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Animal behaviour

Natal origin of Namibian grey whale implies new distance record for in-water migration

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We use genomics to identify the natal origin of a grey whale found in the South Atlantic, at least 20 000 km from the species core range (halfway around the world). The data indicate an origin in the North Pacific, possibly from the endangered western North Pacific population, thought to include only approximately 200 individuals. This contributes to our understanding of Atlantic sightings of this species known primarily from the North Pacific, and could have conservation implications if grey whales have the potential for essentially global dispersion. More broadly, documenting and understanding rare extreme migration events have potential implications for the understanding of how a species may be able to respond to global change.

1. Introduction

Animal migrations are often driven by habitat requirements that may change seasonally or among years. In some baleen whales, there can be vast distances between suitable seasonal breeding and feeding habitats, necessitating long annual migrations, and the grey whale (*Eschrichtius robustus*) is an extreme example (known to migrate as much as 8500 km between breeding and feeding grounds). Here, we investigate the origins of the first grey whale ever recorded in the South Atlantic [1] to better understand the process and context of long-distance migrations.

Extant grey whales likely comprise at least two stocks in the North Pacific [2]. One is the eastern grey whale (EGW) stock, which migrates along the North American west coast from wintering grounds in Baja California to feeding grounds in northern California to Southeast Alaska (the Pacific coast feeding group) or the Bering, Chukchi and Beaufort Seas (known as the northern feeding group; [2]). This putative population is now relatively abundant and was removed from the US list of endangered species in 1994. The other is the endangered western grey whale (WGW) stock (approximately 200 individuals remaining; [3]), found mostly around the northeastern coast of Sakhalin Island and southern Kamchatka Peninsula, Russia, with occasional sightings off Japan and China. Historic winter breeding grounds for the western stock are thought to have been off China [4], but photo-ID matches [5] and telemetry data [6] also show individuals from this population wintering in the eastern North Pacific [5], including in the lagoons off Baja California. Genetic data based on 84 SNP (single nucleotide polymorphism) loci clustered the EGW and WGW stocks separately, but with evidence for migration and admixture [7]. There was no strong lineage sorting in mitochondrial DNA (mtDNA) phylogenies, but significant differentiation based on F_{ST} and ϕ_{ST} [8]. A review of International Whaling Commission considerations of grey whale stock structure is provided in [2].

There are historical records of grey whales on both sides of the North Atlantic Ocean basin. A mtDNA phylogeny incorporating 33 sub-fossil grey

Table 1. Calculations for heterozygosity ratio (which is shown in the right-hand column) based on the minke whale reference. Het, heterozygous sites; Hom, homozygous sites; sites, total number of single nucleotide sites that passed our filtering after variant calling with a minimum of 5× coverage. The heterozygosity ratio for the Namibian sample is italicized.

sample	Het SNPs	Hom SNPs	sites (≥5×)	Het/total	Hom/total	Het/Hom
UAM117578	361 323	9 513 499	940 733 654	0.000384	0.010112	0.03798003
UAM9957	352 441	9 011 134	915 233 802	0.000385	0.009845	0.03911172
Namibia	861 596	21 581 284	1 859 257 776	0.000463	0.011607	<i>0.03992329</i>
WGW ER-14-168	1 133 070	26 913 173	2 053 083 297	0.000551	0.013108	0.04210094
WGW ER-14-0147	784 473	18 692 110	1 634 909 319	0.000479	0.011433	0.04196813
EGW GFD-02	1 015 510	21 507 638	1 815 801 841	0.000559	0.011844	0.04721624

whale samples from the North Sea and North Atlantic ranging in age from 150 to greater than 48 000 years old was polyphyletic and provided no clear indication of ocean basin differentiation at the species or sub-species level [9]. The authors inferred that movement between the Pacific and Atlantic was associated with Pleistocene climate cycles supporting passage across the Arctic when sea-level and climatic conditions made that possible. Sub-fossil remains from Gibraltar and the Mediterranean Sea dated to Roman times have also been reported [10]. More recently, there was a sighting of a single grey whale off Israel in the Mediterranean (on 8 May 2010), sighted again weeks later off Spain [11]. To date there are no genome sequences available for samples from the North Atlantic region.

In May–July 2013, a single grey whale was seen in the South Atlantic off the coast of Namibia. Here, we report on genomic analyses of this individual to identify its likely population of origin.

2. Methods

Photo-identification and sample collection were conducted by the Namibian Dolphin Project. Project work is conducted with the approval of the Namibian Ministry of Fisheries and Marine Resources (MFMR), although no specific research permits are issued by the department. Biopsies were collected on 6 June and 6 July using a crossbow with a modified arrow, and one of those biopsies was used for DNA extraction. DNA was extracted from the skin by standard phenol–chloroform methods, and the genome was shotgun sequenced starting with 1 µg DNA using the Illumina PCR-free Truseq kit (following kit protocols). The library was run in a single lane on a HiSeq 2500 and sequenced to an average read depth of 19.8X. The library size was 225 942 164 paired 125 bp reads. Raw reads from published genomes were downloaded from NCBI Sequence Read Archive [12,13]. See electronic supplementary material, table S1 for details of accession numbers and sample information. Mitochondrial genomes are either from GenBank (see electronic supplementary material, table S1) or derived from raw nuclear genome sequence reads (our Namibian genome together with accessions: SRR5495108, SRR5495100, SRR5495104, SRR5665641, SRR5665642; see electronic supplementary material, methods).

Details of genomic analysis and quality filtering are provided in our electronic supplementary material. We used vcfutils.pl from bcftools to prepare the input for pairwise sequentially Markovian coalescent (PSMC) analysis [14] and ran PSMC (v. 0.6.5-r67) with the settings -N25 -t15 -r5 -p '4 + 25*2 + 4 + 6' (default values establishing the characteristics of the run). We ran 100 bootstraps and plotted the results using psmc_plot.pl

and gnuplot. For generating the plot, the generation time estimate was 18.9 years, after [15], and the mutation rate was set to 2.2×10^{-9} bp yr⁻¹ (a nuclear genome-wide estimate for mammals), after [16]. These values affect the time scale on the x-axis, but will not alter the relative similarity among samples. We also ran a second PSMC analysis using the rate applied in [7]. We generated a maximum-likelihood (ML) tree from the exome data using RAxML [17], executing 100 rapid bootstraps and an ML search thereafter. We used a gamma model for rate heterogeneity, estimated to an accuracy of 0.1 log-likelihood units. There were no partitions and the substitution model was GTR (see electronic supplementary material, methods for further details). The mitochondrial neighbour-joining phylogeny was generated in PAUP (<http://paup.phylosolutions.com/>) using 1000 bootstrap replicates and the Tamura–Nei evolution model (chosen to address likely rate variation across the aligned sequences).

Measures of genomic diversity were based on the heterozygosity ratio method, which Samuels *et al.* [18] propose to provide a more reliable estimate than runs of homozygosity. The heterozygosity ratio is 'the number of heterozygous sites in an individual divided by the number of nonreference homozygous sites'. In order to be able to calculate homozygous SNPs for the grey whale reference sample used in the rest of our study, we chose the minke whale (*Balaenoptera acutorostrata*) genome (accession GCF_000493695.1; [19]) as a common reference, mapping the reads of each grey whale using the bwa mem algorithm and calling the variants using samtools mpileup with the same filtering as described in the electronic supplementary material (for the similar analyses where the grey whale reference was used). To give higher strength to the SNPs based on a divergent species, we also filtered the variant sites to a minimum depth of 5×. Details of each measurement generated are provided in table 1, with the final column showing the heterozygosity ratio for each grey whale genome.

3. Results

We analysed the first known grey whale to be sighted in the Southern Hemisphere. It remained in Walvis Bay, Namibia (23°53' S 14°28' E) from 4 May until 11 July 2013. Photographic documentation (e.g. figure 1) suggested poor body condition and although it remained in a very localized area, no feeding was clearly observed [1]. We sequenced the nuclear genome (to 19.8X coverage, also providing the mitochondrial genome; NCBI accession no. PRJNA694958) of this whale, and compared nuclear and mitochondrial genomes to grey whale genomes available in the NCBI database (figure 1; see Methods). Sex was bioinformatically determined to be male (see electronic supplementary material, methods). In phylogenies based on nuclear exomes (figure 1d), the

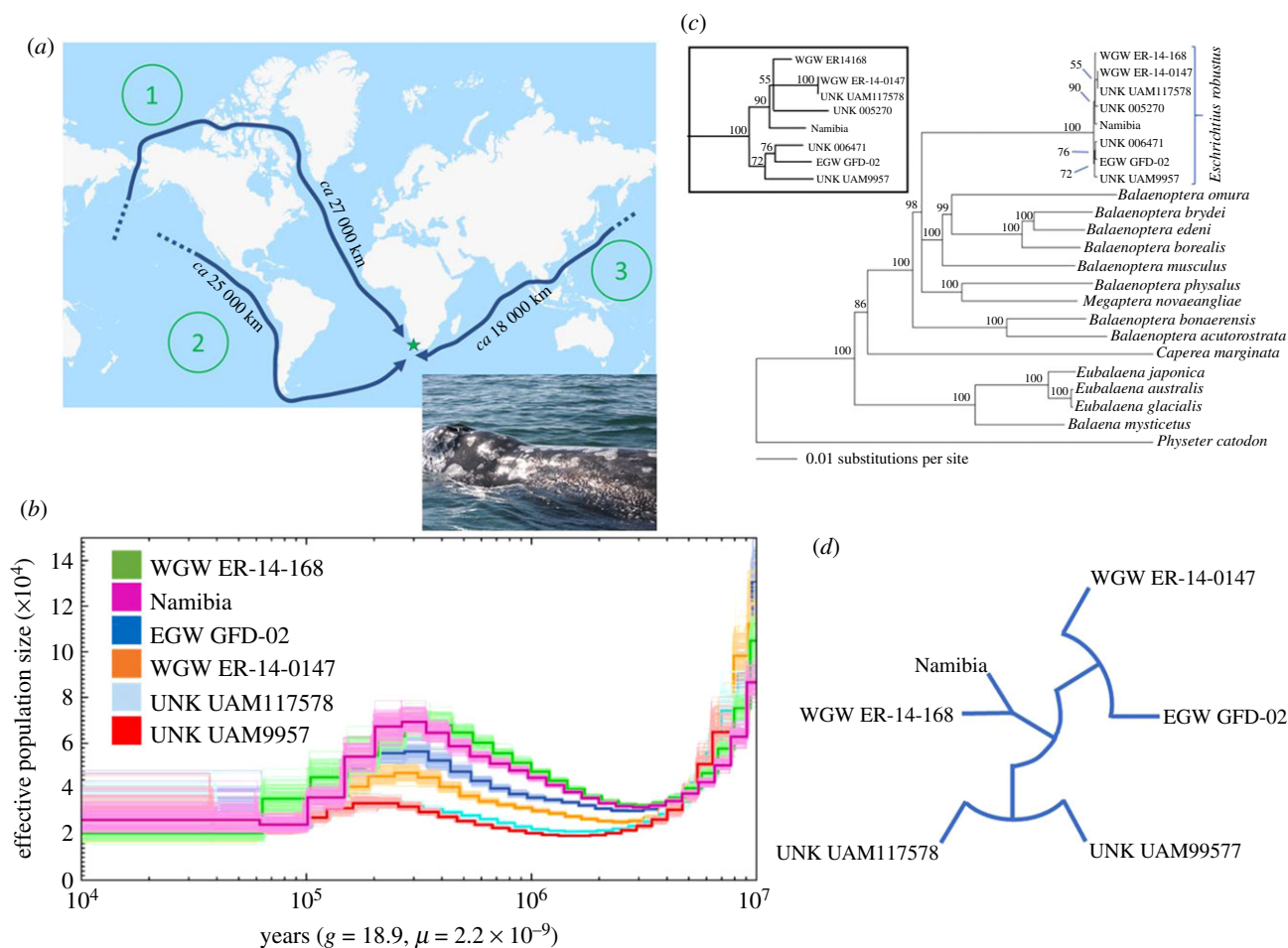


Figure 1. Genetic inference on the origin of the Namibian grey whale. (a) Hypothetical migration routes from the North Pacific grey whale home range to the sighting location in Walvas Bay, Namibia (indicated with a star). Alternative putative migration routes are numbered and estimated geographic distance shown. (b) PSMC of Namibian and database genomes. (c) Mitogenome neighbour-joining phylogeny showing bootstrap support based on 1000 replicates, rooted with *Physeter macrocephalus*. Inset: expansion of the *Eschrichtius robustus* lineage. (d) Unrooted RAxML tree based on exome (minimum node support = 95%). Inset photo of the Namibian grey whale is by S. Golaski. WGW, western grey whale; EGW, eastern grey whale; UNK, unknown breeding population.

Namibian sample aligned most closely to a WGW sample, and in the mitogenome phylogeny was in a lineage together with both samples identified as WGW, separate from a lineage including the sample identified as EGW (figure 1c). Genetic distances between the Namibian whale and the closest available North Pacific reference (WGW ER-14-168) are very low: 2.349×10^{-4} for the nuclear genome based on homozygous differences and 0.067% (uncorrected) for the mitogenome. These values are smaller than expected for comparisons among separate breeding populations. For example, comparisons among EGW and WGW samples found 1.9% difference on average [8], though this was for the mtDNA control region, which evolves more quickly than the full genome. PSMC profiles of historical demography also showed the closest relationship between the trajectory of the Namibian and the WGW sample ER-14-168 ([15]; figure 1b). These relationships remained the same when we applied the mutation rate used in [7] (electronic supplementary material, figure S1). Genomic diversity measured as the heterozygosity ratio [18] was relatively high for the EGW sample, and lower for the Namibian, WGW and Alaskan samples (table 1).

4. Discussion

Given the small genetic distance between the Namibian and available genomes, the data clearly indicate a North Pacific

origin for the Namibian whale, and possibly from the WGW population. While WGW ER-14-0147 has been sighted in the EGW wintering area off Mexico [15], ER-14-168 has not [20]. The EGW population is very much larger, and so ER-14-168 may have migrated to eastern regions undetected. However, ER-14-168 has been sighted 11 times between 2003 and 2019 in both near-shore and offshore areas, confirmed by photo-ID and always near Sakhalin Island (see https://www.iucn.org/sites/dev/files/wgwap20_report_final_en.pdf and links therein). Genetic assignment to a population is difficult for this species based on mtDNA given the lack of full lineage sorting and the putative WGW sample ER-14-0147 clusters with an EGW genotype in the exome phylogeny (figure 1d). However, the assignment of the Namibian whale to the WGW population is supported by the closest match to ER-14-168 (for genetic distance, phylogenetic placement and historical demography), and relatively low genomic variation (consistent with the proposed small population for the WGW; table 1).

Approximate geographic distances for putative migration paths from the North Pacific to Namibia are shown in figure 1a. Historical and modern data placing grey whales in the North Atlantic suggest path 1 in figure 1a as the most plausible when ice-free, though this may also be the longest route (requiring approximately 140 days at 8 km h^{-1}). This would be further than the previous record for a marine vertebrate, the

leatherback turtle (*Dermochelys coriacea*) moving through the water [21]. The northeast passage above Russia may also be possible during brief ice-free periods, with a distance similar to that for path 1. There are no fossil or sighting data to support either route 2 or 3. Furthermore, grey whales feed in relatively shallow water, which may limit the potential for long transits over deep water. If the whale began its journey southward from the wintering grounds in Baja California, that distance could be similar to a direct path through the Indian Ocean (route 3 in figure 1), about 18 000 km. This is still nearly halfway around the world (circumference = 40 075 km).

Confirming that this individual whale, sighted and sampled in the South Atlantic, was most likely born in the North Pacific indicates a remarkably long excursion from a core species range in the North Pacific, rather than origins in a remnant or newly established Atlantic population or taxon. Of course, this individual may reflect aberrant behaviour. However, this is one among the number of grey whales recorded in the Atlantic in recent or historical times. Various studies have speculated on the nature of the historical records in the Atlantic and the recent sightings. Alter *et al.* [9] note that ‘the extirpation of the Atlantic population during historical times has been attributed to whaling’, which implies a separate population there and its extinction. They propose that recent sightings may reflect ‘the beginning of the expansion of this species’ habitat beyond its currently realized range’ to re-establish a new Atlantic population. Dated fossils had placed the grey whale in the North Atlantic during both the Holocene [22] and the Pleistocene [23]. Rodrigues *et al.* [10] propose a ‘forgotten Mediterranean calving ground’ for grey whales based on three fossils dated to Roman times. The bones were not proposed to be from calves, but the location and the writings of Pliny the Elder led them to propose a breeding population.

Garrison *et al.* [24] provide evidence for the presence of grey whales in the western North Atlantic during the Holocene, and based on records up to the eighteenth century proposed a North Atlantic population that went to extinction. Scheinin *et al.* [11] report a grey whale sighting in the Mediterranean Sea in 2010 and offer as one possible explanation that it ‘represents a surviving individual from an extant (rather than extinct) North Atlantic population’ though they later dismiss this idea based on the rarity of sightings. They favour instead the idea that it may be a vagrant. For the sake of discussion, we will consider a ‘vagrant’ to be an individual well outside its normal range for what may be accidental reasons. Grey whales in the North Pacific are generally sighted at or apparently on their way to either feeding or breeding grounds. Although beyond their normal range if

from the Pacific, we cannot actually know if animals in the Atlantic are vagrants or instead rare intentional migrants.

If the Namibian whale (a male) can represent the longest known migration for this species, perhaps historical sightings were also migrants, rather than lost vagrants or members of established Atlantic populations that later went extinct (or migrants or vagrants on their way to establishing a new Atlantic population). Although we have no further data or means of testing the idea, we consider the possibility that some grey whales extend their range on foraging excursions across the Pole when this is possible (when sufficient ice has melted to allow passage), as has been in recent times and during historical periods of warming. Under this scenario, the lack of records during certain periods may be due to difficult access (relatively cold climate) rather than the extinction of an Atlantic population. This potential for global dispersion (even if rare or aberrant) could have conservation implications, especially given the possibility that this whale is from the endangered western stock. Rare excursions on a very large geographic scale are hard to document for marine species, but may have important implications for a species’ potential to adapt to a changing world.

Ethics. Photo-identification and sample collection were conducted by the Namibian Dolphin Project. Project work is conducted with the approval of the Namibian MFMR, although no specific research permits are issued by the department. All approaches to the whale were gradual and designed to minimize disturbance. Biopsy darts were sterilized prior to deployment, and samples were collected from high on the back near the dorsal ridge to minimize impact.

Data accessibility. All sequence data are available on the Sequence Read Archive public database under accession project no. PRJNA694958 (<https://www.ncbi.nlm.nih.gov/search/all/?term=PRJNA694958>).

Additional data are provided in the electronic supplementary material.

Authors’ contributions. A.R.H. sequenced the Namibian grey whale genome, drafted the paper and contributed analyses; F.S. did the bioinformatics and most analyses and revised the article for important intellectual content. T.G. and S.H.E. collected the sample and field data in Namibia and revised the article for important intellectual content. All authors approved the final version of the manuscript and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

Competing interests. We declare we have no competing interests.

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