*Graptemys barbouri*	VU	Decreasing
Turtles	Testudines	Emydidae	*Graptemys ernsti*	NT	Decreasing
Turtles	Testudines	Emydidae	*Graptemys geographica*	LC	Stable
Turtles	Testudines	Emydidae	*Graptemys pseudogeographica*	LC	Unknown
Turtles	Testudines	Emydidae	*Pseudemys alabamensis*	EN	Unknown
Turtles	Testudines	Emydidae	*Pseudemys concinna*	LC	Unknown
Turtles	Testudines	Emydidae	*Terrapene carolina*	VU	Decreasing
Turtles	Testudines	Emydidae	*Terrapene carolina carolina*	VU	Decreasing
Turtles	Testudines	Emydidae	*Terrapene carolina major*	VU	Decreasing
Turtles	Testudines	Emydidae	*Terrapene mexicana triunguis*	VU	Decreasing
Turtles	Testudines	Emydidae	*Terrapene ornata*	NT	Decreasing
Turtles	Testudines	Emydidae	*Trachemys emolli*	Unspecified	Unspecified
Turtles	Testudines	Emydidae	*Trachemys decorata*	VU	Unspecified
Turtles	Testudines	Emydidae	*Trachemys decussata*	Unspecified	Unspecified
Turtles	Testudines	Emydidae	*Trachemys stejnegeri*	NT	Unspecified
Turtles	Testudines	Emydidae	*Trachemys terrapen*	VU	Unspecified
Turtles	Testudines	Emydidae	*Trachemys venusta*	Unspecified	Unspecified
Turtles	Testudines	Geoemydidae	*Cyclemys atripons*	EN	Decreasing

Annex 1. (Cont).

Grupo	Order	Family	Species	CS	PT
Turtles	Testudines	Geoemydidae	*Cyclemys oldhamii*	EN	Decreasing
Turtles	Testudines	Geoemydidae	*Cuora mouhotii obsti*	EN	Decreasing
Turtles	Testudines	Geoemydidae	*Cuora picturata*	CR	Decreasing
Turtles	Testudines	Geoemydidae	*Cuora trifasciata*	CR	Decreasing
Turtles	Testudines	Geoemydidae	*Mauremys cf. annamensis*	CR	Decreasing
Turtles	Testudines	Geoemydidae	*Mauremys japonica*	NT	Unknown
Turtles	Testudines	Geoemydidae	*Mauremys mutica*	EN	Unspecified
Turtles	Testudines	Geoemydidae	*Mauremys reevesii*	EN	Unknown
Turtles	Testudines	Geoemydidae	*Mauremys sinensis*	EN	Unspecified
Turtles	Testudines	Geoemydidae	*Sacalia quadriocellata*	CR	Decreasing
Turtles	Testudines	Kinosternidae	*Sternotherus peltifer*	LC	Unknown
Turtles	Testudines	Kinosternidae	*Sternotherus depressus*	CR	Decreasing
Elasmobranchs	Carcharhiniformes	Carcharhinidae	*Carcharhinus galapagensis*	LC	Unknown
Elasmobranchs	Carcharhiniformes	Carcharhinidae	*Carcharhinus limbatus*	NT	Unknown
Elasmobranchs	Carcharhiniformes	Carcharhinidae	*Carcharhinus obscurus*	EN	Decreasing
Elasmobranchs	Carcharhiniformes	Carcharhinidae	*Carcharhinus tilstoni*	LC	Stable
Elasmobranchs	Carcharhiniformes	Sphyrnidae	*Sphyrna gilberti*	DD	Unknown
Elasmobranchs	Carcharhiniformes	Sphyrnidae	*Sphyrna lewini*	CR	Decreasing
Elasmobranchs	Carcharhiniformes	Triakidae	*Mustelus mustelus*	VU	Decreasing
Elasmobranchs	Carcharhiniformes	Triakidae	*Mustelus punctulatus*	VU	Decreasing
Elasmobranchs	Myliobatiformes	Myliobatidae	*Manta alfredi*	VU	Decreasing
Elasmobranchs	Myliobatiformes	Myliobatidae	*Mobula birostris*	EN	Decreasing
Elasmobranchs	Myliobatiformes	Potamotrygonidae	*Potamotrygon falkneri*	DD	Unknown
Elasmobranchs	Myliobatiformes	Potamotrygonidae	*Potamotrygon motoro*	DD	Unknown
Elasmobranchs	Pristiophoriformes	Pristiophoridae	*Pristiophorus cirratus*	LC	Stable
Elasmobranchs	Pristiophoriformes	Pristiophoridae	*Pristiophorus nudipinnis*	LC	Stable
Elasmobranchs	Rajiformes	Rajidae	*Raja montagui*	LC	Stable
Elasmobranchs	Rajiformes	Rajidae	*Raja polystigma*	LC	Unknown
Elasmobranchs	Rhinopristiformes	Trygonorhinidae	*Trygonorrhina dumerilii*	LC	Stable
Elasmobranchs	Rhinopristiformes	Trygonorhinidae	*Trygonorrhina fasciata*	LC	Unknown
Elasmobranchs	Squaliformes	Somniosidae	*Somniosus microcephalus*	VU	Decreasing
Elasmobranchs	Squaliformes	Somniosidae	*Somniosus pacificus*	DD	Unknown