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Molecular ecology and evolution of the porpoises

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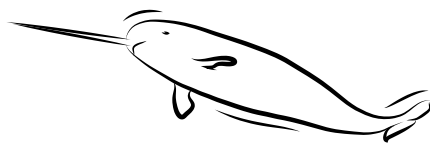
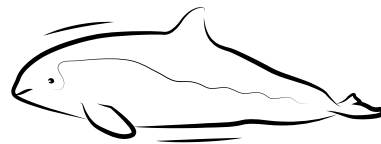
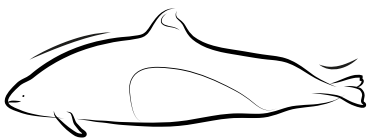
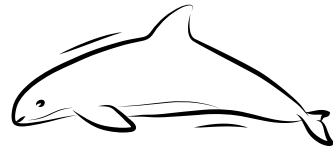
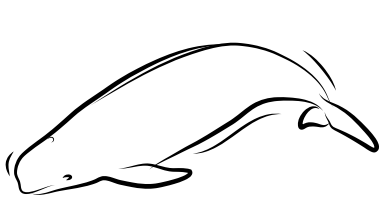
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Summary



The porpoise family (Phocoenidae) comprises seven species that are among the smallest cetacean species. While some are widely distributed, others have a much more localized distribution, with the vaquita (*Phocoena sinus*) being the most restricted of all marine mammals and on the brink of extinction. Despite major conservation issues in most of the species, we still know little about their biology, particularly those from the southern hemisphere (i.e. the Spectacled porpoise, *Phocoena dioptrica*, and the Burmeister's porpoise, *Phocoena spinipinnis*), the exception to this being the finless porpoise species (*Neophocaena*) and the harbor porpoise (*Phocoena phocoena*). Porpoises inhabit a broad range of climatic zones (polar, temperate, tropical), and display a high disparity in types of habitat occupied (pelagic, coastal, and freshwater). Many porpoise species and subspecies show specific behavioral, ecological, physiological, and morphological adaptations to their respective environments. This thesis aims to understand how porpoises adapted to their respective habitats by studying how historical environmental changes and recent human habitat perturbations affected their evolutionary trajectories. Present and historical mechanisms driving population structure, adaptation, and speciation are presented across different evolutionary time scales: (1) between species (or macro-evolution); and (2) within species (or micro-evolution). In this regard, this thesis is divided into a macro-evolutionary chapter (Chapter 2) and four micro-evolutionary chapters (Chapter 3-6). The other major purpose of this thesis is to gather knowledge intended to guide the management and conservation of certain members of the porpoise family. That is why conservation biology is a recurrent theme, discussed in all the chapters.

Chapter 1 starts by introducing key topics related to speciation, phylogeny, phylogeography, and conservation genetics necessary to understand the content of the thesis. When possible, most of the concepts are illustrated with examples in cetaceans. The last part of this chapter is dedicated to the presentation of the biological model used: the porpoise family. A large focus is given to the conservation issues faced by many porpoise taxa and on the role that genetics could play to inform management plans.

Chapter 2 explores the phylogenetic and phylogeographic history, and the evolutionary processes underlying the diversification of the porpoise family resulting in their antitropical distribution. Furthermore, despite severe conservation issues reported in members of the family and their crucial ecological role in the ecosystem, the evolutionary history of Phocoenidae remains understudied. My study fills this gap by providing the first robust estimation of the porpoise phylogeny shedding light on their biogeographical history. This chapter examines the mechanisms driving porpoise divergence across the speciation continuum by attempting to

bridge macro and micro-evolutionary processes. The results indicate that the processes governing the diversification of the Phocoenidae at the macro-evolutionary scale find their origins at the micro-evolutionary scale. More precisely, the main findings of this study are six-fold: (1) like other Delphinidae, porpoises radiated during the Late Miocene and the Pliocene as a response to past climatic changes by specializing to different environments and food resources; (2) the mechanisms driving species diversification in the northern hemisphere are mirrored in the poorly-known species of the southern hemisphere; (3) the southern species are more closely related to one another than they are to the vaquita; (4) the phylogenetic analyses revealed cryptic subdivision for the harbor, Dall's and spectacled porpoises suggesting a more complex evolution than previously thought; (5) the level of mitochondrial genetic diversity within each species is primarily driven by demographic processes rather than natural selection and (6) the level of genetic diversity seems to be a good proxy of their conservation status.

Chapter 3 aims at investigating the population structure and dispersal of the North Atlantic harbor porpoise (*Phocoena phocoena phocoena*) and testing fundamental phylogeographic predictions. Understanding the population structure is paramount to defining management units and designing the best strategies to assess the impact of commercial fisheries and environmental changes on natural populations. This information is required to advise authorities on how to mitigate threats to the species. In the Atlantic, the populations of harbor porpoises are continuously distributed with no obvious barriers to dispersal and are heavily impacted by accidental catches in commercial fisheries. The magnitude of the threat caused by these commercial fisheries remains hard to quantify because of the poor understanding of the population structure. Over the past 20 years, multiple population genetic studies have assessed the genetic structure of harbor porpoises in the North Atlantic. However, these previous genetic studies relied also on limited and disparate geographic sampling together with heterogeneous genetic markers and methodologies. These limitations contributed to blurring our understanding of what factors shaped the genetic variation in harbor porpoises and how populations are structured. Chapter 3, fills the gap by analyzing an exceptionally large genetic sample covering the entire distribution range of the harbor porpoise in the North Atlantic and in the adjacent seas. The genetic analyses were also complemented with environmental-based suitable habitat modelling of the porpoises for three time periods: at present, during the height of the last glacial maximum (LGM), and by 2050 under the most aggressive scenario of the Intergovernmental Panel on Climate Change. These models provided a useful perspective to interpret how past environmental variation shaped the population genetic variation of porpoises during the LGM, how it evolved until the present day, and what will happen in the near future

under the most extreme climate models. Overall, this chapter offers the first complete picture of the population genetic structure at the scale of the broad distribution range of the species in the North Atlantic. The main findings of this chapter are five-fold: (1) populations of the harbor porpoises from the North Atlantic and North Pacific are completely isolated from each other and genetically deeply divergent; (2) porpoise populations from Northwest to Northeast Atlantic waters north of Biscay form a large-scale continuous system under isolation-by-distance without any obvious physical barrier to gene flow; (3) the analysis of the mitochondrial genome revealed, for the first time, a new divergent lineage in West Greenland; (4) the comparison of maternally inherited (mtDNA) and biparentally inherited (microsatellites) markers confirmed previous findings that gene flow is mainly male-mediated and females are philopatric; and (5) the spatial variation in genetic diversity shows no evidence of post-glacial re-colonization of northern habitats typically associated with a pattern of leading-edge effect as reported in many cetacean species (e.g., bottlenose dolphins or killer whales). Instead, the results suggest that population genetic variation in the harbor porpoises has reached an equilibrium state between migration and genetic drift. The genetic variation in the North Atlantic thus reflects the combination of recent intergenerational dispersal and local effective population size.

Chapter 4 leverages genetic time series to investigate the demographic trends of the small and potentially highly endangered Iberian harbor porpoise. The Iberian population of harbor porpoise inhabits the cold upwelling waters along the Atlantic coasts of Spain and Portugal. This isolated population is one of the two populations of a distinct ecotype and possibly a distinct sub-species (*Phocoena phocoena meridionalis*) adapted to the upwelling ecosystem, the other population being located off the Mauritanian coasts. Like the Mauritanian porpoises, the Iberian individuals are known to be morphologically, ecologically, and genetically distinct from other harbor porpoises. Furthermore, previous genetic studies suggested a relatively strong isolation from the other neighboring populations. Despite their unique characteristics, the Iberian harbor porpoises are subject to intense fishing pressures resulting in unsustainable bycatch mortality rates, one of the most important reported in cetaceans. In addition, this population occurs at the margin between two biogeographical zones where the ecological conditions are rapidly changing and therefore it might be particularly sensitive to the strong effect of the ongoing climate change on the Iberian Upwelling System. Employing different genetic approaches, this chapter compares the population genetic structure and diversity between two temporal cohorts (1990-2002 vs. 2012-2015) and revealed two major findings. First, phylogenetic analyses revealed the existence of an unreported divergent

mitochondrial haplotype in the south of Iberia. This could suggest that other distinct populations of this ecotype, overlooked so far, may occur and it calls for further study between Iberia and Mauritania. Second, the comparison of the genetic diversity between the two cohorts showed that a drastic decline in mitochondrial genetic diversity occurred over less than 30 years, possibly reflecting a rapid decrease in effective population size. These results add supplementary concerns to the growing line of evidence suggesting that this population might be rapidly declining. These results underline the crucial need to undertake immediate actions to obtain an IUCN assessment for this population and to officially recognize these porpoises from Iberia and Mauritania as a distinct subspecies. This chapter brings important information and incentive to gain additional knowledge and to apply effective conservation efforts to mitigate incidental catches in commercial fisheries to protect the Iberian population, and to ensure the viability of this small, unique, and possibly endangered population.

Chapter 5 examines the population genetic structure in the isolated population of harbor porpoises from the Black Sea and adjacent waters (*Phocoena phocoena relicta*). While morphological heterogeneity suggested that population differentiation may exist between individuals from the Black and Azov seas, previous analyses of the genetic structure pointed towards a nearly complete genetic homogeneity. However, a report of population genetic homogeneity does not necessarily mean that the focal population is demographically homogeneous. Under some conditions, genetic data may be unable to capture demographic differentiation, an issue often referred to as the "grey zone" of population differentiation. Such a phenomenon can be observed if, for example, genetic drift is inefficient and leads to slow changes in allelic frequencies. This may lead to an absence of significant genetic differentiation between demographically independent populations. This effect has been reported in species exhibiting high fecundity, large population size, and large dispersal abilities such as marine fishes and invertebrates. It may also occur in species exhibiting low fecundity and small population size such as cetaceans with high dispersal abilities, for example, if the population subdivision has been very recent, creating a time-lag between demographic and genetic signals. Using genetic simulations, we assessed the probability that the observed genetic homogeneity in the harbour porpoise from the Black and Azov Seas resulted from a lack of power in our analyses or from a population grey zone effect. In other words, we evaluated if a population grey zone effect exists during which genetic homogeneity may not reflect demographic heterogeneity. Simulations under various demographic models rule out the hypotheses of a lack of power or a grey zone effect. They suggested instead that panmixia is the most likely hypothesis explaining the genetic homogeneity observed in the Black Sea porpoises. The

simulations indicate that considering a realistic effective population size of 1,000 individuals for the Black Sea harbour porpoise, the expected "grey zone" would last at most 20 generations under moderate levels of gene flow (≤ 10 migrants per generation). Morphological heterogeneity reported between the Black Sea and the Azov sea harbour porpoises may thus reflect biological processes other than population subdivision (e.g., plasticity, selection).

Chapter 6 explores the dynamic processes underlying range contraction and fragmentation, patterns of connectivity, and demographic trends in a critically endangered freshwater cetacean species, the Yangtze finless porpoise (*Neophocaena asiaorientalis asiaorientalis*). This species is the only surviving freshwater cetacean in China and the world's only freshwater porpoise. The Yangtze porpoise is now critically endangered due to rapid decline as a consequence of industrial activities, resources depletion, and construction projects that fragmented the river habitat. The application of different population genetic approaches shows that three genetically well differentiated populations occur in the Yangtze River and adjacent lakes with an admixture zone between them; their contemporaneous effective population sizes are among the lowest values ever reported in a cetacean species; that gene-flow seems to occur, but is highly asymmetric and inefficient for connecting populations. Furthermore, using the coalescent-based approximated Bayesian computation statistical framework, the results showed that all the populations in the Yangtze descended from a small number of founders, likely coming from the sea, which colonized the river during the last Ice Age. The simulations showed that the split occurred within the last millennium, but the population decline and loss of connectivity happened during the boom of Chinese industrial activity. Indeed, the genetic diversity of each population shows a clear genetic footprint of massive population contraction during the last 50 years, with effective population sizes of 2% of the pre-collapsed sizes. From a practical perspective, conservation actions have now been implemented that were guided in part by the results presented in this chapter.

Chapter 7 offers an integrative view of the results of this thesis. The first part combines all results to draw parallels between chapters and describes how population split, divergence, and speciation have been occurring in the porpoise family. The second part examines how the knowledge acquired in this thesis can be applied to improve conservation and management plans and more generally guide the conservation of many threatened porpoise taxa. The last part discusses the limits of this thesis, in particular the use of traditional molecular markers (e.g. mitochondrial and microsatellites genetic markers). The final section considers the prospects and perspectives offered by the forthcoming large scale genomics data set and other biological disciplines to improve our understanding of the evolution of porpoises.

