Environmental factors to population structure in mobile marine organisms: a

combined genetic-oceanographic approach in coastal cetaceans

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Abstract

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Multidisciplinary analyses of genetic and environmental data for cetacean population structure studies allow investigating hypotheses of environmental drivers to dispersal, and provide valuable information for the conservation of these species. This dissertation combines microsatellite and mitochondrial DNA (mtDNA) data of coastal cetaceans with remote sensing oceanographic information to assess the degree of overlap between genetic and environmental breaks, and provide recommendations for the designation of cetacean management units associated to important geographical areas for distinct populations. Genetic and demographic data are used to evaluate potential demographic and genetic impacts of by-catch to cetacean species, and species distribution data to evaluate the appropriateness of existing Marine Protected Areas in South America for the conservation of local cetaceans.

Issues of environmental agents to population structure are comparatively explored in two coastal cetacean species that inhabit different ocean basins. Chapter 1 evaluates the regional population structure of Franciscana dolphins (*Pontoporia blainvillei*) through a population genetic analysis using mtDNA data, covering the entire species distribution in the Western South Atlantic. The results show significant population structure between

dolphins occurring in Brazilian, Uruguayan and Argentinean waters, and suggest further genetic structure within the groups of animals collected in Argentina. Chapter 2 narrows the spatial scale of analysis focusing on the Argentinean coastline, includes previously unsampled localities, doubles the sample size, and incorporates 12 microsatellite markers into the previous genetic dataset. Using a combination of frequency, likelihood and Bayesian analytical methods, this chapter supports the previously hinted genetic patterns of finer-scale population structure within Argentina. Moreover, this chapter couples the genetic data with remote sensing oceanographic information and shows a concordant spatial arrangement of the genetic and environmental breaks. In addition, this evidence suggests that a mechanism termed here "isolation by environmental distance" may explain some of the observed patterns. Analogous issues of environmental and population structure are evaluated for humpback dolphins in the Western Indian Ocean in Chapter 3. Contrasting mtDNA sequence data with a suite of remotely driven oceanographic variables, the results of this analysis show concordant regional oceanographic breaks to the strong and highly significant genetic structure, and suggest that surface currents and ocean color properties may play a significant role in dispersal of humpback dolphins in this region.

Addressing relevant aspects of cetacean conservation, an evaluation of genetic and demographic impacts of by-catch to Franciscana dolphins is provided in Chapter 4. Through an analysis of relatedness between dolphins entangled in fishing gear it is demonstrated that, in addition to removing large numbers of individuals from their populations, by-catch also impacts mother-calf associations and reproductive pairs, exacerbating the process of population decline. Finally, in order to evaluate the suitability

of the existing Marine Protected Areas to conserve cetacean populations in South America, a spatial analysis of the extent of cetacean distribution coverage by the existing MPAs is performed in Chapter 5. These data show that, on average, MPAs in South America cover less than 2% of the cetacean distribution, and that 19 species in this region have less than 1% of their distribution covered by protected areas.

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Those long hours on the computer, the indoor weekends, months away, and my awfully frequent crankiness! I dedicate all the time, effort and passion to my favorite person, my love, and my bodyguard - *Laura*.

Introduction

The issue of population structure is one of the most relevant topics in ecological and evolutionary research, a key concept for conservation practitioners, and likely one of the most complex aspects of cetacean studies.

Populations are considered the units at which the most significant ecological processes take place. For instance, demographic expansion and reduction (Beaumont 1999; Kaliszewska *et al.* 2005; Storz & Beaumont 2002), emigration and immigration (Beerli 1998), and behavioral strategies associated with feeding and mating (Alexander 1974; D'Vincent *et al.* 1985; Darling 1983; Hamilton 1964) develop and can be observed most significantly at the population level. Although evolutionary change occurs at many levels ranging from the cellular to the species at least, populations are considered the most significant (or perhaps the simplest models to observe and test) evolutionary units (Futuyma 2009; Hartl & Clark 1997). Therefore, knowledge about the spatio-temporal configuration of demographically distinct groups of individuals of the same species (i.e. population structure) is essential to properly circumscribe ecological and evolutionary studies. In turn, the ecological and evolutionary importance of populations motivated targeting these units for conservation research and action even if the ultimate goal is to preserve species, habitats and ecosystems (Meffe & Carroll 1997; Soule 1987; Soule & Kohm 1989).

The scientific challenge is to translate the theoretical population definitions into empirical assessments of such units within real species (Waples 1998; Waples & Gaggiotti 2006). In particular, cetaceans are cryptic species and therefore questions regarding their ranging patterns, behavior and population structure are difficult to address

by direct observation. Extremely rare and valuable longitudinal studies have provided direct evidence of individual associations and ranging patterns, and may even hint to issues of population structure (i.e.Mate *et al.* 1995; Wells *et al.* 1999; Wells *et al.* 1987). However, accurate genealogical and lineage data are needed to delimit populations, and therefore most of our knowledge about cetacean population structure has come as a result of molecular evidence (i.e. Baker *et al.* 1993; Hoelzel & Dover 1991; Rosel *et al.* 1999; Rosenbaum *et al.* 2009; Secchi *et al.* 1998). Such knowledge is not unequivocal; because cetaceans are characterized by strong social bonds and varying dispersal even within the same species, the resulting genetic patterns cannot always be interpreted in a straightforward manner (Connor *et al.* 2001; Hoelzel 1998). In addition, despite evidence of environmental heterogeneity in the marine environment (Longhurst 2006), the scarcity of relevant empirical data has been reflected in a systematic lack of attention to environmental agents in relation to cetacean population structure. As a result, most cetacean population structure studies have been framed solely in relation to behavioral drivers to dispersal, such as phylopatry and gender-biased dispersal (Escorza Trevino & Dizon 2000; Möller & Beheregaray 2004; O'Corry-Crowe 2008), or in relation to spatial considerations to genetic structure patterns, such as genetic isolation by distance patterns (Hoelzel 1994; Wright 1943) or gaps in the species distribution (Bräger *et al.* 2002; Cassens *et al.* 2005; Rosa *et al.* 2005).

My main goal in this dissertation is to integrate the well-established genetic approaches to population structure with spatially explicit high-coverage and high-resolution environmental data, to evaluate plausible environmental drivers of cetacean population structure. My second goal is to address three issues related to cetacean

conservation: the identification of demographically relevant management units and geographical areas that serve to protect this units; an evaluation of demographic and genetic impacts of the greatest threat to cetacean populations, by-catch; and a preliminary evaluation of the appropriateness of existing Marine Protected Areas (MPAs) for cetacean conservation in South America.

An exploration of plausible environmental drivers for cetacean population structure is carried out comparatively between two coastal cetacean species, Franciscana dolphins (*Pontoporia blainvillei*) in the Western South Atlantic, and humpback dolphins (*Sousa chinensis*) in the Western Indian Ocean. Because coastal areas are typically characterized by notable environmental heterogeneity, coastal cetaceans are likely to experience such heterogeneity and are therefore appropriate study species to evaluate the influence of environmental variation on population structure. Both species exhibit comparable dispersal capabilities, ranging from localized to larger range movements (Bordino & Wells 2005; Hung & Jefferson 2004), occupy the same ecological niche (Barros *et al.* 2004; Bordino *et al.* 2004), and occur in comparable marine environments, which makes them likely to be constrained by similar types of ecological processes. Yet, environmental variation between both ocean basins allows assessing the influence of localized conditions to dispersal. Chapter 1, published in *Conservation Genetics* (9: 419-435), uses mtDNA sequence data to evaluate the regional genetic structure of Franciscana dolphins along their entire distribution range, and the appropriateness of the current Franciscana Management Areas. Chapter 2, published in *Molecular* Ecology (doi: 10.1111/j.1365-294X.2010.04647.x)*,* follows the line of work in the previous chapter and incorporates mtDNA and microsatellite data for a larger and more comprehensive

sampling scheme within Argentina. Most significantly, this chapter uses remote sensing data to explicitly test the influence of three oceanographic variables in the population structure patterns of Franciscana dolphins. Additionally, combining genetic and environmental data, suggestions are made related to specific geographical areas that should be a priority for conservation in order to protect Franciscana populations. Chapter 3 evaluates regional environmental agents to dispersal for humpback dolphins in the Western Indian Ocean. Here, mitochondrial DNA sequence and spatially explicit oceanographic data are jointly analyzed to test for overlapping genetic and environmental discontinuities for the study species.

I evaluate genetic and demographic impacts of by-catch through a relatedness analysis between dolphins simultaneously entangled in fishing gear. Despite the known impacts of by-catch on population abundance, there is little knowledge about the potential impacts of by-catch to specific demographic associations in cetaceans. In Chapter 4, a combination of field, demographic and genetic data is used to evaluate the potential impact of by-catch to important demographic associations of Franciscana dolphins. In particular, this chapter investigates the simultaneous impact of fisheries to Franciscana dolphin reproductive pairs and mother-calf pairs.

Finally, I attempt a preliminary evaluation of the suitability of the existing Marine Protected Areas (MPAs) to conserve cetacean populations in South America. Although MPAs worldwide have largely proven successful in protecting marine taxa and habitats (Guenette *et al.* 1998; Halpern 2003), the appropriateness of existing MPAs to adequately protect cetaceans may be limited (Reeves 2000). Chapter 5, published in the *Latin*

American Journal of Aquatic Mammals [6:2 (203-207)], offers a spatial analysis of the

extent of cetacean distribution covered by the existing MPAs in South America.

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Final remarks

This dissertation combines molecular and environmental data with a range of analytical techniques to address fundamental questions regarding the population structure of coastal cetaceans, and to contribute to conservation efforts in these species.

Using mitochondrial (mtDNA) and nuclear (nuDNA) genetic data, I found evidence of significant population structure at varying spatial scales for both study species. Whereas local scale structure of the mtDNA (i.e. Franciscana dolphins within Argentina) seemed associated with geographical distance, mtDNA regional structure (i.e. Franciscana dolphins across their entire distribution range and humpback dolphins in the Western Indian Ocean) and nuDNA local structure (i.e. Franciscana dolphins within Argentina) do not show significant IBD. Since cetaceans, and especially female cetaceans, are generally phylopatric, it would be expected that IBD be apparent for the mtDNA data. However, it is possible that regional scale assessments are above the species' capability for dispersal and that IBD patterns at such spatial scale become irrelevant. While it is not immediately obvious why male-biased dispersal (assessed indirectly though the nuDNA patterns) seems not constrained by geographical distance at local scales, it is possible that environmental factors become more relevant for animals that do disperse (i.e. males), therefore obscuring the purely spatial patterns. The IBED patterns in the nuDNA data and the fact that males exhibited weaker genetic structure support this possibility.

By combining spatially explicit environmental information with genetic data, it was found that environmental discontinuities and genetic breaks exhibit a considerable

degree of overlap for both studied species. Even though environmental heterogeneity is common in the marine environment, strong and conspicuous breaks are not frequent enough to justify this overlap as a random occurrence. Moreover, the fact that such an overlap is present for both species and for related environmental variables suggests that there is some biological significance behind these patterns. At least two different scenarios could explain such correlations between the environmental and genetic data. First, environmental variation could be directly related, in a functional way, to the observed genetic structure patterns. For instance, areas of relatively high primary productivity, which are conspicuous in ocean color images and are known to hold relatively high fish biomass, could function as feeding areas for top predators like odontocetes. Since feeding areas can drive population structure patterns, this hypothesis would help explain the relationship between the environmental and genetic data. In addition, surface current patterns are known to influence nutrient distribution and have the potential to impact the distribution of mobile marine animals. Thus, marine currents and ocean color features (i.e. productivity) could work synergistically influencing marine population structure from a direct functional perspective. Secondly, the observed environmental variation could be a proxy for environmental or ecological features not directly quantified by this variable. For instance, typical breeding areas for cetaceans are relatively shallow and geographically sheltered areas such as bays, gulfs and estuaries. As these areas have particular circulation patterns, they are conspicuous in ocean color images, and are most likely to be singled out by statistical approaches assessing environmental variation. In this second scenario, particular habitats that influence the population structure patterns of cetaceans would be distinguishable via remote sensing,

explaining the overlap between the environmental and genetic data. In these two

plausible scenarios, coupling of biological proxies (i.e. population structure patterns) and

environmental indicators has the potential to uncover important ecological relationships

between populations and their environment, and to identify specific geographical areas

associated to such relationships. Bringing the presented data to this context, Bahia

Samborombon, in northern Buenos Aires, is characterized by relatively high productivity,

shallow waters, and in some cases presents sandbank systems that offer shelter from the

rougher waters at the mouth of the La Plata Estuary. This area is environmentally

different from any of its adjacent areas and houses a distinct Franciscana population.

Both previous scenarios of breeding or feeding areas for Franciscanas would be plausible

in Samborombón. Interestingly, humpback dolphins at both sides of the splitting of the

South Equatorial Current show significant genetic structure. In addition, all areas

showing no environmental data overlap in the Western Indian Ocean are inhabited by

genetically distinct humpback dolphins, and the only case of environmental overlap

showed concordant lack of population structure. Taken altogether, these results highlight

the potential importance of environmental heterogeneity in the spatial genetic structure of

coastal cetaceans. Although it would be difficult to generalize about the role of

environmental breaks to marine dispersal patterns having assessed only two different

species that are ecologically related, these results have the potential to be indicative of

analogous patterns in other mobile marine species with similar ecological niches.

 Whereas it is intuitively straightforward to assume that environmental variation, if

biologically relevant, should have a proportional effect on population partition, this is a

hypothesis that remained largely untested. An interesting result of this dissertation is the

observation of IBD-like patterns when assessing the spatial variation of environmental and genetic data (Chapter 2). These findings motivated a formal proposition of a pattern of isolation by environmental distance (IBED) for cetaceans. As IBED patterns were present only for the nuDNA data on local scale analyses (i.e. Franciscana dolphins in Argentina), it is possible that such patterns require a combination of small effects of phylopatry and a spatial scale that is within the dispersal capabilities of the species under study, so that dispersing individuals (i.e. male Franciscana dolphins) have the potential to actually experience environmental variation. A similar analysis utilizing bi-parentally inherited molecular markers for humpback dolphins in the Western Indian Ocean would allow one to either generalize about this issue, if analogous patterns are found, or assume that some of these issues could be driven, for instance, by behavioral aspects that might be idiosyncratic to each species. Given the suggestions of small dispersal capabilities for humpback dolphins, such an analysis would be most informative with a more comprehensive sampling, particularly in areas that are currently not studied.

The use of molecular data also served to address important conservation-related aspects of the species under study. First, genetic evidence was used to assess potential demographic and genetic impacts of cetacean by-catch, which could be cryptic to conventional observational studies. Although it is well known that by-catch is one of the greatest threats to small cetaceans as it removes large numbers of individuals from their populations, the potential impacts to specific demographic segments in those populations has received relatively little attention. Chapter 4 shows that both members of Franciscana mother-calf pairs and potentially reproductive pairs are caught together in fishing gear.

Because many cetaceans are highly social, it is not unlikely that these kind of impacts apply more broadly to the taxonomic group than to particular species.

Secondly, genetic evidence provided a transparent and replicable framework for propositions of species management units based on quantitative genetic data. Chapters 1 and 2 support previous suggestions that at least four Franciscana Management Areas (FMAs) need to be designated along the entire species distribution to protect discrete Franciscana dolphin populations: two areas in Brazilian waters (FMAs I and II), one to protect the Franciscana distribution area in Uruguay (FMA III), and the last one in Argentina (FMA IV). However, the combined mtDNA and nuDNA data presented here suggest that Franciscana dolphins are locally structured in Argentina, and that the FMA framework should reflect this updated spatial arrangement of Franciscana populations at their southern range. In the Western Indian Ocean, the very strong and significant population structure observed for humpback dolphins in Oman, Tanzania and the Mozambique-South Africa grouping should leave little doubt that these groupings should be independently considered for management.

Third, coupled genetic and environmental information allow applying the concept of biological management units to specific geographical areas that make ecological sense. Because biological populations cannot be understood if they are removed from their habitats and the ecological connections with them, a framework that takes into account relevant environmental and ecological data will be closer to a more relevant population concept. Protecting areas that have the environmental characteristics and ecological resources to sustain wild populations may be the most, of not only, feasible strategy to conserving such populations. In South America, the very small potential of current MPAs

to protect cetaceans, highlights the importance of a framework that combines species distribution, population structure and environmental breaks to re-examine the presence of critical habitat for cetaceans in the area, and prioritize these habitats for protection.

In conclusion, the combination of high-resolution genetic data, high-coverage environmental information, and a suite of analytical approaches has provided relevant evidence to increase our understanding of timely ecological questions and conservation issues in coastal cetaceans, and could hint at useful frameworks for other mobile marine species.