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Genetic and behavioural data confirm the existence of a distinct harbour porpoise ecotype in West Greenland

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ABSTRACT

Elucidating the evolutionary and ecological characteristics of distinct populations constitutes a cornerstone in the classification of ecotypes, and in assessing their specific responses to environmental changes and potential impacts from human activities. In this study, two complementary approaches were deployed to investigate the existence of a putative harbour porpoise (Phocoena phocoena) ecotype in West Greenland. Genetic differentiation of 68 porpoises from West Greenland, and neighbouring Canada and Iceland were studied by ddRADseq analysis, and 18 porpoises instrumented with satellite transmitters were used to study their movement behaviour and site fidelity. The results suggest a genetically distinct harbour porpoise population in West Greenland, with strong site fidelity during the August breeding period and wide-ranging dispersal in the North Atlantic at other seasons. This adds to previously described unique characteristics of West Greenland harbour porpoises, including mesopelagic foraging behaviour, distinct skull morphology and tooth ultrastructure, and shorter, yet heavier, body; all pointing to the existence of a distinct West Greenland ecotype. We hypothesize that this ecotype arose through gradual adaptation to the local environmental conditions of the West Greenlandic shelf area, including high summer primary productivity and seasonal sea ice coverage. Consequently, this distinct ecotype of harbour porpoises necessitates a focused conservation plan.

1. Introduction

Originally coined for the description of plants [1], the classification of ecotype as an “ecological unit to cover the product arising as a result of the genotypic response of an ecospecies to a particular habitat” quickly found its way into a range of animal systems [2–4]. Having been adopted across a range of studies, the exact definition of what constitutes an ecotype remains a matter of debate [5,6], but it is typically applied to populations characterised by divergent genetic, ecological, behavioural, physiological, demographic and/or morphological adaptations to a particular environment. Ecotypes are thus non-static entities situated somewhere along the speciation continuum between populations and subspecies (or species), and they may merge or evolve depending on whether or not local adaptation is stronger than gene flow [7].

Ecotypes also occur in a range of marine mammal species [8–10]. In these, ecotypes do not appear to be specialised to specific environmental conditions (e.g. salinity and oxygen), but rather to specific prey or habitat types. For instance, bottlenose dolphins (Tursiops truncatus) comprise pelagic and coastal ecotypes [11], and among killer whales (Orcinus Orca) several ecotypes with particular dietary and/or habitat preferences have been recognised [9,12,13]. Moreover, in marine mammals, it seems that ecotype diversification mainly occurs in species with strong social systems where it is associated with the rise of unique ‘cul-
tures’ [14–16]. This raises the question of whether more solitary marine mammal species, not typically linked to the evolution of culture, also exhibit genetic, phenotypic and behavioural characteristics associated with adaptation to local prey sources and habitats. Documenting such unique characteristics, and ultimately disentangling their genomic background, constitutes a cornerstone in evolutionary biology and is a prerequisite for understanding and mitigating population- and species-specific responses to environmental changes and diverse human impacts, including hunting, bycatch and ocean noise.

The harbour porpoise is a small and widely distributed odontocete, occurring in subarctic and temperate waters across the northern hemisphere. Throughout its range, the harbour porpoise appears to prefer coastal waters along the continental shelf, where they can locate high and predictable densities of prey to maintain their relatively high metabolism [17–19]. Harbour porpoises are characterised by limited genetic structure approaching panmixia across large portions of their North Atlantic range, from northeastern United States to northern Norway [20–22]. It is increasingly clear that some harbour porpoise populations situated at the periphery of the core North Atlantic range (e.g. Black Sea, Iberia, Mauritania and Baltic Sea) display unique genetic and/or morphological characteristics possibly related to local habitats, which may merit Ecotype classification [23–29].

It has recently been documented that harbour porpoises from West Greenland display a unique migratory behaviour compared to other porpoise populations, undertaking long-range trips into the deep waters of the North Atlantic in autumn and winter [30,31]. This offshore winter migration is in striking contrast to the year-round coastal distribution so far reported for other harbour porpoise populations [32–35]. Moreover, multiple previous studies have found that West Greenland harbour porpoises differ from other populations in terms of their body shape and size, a mesopelagic diet, and their tooth ultrastructure and skull morphology [36–40]. These unique characteristics hint at dietary and/or habitat specialisations in West Greenland harbour porpoises reminiscent of those described for other odontocete species commonly regarded as harbouring multiple distinct ecotypes.

To date, genetic data have been inconclusive with regard to the genetic distinctiveness of West Greenland harbour porpoises [41–45]. A recent study detected a novel and highly divergent mtDNA haplotype in a single individual out of 29 collected from West Greenland [46], but the overall frequency and affinity of this haplotype is unknown. Moreover, it is unclear whether West Greenland porpoises visit and/or admix with neighbouring populations in Iceland and Canada during the long-range movements described from satellite tracking by Nielsen et al. (2019). Satellite tracking is a powerful tool for obtaining information on movements and behaviour at individual and population level [30,32,47–53]. However, although genetics and satellite tracking have complementary strengths, they have only been jointly employed in few studies of marine mammals to examine both long-term and contemporary structure of populations [54–56]. The lack of integrated approaches is problematic in that evolutionary genetic barriers may not reflect contemporary ecological barriers and behavioural patterns, and vice versa. This is particularly true for marine systems because of limited knowledge of what constitute barriers in oceans, and the potential ease with which these may form or break down; for example, as a result of seasonal, annual, or long-term shifts in temperature, salinity, ice conditions, or primary production, along with the distribution and abundance of prey and predators. The aim of the present study is to shed additional light on whether West Greenland harbour porpoises may qualify as a distinct ecotype. We do so by i) generating ddRADseq nuclear genome data to assess the genetic uniqueness of the West Greenland harbour porpoises in relation to neighbouring populations, and ii) re-analysing the satellite tracking data from Nielsen et al. (2019) to assess whether West Greenland porpoises, despite their long-range movements, exhibit site fidelity to West Greenland during the summer breeding period.

2. Materials and methods

2.1. Sampling and DNA extraction

A total of 68 harbour porpoise samples were collected between 1991 and 2014 from four localities across the species’ temperate and subarctic Atlantic range, including West Greenland (n = 30), Iceland (n = 12) and Newfoundland (n = 14) and the Gulf of St. Lawrence (n = 12) in Eastern Canada (Fig. 1; Supplementary Table 1). The samples consisted of muscle tissue from the subsistence hunt in West Greenland, skin biopsies from animals instrumented with satellite transmitters in West Greenland, and muscle from stranded or bycaught specimens from Canada and Iceland. Total genomic DNA was extracted from approximately 25 mg of tissue using the DNeasy Blood and Tissue Kits (Qiagen) for the West Greenlandic and Canadian samples, or the NucleoSpin Tissue Kit (Macherey-Nagel) for the Icelandic samples, following the manufacturer’s recommendations. DNA concentrations were measured using a Qubit® 2.0 Fluorometer (West Greenlandic and Canadian samples) or a NanoDrop 1000 (Thermo Scientific) (Icelandic samples), and DNA quality and quantity was further assessed with the Genomic ScreenTape System for the Agilent 2200 TapeStation (Agilent Technologies). The average peak molarities of the DNA extracts was 52.4 ng/μl (range: 6.08–347 ng/μl, SD = 50.0) and the average DNA fragment size was 19,488 bp (range: 7909 bp – and 54,561 bp, SD = 8986). The extracted DNA was turned into libraries using a double digested RAD-tag (ddRAD-tag) library cut by the restriction enzymes PstI (rare cutter) and MspI (common cutter), as described in detail by Lah et al. [27]. Sequencing was conducted at LGC Genomics, Berlin, Germany, on two lanes of an Illumina NextSeq platform (Illumina Inc.) with the 150bp paired-end read module.

2.2. DNA data filtering and quality control

Samples were de-multiplexed using LCG-developed software and clipped to remove Illumina TruSeq™ adapters and inline barcode remnants of all reads. Reads shorter than 20 bases were discarded, while the remaining paired reads were stored in a spate of FASTQ files for single reads. The DNA sequence reads were further processed using the de novo approach of Stacks v1.45 software package for analysing RAD-seq data [57,58]. First, process_radtag, was used to trim the de-multiplexed paired-end reads to a length of 85 basepair (bp), discard reads with a phred score <10 and concatenate them into a single FASTQ file per individual. Then, the ustacks program was used to align reads into matching stacks from identified loci and SNPs at each locus. We used a minimum depth of coverage of m = 3 to create a stack, a maximum distance of M = 3 nucleotides between stacks, removal of highly repetitive RAD-tags and the bounded-error SNP calling model (upper bound 0.01) to increase heterozygote calls. Next, the stacks and stacks programs were used to create a catalogue of all loci among all the individuals with two mismatches allowed between loci, and for matching loci in each individual to the catalogue, respectively. Loci with poor coverage or high sequencing error were removed with rstacks using a log likelihood value below –10, and this rstacks output was in turn used to rebuild a loci catalogue with stacks before reads were re-matched with stacks. Finally, the population program was used to generate a SNP data set for downstream analyses, retaining only loci that were present in 97% of all individuals and had a minimum depth coverage of six. Also, only a single SNP was kept per locus to avoid linkage disequilibrium. Following these procedures, the initial dataset of more than 690 million reads was reduced to an average of 7,418,410 reads per animal (range: 43,794–10,722,537, SD = 1,870,941). The resulting RAD-tag catalogue contained 548,556 loci, with an average of 114,808 loci per animal (range: 69,564–162,482, SD = 27,942), once sample PNPF_04 with a very low number of loci (n = 55) had been discarded (Supplementary Figs. 1A–B). Ultimately, when including only loci pre-
sent in 97% of the individuals, a total of 1023 SNPs was retained for population genetic inference across 67 individual harbour porpoises.

2.3. Genetic population structure, migration rates and demographic history

The population genetic ancestry of samples and populations was assessed using a principal component analysis (SmartPCA) available in the Eigensoft package [59] and the maximum likelihood approach implemented in ADMIXTURE v. 1.23 [60]. The admixture analysis was conducted using default parameters for 1 to 10 clusters and Cross Validation (CV) error to infer the most likely number of clusters; the output was plotted using the R package Pophelper 2.1.0. [61]. For each of the populations, we estimated basic population genetic summary statistics and pairwise $F_{ST}$ values in GenoDive 2.0 [62]. Moreover, to infer recent migration rates we used the BayesAss [63] algorithm for SNP data implemented in BA3-SNPs [64]. Migration rates were inferred between the two inferred population genetic clusters (West Greenland and Canada-Iceland), as well as among all three sampling regions (Canada, West Greenland, and Iceland) using 50,000,000 iterations, a burn-in period of 5,000,000 iterations, and sampling at every 1000 iterations. Following initial adjustments, a satisfactory acceptance rate for the MCMC chain was obtained by using the following mixing parameters for migration rates $m = 0.20$, allele frequencies $a = 0.40$ and inbreeding coefficients $f = 0.03$ for the two-population model, and $m = 0.20$, $a = 0.55$ and $f = 0.08$ for the three-population model, respectively.

2.4. Contemporary movement data

In order to investigate the behaviour of West Greenland harbour porpoises during the August breeding period we supplemented the genetic data with contemporary movement data from 18 harbour porpoises satellite tagged in West Greenland as described in Nielsen et al. [30]. Briefly, the tagged animals were live-captured with floating large-mesh gillnets on the continental shelf approximately 50 km south-west of Maniitsoq, West Greenland (Fig. 1), and instrumented with Argos satellite transmitters (Wildlife Computers, Seattle, USA). For a detailed analysis of individual behaviour and putative site fidelity during the August breeding month, we plotted the waterway distance between the tagging site of Maniitsoq and each satellite position obtained. The waterway distance between satellite positions and tagging site was estimated based on the Euclidean shortest path between tagging area and the porpoise position according to Li & Klette [65]. Satellite positions were provided through the Argos Data Collection and Location System and were filtered using the R package Argosfilter [66] as described in Nielsen et al. [30]. The West Greenland coast was modelled as an obstacle polygon and a visibility graph [67] was produced to calculate the waterway distance, using R version 3.4.3 [68] and the package Pyvisgraph [69] in Python 3.6.5 (Python Software Foundation).

3. Results

3.1. Genetic clusters, diversity and migration rates

The genetic data consisted of 1023 Single Nucleotide Polymorphisms (SNPs) that unequivocally pointed to the genetic separation of West Greenland harbour porpoises from porpoises sampled in neighbouring Canada and Iceland. This was evident from the PCA analyses with more than 25% of the genetic variation attributed to the separation between West Greenland and the other regions (Fig. 2A; Supplementary Fig. 2). The genetic uniqueness of West Greenland porpoises was also indicated by the Admixture analysis, supporting the existence of two ancestral populations ($K = 2$; CV error rate $= 0.445$)
with the sample regions divided into a cluster consisting of harbour porpoises from Gulf of St. Lawrence, Newfoundland, and Iceland, and a cluster including only harbour porpoises from West Greenland (Fig. 2B; Supplementary Fig. 3). Notably, the admixture analysis indicated some introgression with on average 15% (range 0–40%) of the West Greenlandic animals’ genome originating from neighbouring populations in Canada and Iceland.

The analyses of migration rates in BA3-SNP indicate that such introgression may be of recent origin, with relatively high proportions of recent migrants (~30%) in West Greenland and Iceland originating from Canada in the three-population model, as well as in West Greenland originating from the combined Canada-Iceland population in the two-population model (Table 1). In contrast, the proportion of recent mi-

Table 1

<table>
<thead>
<tr>
<th>Migration into</th>
<th>From</th>
<th>WGR</th>
<th>CAN-ICE</th>
<th>WGR</th>
<th>CAN</th>
<th>ICE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>WGR</td>
<td>0.677</td>
<td>0.009</td>
<td>[0.667, 0.698]</td>
<td>0.025</td>
<td>[0.000, 0.005]</td>
</tr>
<tr>
<td></td>
<td>CAN</td>
<td>0.332</td>
<td>0.991</td>
<td>[0.302, 0.975]</td>
<td>0.000</td>
<td>[0.000, 1.000]</td>
</tr>
<tr>
<td></td>
<td>ICE</td>
<td>0.677</td>
<td>0.012</td>
<td>[0.667, 0.000]</td>
<td>0.022</td>
<td>[0.000, 0.730]</td>
</tr>
</tbody>
</table>

grants from West Greenland to Canada and Iceland, and from Iceland to Canada and West Greenland, were low (1–2%) and not statistically different from zero in both the two- and three-population models.

Overall, the levels of genetic differentiation were moderate and only statistically significant for comparisons including West Greenland (Fst = 0.041–0.043), and not significant for comparisons between Iceland, Gulf of St. Lawrence and Newfoundland, respectively (Fst = 0.001) (Supplementary Table 2). The estimated effective numbers of alleles (Eff Num = 1.401), expected heterozygosity (Het = 0.263), and observed heterozygosity (Hobs = 0.280) were all higher for West Greenland than for Canada and Iceland (Supplementary Table 3).

3.2. Contemporary movement data

The satellite tagging data revealed large individual variation in movements with nine of the tagged animals leaving the West Greenland shelf in early fall-early winter and moving several thousand kilometres into the deeper North Atlantic Ocean, whereas nine animals remained within the shelf area during the duration of contact with the tag (Fig. 1; Supplementary Table 1). Strikingly, despite these long-distance oceanic movements, the four animals with tags transmitting a full migration cycle returned within 100 km of the tagging area during the August breeding period, illustrating a strong breeding site-fidelity to West Greenland (Fig. 3; Figs. 4A-D). Quite extraordinarily, the tag on animal ID 21792 lasted for more than 1000 days, documenting two full migration cycles from summer to winter sites. The nine animals that left and those nine that stayed had similar gender composition and overall similar body length (average 130.0 cm vs 134.1 cm), but differed substantially in tag duration, with those leaving doing so after 128 days (SD = 81.7) and on average transmitting for 375 days (SD = 306.2 days), whereas those staying only transmitted for an average of 122 days (SD = 91.5 days). Thus, the observed variation in movements may mainly owe to differences in tag duration.

4. Discussion

4.1. A distinct West Greenland harbour porpoise ecotype

It has long been questioned as to whether harbour porpoises in West Greenland comprised their own population or were part of the largely panmictic North Atlantic population ranging from northern Norway to
the United States. Genetic studies based on mtDNA and microsatellite markers have hinted that porpoises in West Greenland were different from other populations [20,21,43], and a recent study encompassing samples from much of the harbour porpoises’ North Atlantic range detected a unique mtDNA haplotype in West Greenland porpoises [46]. Still, none of these studies have provided solid evidence. The genomic data presented here unequivocally confirm that harbour porpoises in West Greenland are genetically distinct from harbour porpoises in Iceland and Canada. Moreover, by inclusion of harbour porpoise satellite tagging data, we demonstrate that despite its unique long-range offshore movements and opportunity to mix with neighbouring populations, the West Greenland porpoises exhibit strong site-fidelity during the August breeding period to the West Greenland shelf area. Thus, the behavioural data are congruent with the genetic data.

In addition to the genetic differences highlighted here and previously [43], West Greenland porpoises are generally smaller in length and heavier in body mass compared to other North Atlantic porpoises [37], have a characteristic tooth ultrastructure [39] and unique skull morphology with a short rostrum and forward orientated skull vertex, indicative of pelagic feeding [31,38]. Furthermore, West Greenland porpoises are characterised by distinct reproductive traits [70], fatty-acid profiles [Meller 1999 cited in 68], contaminant levels [71–73], and parasite and bacterial composition [74,75]. While some of these observations may simply reflect environmental variability, together they comprise a long list of characteristics pointing to the uniqueness of harbour porpoises in West Greenland, as summarised in Supplementary Table 4.

In other harbour porpoise populations, the levels of genetic differentiation and unique ecological, behavioural, and morphological characteristics reported in our study for West Greenland harbour porpoises have led to a classification as distinctive ecotypes or subspecies [26,76,77]. In this light, we propose that the West Greenland harbour porpoise should also be classified as a separate ecotype. Indeed, it could prove to be a separate subspecies, which tentatively could be referred to as Phocoena phocoena kalallit given its close association with West Greenland. Additional analyses of morphological and mitogenome data are needed to shed light on this.

4.2. Origin and adaptations of porpoises in West Greenland

The West Greenland harbour porpoises join the ranks of other distinct North Atlantic harbour porpoise populations in the Black Sea, Mauritania, Iberia, southern United Kingdom, and the Kattegat-Baltic Sea region [20,23–25,27,28,76,78,79]. Overall, it seems likely there is one large semi-pammictic population at the core of the porpoise’s North Atlantic range (i.e. northeastern USA, Canada, Iceland, the North Sea, and Norway), with more or less genetically isolated pockets at the periphery of this range. In marine mammals – as well as many other species groups – the existence of distinct populations at the periphery of the core range are typically associated with isolation during glaciations or founder events as new habitats became available upon glacial retreat [80–82]. Similarly, the divergence of harbour porpoise populations in Iberia, Mauritania, and the Black Sea from the larger North Atlantic population have all been attributed to postglacial climatic events [24]. Unfortunately, our genetic dataset did not allow for reliable estimation of the site frequency spectrum and hence we could not reconstruct the demographic history of the West Greenland harbour porpoises or estimate its divergence from neighbouring populations. Much of its current habitat was covered by advancing glaciers and sea ice during the recent glacial period [83]. The exact timing of the glacial retreat in West Greenland is uncertain, but recent studies suggest that deglaciation of the shelf area, on which contemporary West Greenlandic harbour porpoises forage and breed during the summer, started as early as 17,000 years BP [83–86]. Until tested thoroughly with more extensive genome data we hypothesize that the glacial retreat facilitated the colonisation of West Greenland by North Atlantic harbour porpoises, which gradually adapted to the region’s seasonal changes in sea ice coverage and primary productivity.

Arctic cetaceans, such as the bowhead whale (Balaena mysticetus), narwhal (Monodon monoceros), and beluga (Delphinapterus leucas), have adapted to seasonal changes in sea ice coverage by migrating between open-water feeding and breeding sites during the summer and areas with open pack-ice and polynyas during the Arctic winter [87–90]. In contrast, more temperate cetacean species, such as the humpback whale (Megaptera novaeangliae) and fin whale (Balaenoptera physalus) mainly visit the Arctic during the summer feeding season when primary
productivity is high, and leave for warmer waters for breeding during winter [91]. As documented by satellite tagging data, harbour porpoises in West Greenland appear to have adapted a somewhat intermediate strategy, feeding and breeding in the productive waters of West Greenland during the summer, and migrating to ice-free waters in the south-eastern Davis Strait, eastern Labrador Sea, and central North Atlantic during winter [30]. The observation that half of the tagged animals did not leave the Greenland shelf area during the study may mainly owe to differences in tag duration and we hypothesize that most West Greenland porpoises leave the shelf and forage in the deep waters of the North Atlantic during winter. As detailed by Nielsen and co-authors [30,31], formation of sea ice is likely a major driver of the West Greenland harbour porpoise's migration into open waters during winter and spring. In addition, given the observation that the tagged porpoises – rather than just following the edge of the sea ice – moved far into the open waters of the North Atlantic where they performed deep dives, it may be that the winter migration also presents an opportunity to forage and build energy reserves for the summer breeding period [30,31]. Future studies should assess the energetic cost-benefits of these long-distance seasonal migrations.

While the West Greenland harbour porpoises exhibit multiple unique genotypic and phenotypic characteristics, including a strong breeding site-fidelity, our genetic data also pointed to some admixture of its genome. On average 15% of the West Greenland harbour porpoise
genome originates from neighbouring populations in Canada and Iceland, and Canada appears to be a source to a relatively high proportion of recent migrants in West Greenland. It is unclear whether this introgression reflects past or ongoing immigration, and to what extent it may be facilitated by climate change and recent warming of the West Greenland marine ecosystem [92]. In time, immigration may break down the genetic and phenotypic characteristics of West Greenland porpoises, or alternatively the population may carry yet-to-be-identified adaptive alleles that maintain its distinctiveness in the face of ongoing gene flow, as demonstrated for a wide range of fish, birds and mammals [7,93–95]. More studies like ours – integrating genetic and behavioural data – are needed to shed light on the complex interplay between environment, phenotypes, genes and behaviour in the evolution of marine mammals.

4.3. Management implications

The most recent estimate of abundance for harbour porpoises in West Greenland was 83,321 (95% CI: 43,377–160,047) in 2015 [96], which - taking satellite tracking data into account to include porpoises outside the surveyed area - gives a total abundance of 106,822 animals (55,149–206,909) [97]. An average of 2139 harbour porpoises were reported taken annually by subsistence hunters in West Greenland during 1993–2012, which is higher than the recommended catch level of no more than 1869 animals [97]. Although not alarming, this level of removals in proportion to uncertain population size estimate triggers concerns about a population in decline in the future. The importance of a strict management regime in terms of designating managing units and hunting quotas becomes even more important when considering that
porpoises in West Greenland may constitute a distinct ecotype or sub-species. Also, given the observed long-distance migrations, West Greenland porpoise populations may be impacted outside of the Greenland shelf area, e.g. noise pollution and bycatch. For now, we recommend that the West Greenlandic harbour porpoise population is managed as a separate unit, and that future work should focus on understanding its conservation status and monitor the putative effects of anthropogenic stressors e.g. hunting and climate change.

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**Author contributions**


**Data**

Genetic data and codes are available as supplementary files.

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**Appendix A. Supplementary data**

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecgg.2021.100108.

**References**
