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Low genetic diversity, limited gene flow and widespread genetic bottleneck effects in a threatened dolphin species, the Australian humpback dolphin

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ABSTRACT

Numerous species of marine megafauna are at risk of extinction and understanding their genetic population structure and demographic history is essential for their conservation. We used mitochondrial DNA and 18 nuclear microsatellite loci, on the largest genetic dataset compiled to date on Australian humpback dolphins (eight sampling sites, 159 samples), to assess their genetic diversity, gene flow and past demographic history along the east coast of Queensland, Australia. Levels of genetic diversity were low (mtDNA: h = 0–0.52, π = 0–0.007; nDNA: Ho = 0.27–0.41; AR = 1.7–2.4). Both mitochondrial (Φ_{ST} = 0.49, P = 0.001) and nuclear markers (F_{ST} = 0.14, P = 0.001) showed strong genetic structure among sampling sites. Four putative populations were identified, with little contemporary gene flow (m = 0.017 to 0.047) among populations. Genetic divergence follows an isolation-by-distance model (r = 0.38, P = 0.0001), with an apparent restriction in gene flow occurring at scales of 382–509 km. Estimates of contemporary effective population size were low (N_e = 11.5–31.2), with signatures of genetic bottlenecks for all putative populations about 50–150 generations ago. The current low levels of genetic diversity, gene flow, and effective population size in Australian humpback dolphins indicate the effects of historical population bottlenecks and/or founder events during the late Holocene period (~1250–3750 years ago); probably associated with sea level fall and increased intensity of El Niño Southern Oscillation-climatic events. Our results raise important conservation concerns and emphasize the vulnerability of Australian humpback dolphins to stochastic demographic, genetic and environmental processes. Conservation strategies should focus on promoting connectivity among local populations and reducing direct causes of human-related mortality.

1. Introduction

The viability of populations is affected by demographic, environmental, and genetic factors (Lande, 1993). Genetic diversity has been identified as having important bearings on both individual and population fitness, as well as population resilience and persistence, and the adaptation to environmental changes (Hughes et al., 2008). There is usually a negative correlation of genetic diversity and population size (Frankham, 1996). Small populations may have generally reduced genetic diversity due to founder events, genetic bottlenecks driven by natural and/or anthropogenic disturbances, genetic drift or a combination thereof (Banks et al., 2013). Regardless of the underlying mechanisms, low genetic diversity is particularly concerning for species characterized by small populations with low migration and gene flow among them, features that exacerbate genetic drift and inbreeding depression (Munson et al., 1996; Roelke et al., 1993). Such loss of evolutionary potential may increase the risk of extinction of local populations and degrade the persistence of the metapopulation (group of spatially structured local populations that may exchange individuals through migration, Frankham, 2005; Hanski, 1998). Hence, maintaining adequate levels of genetic diversity, within and among wildlife populations, is one of the main principles underlying the conservation

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and management of threatened species (Willoughby et al., 2015).

Several species of marine megafauna are at risk of extinction due to increasing human pressures (see review in Estes et al., 2016). Species and populations inhabiting coastal waters, such as inshore dolphins and sharks, are among the most threatened due to high and cumulative human impacts, such as habitat loss via degradation and fragmentation, pollution, incidental capture in fisheries, acoustic disturbance, and vessel traffic (Davidson et al., 2012; Dulvy et al., 2014). The distinctive pattern of coastal settlements in Australia, where 85% of inhabitants live within 50 km of the coast, has resulted in unprecedented pressures on coastal ecosystems in terms of coastal urbanization, ports and shipping infrastructure, particularly along the urban coast of Queensland (Grech et al., 2013). The cumulative impact of these human activities on marine coastal ecosystems, has raised serious concerns about the long-term survival of Australia's tropical inshore dolphins (DOE, 2015).

Australian humpback dolphins (*Sousa sahulensis*) were recently described as a new species, and are endemic to coastal waters of northern Australia and southern New Guinea (Jefferson and Rosenbaum, 2014; Mendez et al., 2013). Humpback dolphins occur in small numbers ranging from 15 to about 200 individuals per study area (see reviews in Brown et al., 2016; Parra and Cagnazzi, 2016) and inhabit mainly shallow inshore and estuarine waters (Parra and Cagnazzi, 2016; Parra et al., 2004). They feed on a wide variety of fish associated with inshore habitats (Parra and Jedensjö, 2014), display strong site fidelity to coastal areas (i.e. tend to remain in the same area or return to it multiple times), and range over relatively small areas (197–349 km^2) (Cagnazzi et al., 2011; Parra, 2006). Combined with the slow life history patterns of delphinids, these features make this species particularly vulnerable to habitat degradation and fragmentation. Currently, Australian humpback dolphins are considered Vulnerable under the International Union for Conservation of Nature (IUCN) Red List of threatened species (Parra et al., 2017; Parra and Cagnazzi, 2016).

Preliminary information suggests that humpback dolphins in Australian waters exist as a metapopulation of small and genetically isolated population fragments (Brown et al., 2014). Given their current small population sizes and apparent fragmented distribution, the loss of genetic diversity and restriction of gene flow poses serious concerns about the conservation and long-term survival of this species in Australian waters (Parra and Cagnazzi, 2016). Quantification of genetic variability and gene flow, or lack thereof, among populations of humpback dolphins is needed to define: 1) appropriate geographical scales for management of populations, and 2) populations or genetic groupings that should be managed separately to best maintain evolutionary processes and adaptive diversity across the geographic range of the species (Moritz, 1994; Palsboll et al., 2007). Such information can contribute significantly towards defining targets for protection (Wood and Gross, 2008) and for understanding the status of Australian humpback dolphin populations.

In this study, we used the largest genetic dataset compiled to date on Australian humpback dolphins to assess the patterns of genetic diversity, population structure, gene flow, effective population size, and past demographic history of this species along the east coast of Queensland, Australia. Our results provide insights into the connectivity and demographic history of Australian humpback dolphins, with important ramifications for their conservation and management.

2. Methods

The methods employed in data collection and analysis are described in detail in the electronic supplementary material (see Appendix A). In summary, skin samples of humpback dolphins were collected between 2006 and 2011 from free-ranging (n = 155) and stranded (n = 4) animals across eight different localities along the urban coast of Queensland (Fig. 1). Biopsy samples were genotyped at 20 microsatellite loci, and a fragment of 428 base pairs (bp) of the mtDNA control region was sequenced. A total of 17 samples were replicates, eight failed to amplify for more than five loci; and four failed to sequence properly, leaving a total of 134 and 138 individual samples for microsatellite and mitochondrial DNA based analysis, respectively. We genotyped 10% of the samples twice independently at all loci to estimate scoring error rate. The average genotyping error rate per multilocus genotype was estimated at 0.3%. Evidence for null alleles using the software MICROCHECKER Ver. 2.2.3 (Van Oosterhaut et al., 2004) was detected at locus EV37 and MK5 and these were removed from further analysis. None of the remaining 18 loci showed significant deviation from HWE (over the complete data set, nor within any of the populations sampled), nor did we find significant linkage disequilibrium for any pair of loci after sequential Bonferroni correction in GENEPOP V4.2 (Rousset, 2008).

Genetic diversity and differentiation within and among sampling localities, and putative populations identified (see below), was assessed by examining variation in microsatellites using GenAlEx 6.5 (Peakall and Smouse, 2012), GENETIX 4.05 (Belkhir et al., 2004), FSTAT 2.9.3 (Goudet et al., 2002) and ARLEQUIN 3.5.1.3 (Excoffier et al., 2005). Variation in mtDNA data was examined using ARLEQUIN 3.5.1.3 (Excoffier et al., 2005). We used the spatial Bayesian clustering approach implemented in program TESS 2.3 (Chen et al., 2007; Durand et al., 2009) to evaluate the most likely number of putative populations (K) based on microsatellite loci. Isolation by distance (IBD) (Slatkin, 1993) was investigated using simple Mantel test implemented in the software package ALLELES IN SPACE (AIS) (Miller, 2005). We tested for sex bias in dispersal across sampling locations and putative populations in FSTAT 2.9.3 using microsatellites data and comparing four different statistics (Goudet et al., 2002).

The Bayesian multilocus genotyping approach implemented in the program BAYESASS 3.0 (Wilson and Rannala, 2003) was used to estimate the magnitude and direction of contemporary gene flow between the sampled locations and clusters identified in TESS. We used the bias-corrected version of the linkage disequilibrium method (Peel et al., 2013; Waples, 2006; Waples and Do, 2010), implemented in the program NeEstimator V2 (Do et al., 2014), to estimate contemporary genetic effective population size (N_e) among the putative populations identified in our analysis. We used the approximate likelihood MCMC approach implemented in VarEff 1.2 R package (https://qgsp.jouy.inra.fr/) for estimating past changes in effective population size from microsatellite data (Nikolic and Chevalet, 2014).

3. Results

3.1. Genetic diversity within sampled locations

Levels of microsatellite genetic diversity were similar and low for all sampling groups, and yet no evidence of inbreeding (F_{IS}) was detected in any of the sampled locations, (Table 1). In mtDNA control region, we found eight unique haplotypes characterized by 17 variable sites (Table 1, Fig. 1). The number of haplotypes detected in each sampled site varied from one to five (Table 1). Overall haplotype (h = 0.52) and nucleotide (π = 0.007) diversities across all sampled locations were low (Table 1) relative to other cetacean species (see review in Alexander et al., 2013). Mitochondrial haplotypic and nucleotide diversity were highest in the north for WS (h = 0.86, π = 0.012) and lowest for NGSS, SGSS and MB in the south (h = 0.00, π = 0.000). The most common haplotypes were H4 (67% of all individuals sampled), found in all sampled locations except in the two most northern locations HB and TV, and H1 (22%), found in individuals from HB, TV, WS in the north and KB in central region (Fig. 1).

3.2. Genetic differentiation among sampling locations

The AMOVA analysis showed significant population differentiation among all sampling locations for both, microsatellites (F_{ST} = 0.14,