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Original Article

Stranding collections indicate broad-scale connectivity across the range of a pelagic marine predator, the Atlantic white-sided dolphin (*Lagenorhynchus acutus*)

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Understanding the extent of population genetic connectivity in highly mobile marine species is vital for delineating management units. However, obtaining samples for generating genetic data is challenging for species inhabiting inaccessible pelagic waters. As a result, management strategies do not always align with underlying population biology. Marine strandings provide an accessible and cost-effective sample source for research on elusive cetaceans and can be used collaboratively among stranding networks to generate ecosystem-wide population genetic assessments. Here, we used samples collected from strandings and free-ranging individuals across the North Atlantic to investigate population structure, genetic diversity, and individual relatedness in the Atlantic white-sided dolphin (AWSD; *Lagenorhynchus acutus*), a widely distributed marine predator. Mitochondrial DNA sequences and nuclear DNA single-nucleotide polymorphisms showed a complete lack of population differentiation across the species' range, implying an unusual pattern of strong connectivity. No differences in genetic diversity among geographic regions and weak within-group relatedness further support the existence of species-wide panmixia in AWSD. This study emphasises the value of long-term stranding collections for cetacean research and has important implications for AWSD conservation management.

Keywords: conservation genetics, dolphin, genomics, *Lagenorhynchus*, molecular ecology, population genetics, strandings.

Introduction

Cetaceans are long-lived, often wide-ranging marine predators with complex life histories that inhabit a variety of ecosystems and occupy almost every part of the world's oceans (Tittensor *et al.*, 2010). Many species undergo long seasonal migrations, and all species can be considered highly mobile (Aidley, 1981). Despite their mobility and the absence of physical dispersal barriers in their open-water habitats, most cetacean species display geographic population differentiation, having evolved distinct genetic populations across their range displaying various levels of connectivity (Hoelzel, 2009). The drivers leading to genetic divergence within a species are multifaceted with some populations being isolated by geographic distance, while others may be in closer proximity, but display differences in social behaviour or habitat requirements mediated through, for example, prey distribution, thermal barriers, or habitat suitability (Amaral *et al.*, 2012; Andrews, 2014; Genoves *et al.*, 2020). In contrast, some marine species may display range-wide connectivity and weak structuring. This pattern is observed less frequently, but can be mediated through continuous gene flow driven by generalist behaviour regarding prey and habitat selection, and strong mobility (Craddock *et al.*, 2009; Oomen *et al.*, 2011; Hernandez-Milian *et al.*, 2016; Beatty *et al.*, 2020). Given the complexity of mechanisms leading to restricted gene flow, some signatures of genetic differentiation within cetaceans have only recently been resolved through next-generation-sequencing (NGS) approaches (Morin *et al.*, 2009; Lah *et al.*, 2016). However, for many elusive pelagic species, few studies utilizing NGS technologies have been conducted and therefore large knowledge gaps remain concerning fine-scale population structure alongside other aspects of their biology. This is largely driven by the inaccessibility of remote marine habitats and legislative difficulties in obtaining permits for the collection of samples from living animals (Jarić *et al.*, 2015).

Opportunistic sampling of deceased cetaceans is regularly conducted by national stranding networks and provides an important yet cost-effective source of information. Such sample archives can aid in understanding the ecology, life history, and pathology of cetaceans as well as the potential impacts of climate change and human interactions (Evans *et al.*, 2005; Adimey *et al.*, 2014; Byrd *et al.*, 2014; Betty *et al.*, 2020; IJsseldijk *et al.*, 2020). Furthermore, tissue samples from deceased animals provide a valuable opportunity for generating high-resolution genetic data for population assessments. Such information can be used to directly inform conservation through the delineation of meaningful management units (MUs; Moritz, 1994). MUs can be defined through detection of genetically differentiated groups or identification of adaptive differentiation to specific habitats (Funk *et al.*, 2012; Car-

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lén *et al.*, 2018), ultimately aiming to conserve a large proportion of species-wide genetic diversity (Hoban *et al.*, 2021). Additionally, several ecological factors, apart from genetics, can warrant regional management even if at odds with genetic units, or in species with an absence of population structure (Crandall *et al.*, 2000). For example, regional differences in anthropogenic threats could benefit from separate MUs through implementation of local measures tackling sources of those pressures (Wallace *et al.*, 2010).

The Atlantic white-sided dolphin (*Lagenorhynchus acutus*; AWSD) is an understudied pelagic cetacean inhabiting large offshore areas of the North Atlantic Ocean (Selzer and Payne, 1988). While it is believed to be among the most abundant cetacean species in the North Atlantic with an estimated 145000–300000 individuals (Braulik, 2019), its restriction to cold-water habitats makes it vulnerable to habitat contraction and climate change (MacLeod *et al.*, 2005). Given the inaccessibility of AWSD habitat, monitoring population trends and assessing structure, beside other ecological factors, are difficult to perform and greatly benefit from the introduction of samples obtained from stranding records. Banguera-Hinestroza *et al.* (2014a) made use of strandings from across the North Atlantic in an assessment of population structure. In doing so, they find evidence for both broad-scale connectivity between eastern and western North Atlantic regions, and fine-scale structure between eastern North Atlantic putative populations. However, this study used mitochondrial control region sequences and a small panel of microsatellites, which may be limited in their statistical power to detect population structure. Fernández *et al.* (2016) generated nuclear single-nucleotide polymorphisms (SNPs) for a more in-depth assessment of structure, but the retained markers have not yet been used to perform a detailed assessment of AWSD population structure.

Resolving fine-scale patterns of population structure enables a more targeted management approach by policy makers through identification of vulnerabilities or low resilience to anthropogenic impact for cetacean populations (Andrews, 2014). Given the above mentioned studies indicating differing patterns of connectivity in AWSD, the species currently receives a localized management approach by either nations (Evans *et al.*, 2003; Fisheries, 2019) or international consortia (ASCOBANS, NAMMCO). This may be justified by some identified ecological variation such as differences in prey composition between regions or seasonal migration throughout the year, which may warrant a more localized management approach (Hátún *et al.*, 2009). However, it is important to thoroughly resolve any population genetic structure present at multiple spatial scales to appropriately inform these management approaches from a genetic perspective. Recent advances in genomic technologies and access to long-term stranding collections present an opportunity to achieve this, alongside increasing our knowledge of genetic diversity and kinship in AWSD.

In this study, we acquired 93 tissue samples of AWSD across its eastern range and used reduced representation nuclear genome sequencing to generate a dataset of SNP genotypes. We further compiled a large dataset of mitochondrial DNA control region sequences across the entire range of the species. To achieve a high-resolution population genetic assessment of AWSD, resolving the above-described uncertainties, we used these data to test the following three hypotheses: (i) AWSD displays strong connectivity over broad and fine spatial scales, (ii) AWSD shows high species-wide genetic diversity and little inbreeding, and (iii) social structure consists of loose associations of unrelated individuals, as opposed to kin-associated family groups. We discuss the implications and challenges of the results for the conservation management of AWSD and propose how strandings can be further used to understand more about cetaceans and their conservation status through multidisciplinary approaches.

Methods

Sample acquisition, DNA extraction, and processing

Tissue samples (muscle, liver, or skin stored at −80°C dry frozen or in >80% ethanol; some transferred under CITES Institutional permits DK 014 and GB 034) were collected from stranded ($n = 76$) and free-ranging ($n = 17$) AWSD along the eastern North Atlantic coastline between 1992 and 2019 (Figure 1). These comprised individuals from Scotland ($n = 67$), the Faroe Islands ($n = 14$; obtained through sampling by the Faroes national history museum of coordinated traditional hunts), Ireland ($n = 8$), Iceland ($n = 3$), and France ($n = 1$). High-quality DNA was extracted using methods described in the Supplementary Material. All 93 samples (plus two technical duplicates) were then submitted to Diversity Arrays Technology for DArTseq™ analysis, under appropriate CITES permits. Supplementary Table S1 contains details on year of sampling, sex, geographic origin, extraction method, and analysis conducted on each sample.

Mitochondrial control region sequencing and analysis

A subset of 21 samples was selected for mitochondrial DNA sequencing (Scotland $n = 10$, Ireland $n = 3$, Faroe Islands $n = 3$, Iceland $n = 3$, Norway $n = 1$, France $n = 1$) focussing on geographic regions that were previously poorly assessed. We sequenced the mitochondrial control region using universal cetacean primers MTCR-F (5′-TTCCCCGGTCTTGTAAACC-3′) and MTCR-R (5′-ATTTTCAGTGTCTTGCTTT-3′) that target a partial 900 bp sequence of the control region (Hoelzel and Green, 1998). PCR conditions are described in the Supplementary Material.

Sequences were trimmed and error-corrected using Geneious Prime® 2021.2.2 and NCBI nBLAST searches conducted to ensure correct species assignment. The data were supplemented with 113 control region sequences from Cipriano (1997; $n = 2$), Mirimin *et al.* (2011; $n = 19$), Banguera-Hinestroza *et al.* (2014a; $n = 64$), and Pugliares-Bonner *et al.* (2021; $n = 28$) (Accession numbers AF113486–AF113487, FR668237–FR682924, KJ456520–KJ456583, and MT450724–MT450751) for subsequent analysis (Supplementary Figure S2). All 134 sequences were aligned using Geneious Prime® and trimmed to 320 bp. The final control region dataset contained information from two locations in the western North Atlantic and eight locations in the eastern North Atlantic (Supplementary Figure S3).

Haplotype and nucleotide diversity were calculated using Arlequin 3.5 (Excoffier and Lischer, 2010). To investigate whether previously detected signatures of structure could be reproduced, the samples were stratified into (i) six regions [SNS = southern North Sea, E_Scot = eastern Scotland, NNA = northern North Atlantic, W_ENA = western

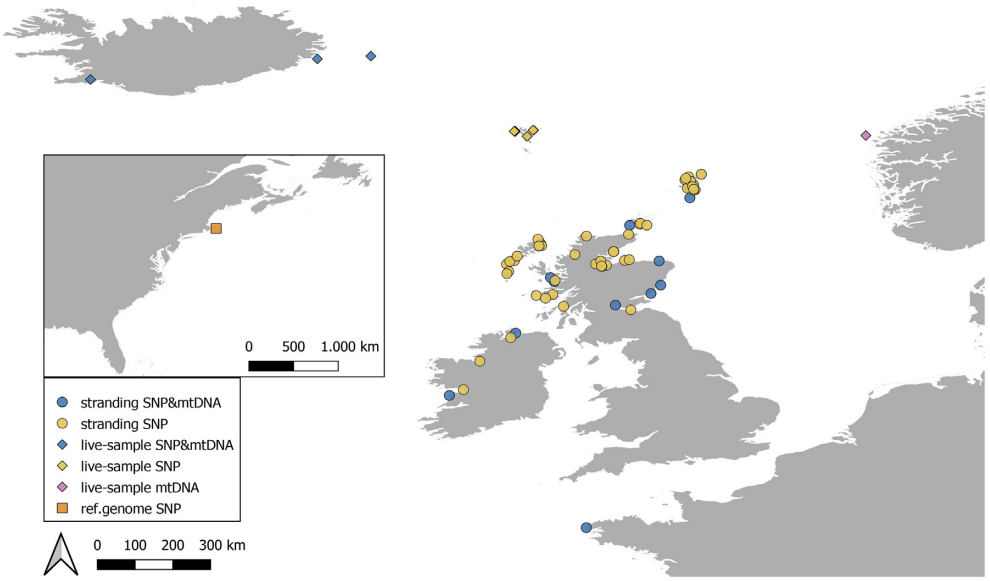

Figure 1. Maps of the North Atlantic Ocean displaying spatial distribution of 93 *L. acutus* tissue samples and the reference genome sample used in this study. Point shapes indicate sample type and point colour indicates data type associated with each sample.

east North Atlantic, SGL = southern England, WNA = western North Atlantic, ENA = eastern North Atlantic; following Banguera-Hinestroza *et al.* (2014a)] to test for fine-scale structure; and (ii) eastern and western North Atlantic to test for broad-scale structure using Wright's pairwise fixation indices.

DArTseq sequence alignment and variant calling

Raw DArTseq sequences were checked for base call quality and errors. Two samples did not produce libraries and were excluded from the dataset ($n = 91$). Barcodes were removed and reads aligned to the reference genome (SRR16086814). Sequencing reads from the reference genome individual were incorporated in the variant calling pipeline to represent the western-most range of the species, increasing sample size to 92. SNP calling and per locus genotype likelihood calculation was conducted using ANGSD (Korneliussen *et al.*, 2014). Individuals with a missing rate $\geq$50% and the sample with the higher missing rate of each replicate pair were removed, reducing the sample size to 90 (Supplementary Figure S2). Genotype likelihoods were recalculated with this corrected sample set, resulting in a total number of 6371 SNPs. See Supplementary Material for details.

Filtering and quality control

Following variant calling, two SNP datasets (A and B) differing in proportion of missing data were generated for separate downstream analyses.

Dataset A was used to infer population genetic parameters such as genetic structure, genetic diversity, and inbreeding. Data were pruned for loci affected by linkage disequilibrium using ngsLD with a maximum kb distance of 5 and a minimum weight of 0.5, reducing the number of loci to 3647 (Fox *et al.*, 2019). Subsequently, all loci not mapped to 1 of the 21 autosomes and markers mapped to the X-chromosome were manually removed to account for sex bias. Lastly, a minor allele frequency (MAF) threshold of 0.01 was applied using the –maf function in PLINK (Purcell *et al.*, 2007), leaving a final dataset of 2381 SNPs.

Dataset B was used for the inference of pairwise relatedness between individuals, which required maximally informative markers. The parameters for linkage disequilibrium filtering and exclusion of unmapped and sex-linked markers remained the same as in dataset A. The MAF threshold for the dataset was set to 0.3, resulting in retention of 391 SNPs.

Population structure

Prior to inferring of population structure, four individuals were removed due to high relatedness scores. A separate ANGSD run to calculate genotype likelihoods across the remaining 86 individuals was then performed using the parameters described above. We performed a principal component analysis (PCA) based on genotype likelihoods in PCAngsd (Meisner and Albrechtsen, 2018). The covariance matrix was used to compute eigenvectors on a two-dimensional scale to resolve population structure in R Studio (R Core Team, 2022). We further investigated multivariate clustering algorithms with pre-defined population assignments for a guided clustering approach that can often help to resolve structure at fine scales. For this, we performed a discriminant analysis of principal components (DAPC) using the dapc function within the *adegenet* package in R (Jombart, 2008) and a novel, non-linear Kernel Local Fischer DAPC, which was shown to exceed the power of the previous two approaches to resolve structure resulting from complex admixture scenarios (Qin *et al.*, 2022). The programme NGSadmix was used to generate admixture proportions for each individual (Skotte *et al.*, 2013). Admixture runs were performed for $K = 1$–6 and the results merged and uploaded to CLUMPAK to identify the optimal K based on Delta K and the Evanno method (Kopelman *et al.*, 2015).

Genetic diversity and inbreeding

To assess levels of genetic diversity and inbreeding, we calculated standardized multilocus heterozygosity (*sMLH*) as a measure of diversity and F_{HATII} as a measure of inbreeding in

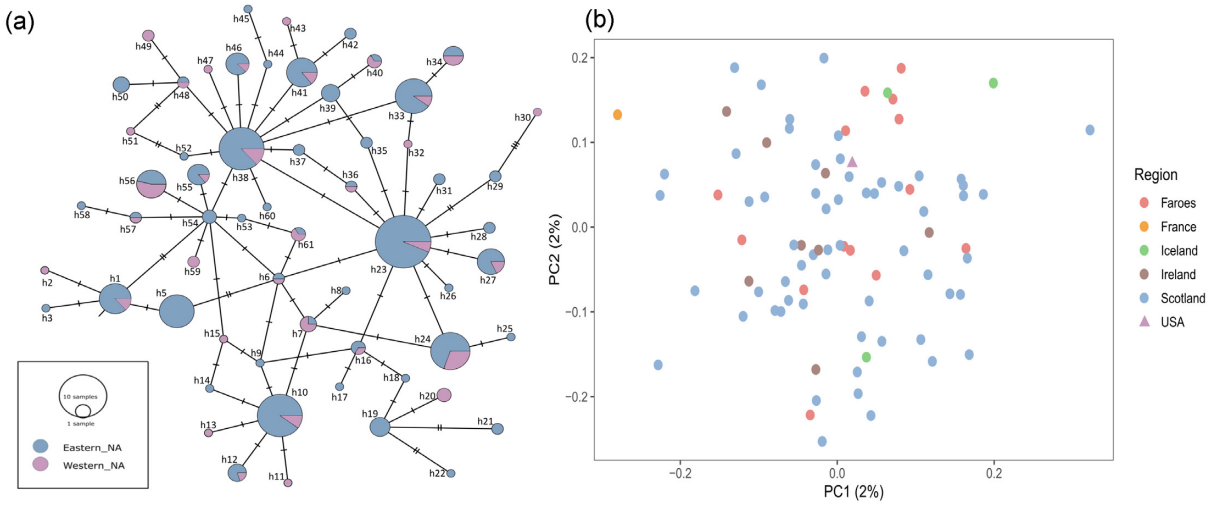

Figure 2. (a) Minimum spanning network of mtDNA haplotypes derived from a total of 134 sequences (combined from this study and available sequences on GenBank) based on a 320 bp fragment. Circle size is relative to the number of individuals sharing each haplotype; colours represent eastern and western North Atlantic. (b) Plot of first two PCA axes for 86 AWSD and 2381 SNPs, displaying an absence of population genetic clustering across six sampled regions of the North Atlantic Ocean (different colours). Each point represents one individual; percentage variance explained by each axis is shown in parentheses.

each sequenced individual and between sampled regions using the *inbreedR* package in R and the PLINK –ibc function. (Stoffel *et al.*, 2016). Both, *sMLH* and F_{HATII} proportions were visualized as distribution across individuals as well as comparison between regions in R.

Relatedness

Detection of potentially related individuals across the sample set was performed prior to assessment of population structure. We investigated overall relatedness through pairwise comparisons of all possible pairings. The sample set included eight mass-stranding or group-sampling events, which provided an opportunity to interpret within-group social structure given that several dolphin species are known to exhibit natal philopatry and aggregation in family groups. Supplementary Table S4 contains details on size of event, coverage by the sample set and date.

The PLINK –genome function and NGSrelate were used to calculate pairwise identity by descent estimates, kinship coefficients (*PI_HAT*), inbreeding coefficients, and relatedness measures. Visualizations of outputs were further processed in R and classified based on predefined thresholds. First degree pairings were assessed based on available metadata, namely records on sex, length, weight, sample location, sample date, and age group, collected from strandings to detect biologically relevant associations.

Results

Species-wide connectivity

We sequenced 21 AWSDs at the mitochondrial control region and combined these with 113 open-access sequences to create a minimum spanning network of control region haplotypes from samples across much of the known species range. The 320-bp long alignment showed a total of 61 haplotypes, thus displaying a high haplotype diversity of $h = 0.973$ with 39 polymorphic sites. Within our sample set, we found six different haplotypes, all of which were shared with samples from previous studies (Supplementary Table S5). A total of 24 haplotypes were unique to the eastern North Atlantic, while 12 were restricted to western North Atlantic individuals (Figure 2a). We found no significant differentiation between eastern and western North Atlantic ($F_{ST} = 0.00553$; $p = 0.08108 \pm 0.0212$). Furthermore, no significant differentiation was detected between any of the six regions defined by Banguera-Hinestroza *et al.* (2014a) when incorporating all available sequences (Supplementary Table S6).

Analysis of population structure at the nuclear genome was performed using a set of 2381 SNPs genotyped across 86 individuals from six regions spanning the eastern (Faroes, France, Ireland, and Scotland), central (Iceland), and western (USA) North Atlantic. PCA results showed no differentiation among sampled regions along PC1 and PC2 (Figure 2b) or PC1 and PC3 (Supplementary Figure S7). Notably, even the sample from which the reference genome was derived, representing the western side of the North Atlantic Ocean, is situated within the single cluster detected by PCAngsd. Guided Bayesian clustering approaches using DAPC and KLFDAPC further supported this finding (Supplementary Figures S8 and S9). Estimation of the optimal *K* based on admixture proportions generated in NGSadmix identified K = 2 as the best fit for the data (Supplementary Figure S10). However, individual admixture proportions across sample regions and $K = 1$–6 (Supplementary Figure S11) showed no clear geographic structure, nor any separation of individuals to separate genetic clusters, concordant with the PCA results.

Diversity statistics

Measures of genetic diversity were based on the two marker systems used in this study. Within the mitochondrial control region, we observed a haplotype diversity of $h = 0.973$ and nucleotide diversity of $\theta_\pi = 0.01107$.

For the nuclear SNP dataset, *sMLH* was normally distributed with a mean of 0.995 ($SD \pm 0.078$) and a minimum

and maximum of 0.707 and 1.242, respectively (Figure 3a). *sMLH* did not differ among most regions, but the French individual showed a smaller value than the mean of all other regions (Figure 3b).

The inbreeding coefficient F_{HATII} was normally distributed across the sample set with a mean of 0.009 ($SD \pm 0.155$). The maximum observed value was 0.288 and three samples showed low F_{HATII} with the minimum observed value being −0.870 (Supplementary Figure S12A). When comparing inbreeding across sampled regions and between mass stranding events and single strandings, values did not differ (Supplementary Figure S12B).

Relatedness

A maximally informative set of 392 SNP loci was used to estimate pairwise relatedness among all 90 individuals, given the absence of population structure. The majority of the comparisons (72.43%) exhibited no relatedness ($PI\_HAT = 0$; Figure 4a). However, four pairwise comparisons had relatedness coefficients >0.4, implying first degree relatedness (Manichaikul *et al.*, 2010). *KING*-robust kinship and the *R1* coefficient clearly identified these four pairs as one parent–offspring and three full-sib relationships (Figure 4b). We observed few second-degree ($n = 7$; 0.17% of all comparisons) and a moderate number of third-degree relationships ($n = 180$; 4.49% of all comparisons). Interestingly, the pair assigned to parent–offspring status and one of those assigned full-sib status each comprised an adult female and juvenile male sampled during the same stranding events. The remaining pairs of individuals assigned full-sib status were sampled 14 and 22 years apart, respectively.

Discussion

The AWSD is one of the most abundant yet least studied North Atlantic delphinid species. It may be vulnerable to increasing ocean temperatures through habitat contraction or prey shifts, alongside other direct anthropogenic impacts (entanglement, contamination, and prey depletion). Increasing population genetic knowledge of the species is important to inform future management and monitoring approaches. To achieve this, we conducted high-resolution SNP genotyping and mitochondrial control region sequencing on a range-wide sample set to investigate population genetics, social structure, and genetic diversity of AWSD.

Species-wide connectivity

The population genetic assessment of AWSD suggests broad-scale connectivity across the North Atlantic Ocean. This is partly in concordance with previous studies (Fernández *et al.*, 2016); however, our data do not support the differentiation of a southern North Sea population as reported by Banguera-Hinestroza *et al.* (2014a). This differentiation was suggested by the authors to potentially represent an artefact of historical structure that could have formed through drift within a population inhabiting isolated parts of the North Sea during the Last Glacial Maximum, which was then later reconnected to the North Atlantic. However, by repeating the analysis using the same population assignments as Banguera-Hinestroza *et al.* (2014a), but with a larger dataset, North Sea individuals were not resolved as a separate population. The low frequency of sightings and strandings along the North Sea coastlines in addition to the known habitat requirements further suggest that this region is unlikely to be a contemporary habitat for a stable AWSD population (Selzer and Payne, 1988). Considering this, together with the high-resolution genetic data presented in this study, it seems likely that signatures of differentiation previously detected in the control region were an artefact of small sample size and restricted DNA marker systems.

Despite high dispersal capabilities, cryptic population structure is regularly observed in cetaceans and can be mediated through factors such as kinship (Beck *et al.*, 2012), adaptation to specific habitats (Louis *et al.*, 2021), isolation by distance, or the complex interplay of several factors (Hoelzel, 2009). Our findings on AWSD connectivity therefore suggest atypically strong dispersal behaviour compared to other species, with panmixia across the species' range. Phylogeographically, the AWSD may not have experienced restricted dispersal during the Pleistocene due to maintenance of its environmental temperature niche and its preference for pelagic waters, forming a continuous refugium. Together with a generalist diet preference and fission–fusion social dynamic, this likely supported a large historic effective population size and facilitated geneflow throughout its range, contrary to differently adapted cetaceans in the North Atlantic (Banguera-Hinestroza *et al.*, 2014b).

Genetic diversity and inbreeding

In terms of genetic diversity, we found values of nucleotide diversity ($\theta_\pi = 0.01107$) and haplotype diversity ($h = 0.973$) comparable to other delphinids such as the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*; $\theta_\pi = 0.0165$, $h = 0.961$; Hayano *et al.*, 2004) and the Atlantic spotted dolphin (*Stenella frontalis*; $\theta_\pi = 0.0147$, $h = 0.9007$; Adams and Rosel, 2006). Nuclear genetic diversity, measured as population-wide multilocus heterozygosity ($sMLH = 0.995$) was normally distributed with little difference across sampled regions. Additionally, we found low levels of inbreeding and relatedness across the sample set, which suggests that genetic diversity is currently not of concern for this population. However, more accurate estimates of genetic diversity and inbreeding in AWSD, as well as predictions of how the species may respond to future environmental changes, could be achieved via whole genome sequencing and should be considered a sensible target for future studies. This would generate measures such as genome wide nucleotide diversity and runs of homozygosity. These data could be used to estimate historical effective population size (N_e) and model historical responses to climate change events, which can provide insight into potential responses to future changes (Louis *et al.*, 2020; Foote *et al.*, 2021). Alternatively, for regular monitoring of population genetic responses to environmental change, targeted panels of SNP markers could be derived from this study as a more cost-effective approach to species conservation management.

Relatedness

Pairwise measures of identity by decent across 90 AWSD showed low levels of individual relatedness overall. Nevertheless, we identified four pairs of first-degree relatives, two of which are likely to be mother and calf that stranded together. Generally, it is interesting to note that across a total of eight multiple stranding or group-sampling events included

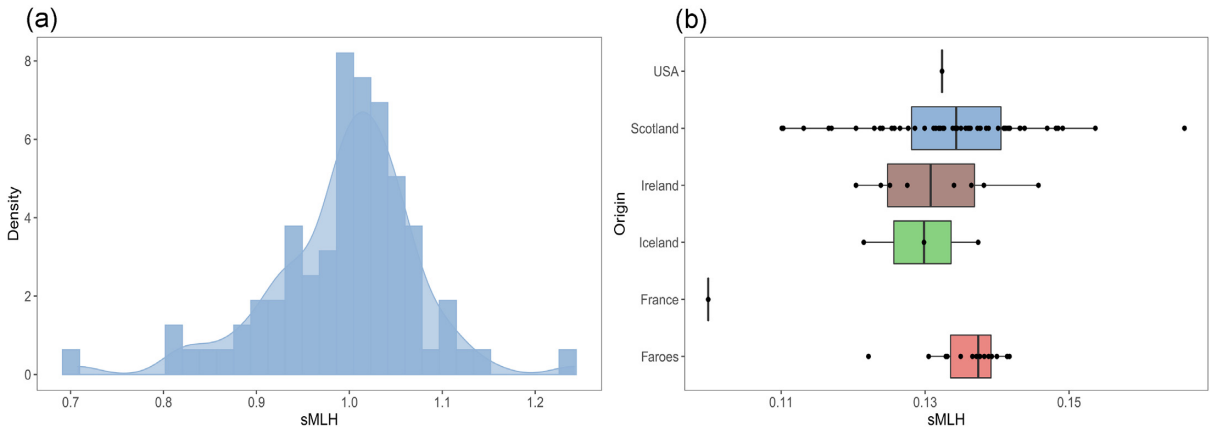

Figure 3. (a) Distribution of sMLH across 86 AWSDs. (b) Distributions of sMLH across the six sampled regions. Centre lines of the boxplots reflect the median, bounds of the boxes extend from the first to the third quartile, and upper and lower whiskers reflect variability outside the interquartile range.

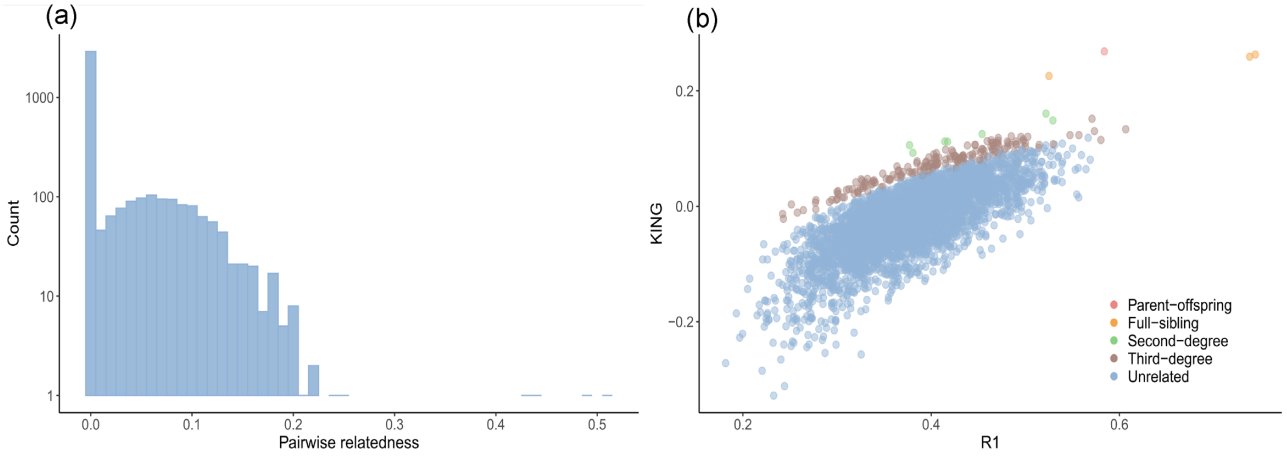

Figure 4. (a) Distribution of genome-wide pairwise relatedness (PI_HAT) across 90 AWSD based on 392 maximally informative SNPs. (b) R1 relatedness coefficient plotted against KING robust kinship for all possible pairings across 90 AWSD, with classification into relatedness categories (colours) based on *Z*-scores, as described in Manichaikul *et al.* (2010).

in the sample set within this study, so few related individuals could be identified. This is consistent with the lack of observed population genetic structure and with previous studies on the social structure of groups of AWSD, which support a fission–fusion dynamic and absence of kin-associated social structure among adult specimens (Mirimin *et al.*, 2011; Pugliares-Bonner *et al.*, 2021); a model which is corroborated through our high-resolution data on pairwise relatedness measures. Altogether, no signature of kin-associated grouping in adult conspecifics was detected, implying low importance of kinship-based social structure. This supports the high dispersal behaviour, which suggests limited tendencies towards aggregation of family groupings, and thus, favourable conditions for geneflow.

Implications for conservation

Conservation strategies often incorporate MUs, which can be delineated by population genetic structure (Funk *et al.*, 2012; Hoban *et al.*, 2021). Our results on the broad-scale connectivity in AWSD suggests the species would be most appropriately managed as a single range-wide MU. However, trends in distribution, seasonality, or increased mortality of a species can inform management strategies that specifically target observed issues, such as the need to mitigate anthropogenically mediated threats (IJsseldijk *et al.*, 2020). It is therefore important to evaluate both genetic and non-genetic factors when assessing management strategies. Given the limited data on non-genetic factors for AWSD, implementing our results on AWSD connectivity in future management strategies would benefit the population by emphasising on conservation of contemporary genetic diversity. Nevertheless, a supplementation of the SNP dataset with additional western North Atlantic individuals should be considered a sensible target to reinforce the results presented here.

To successfully manage this population, we encourage international and national consortia such as ASCOBANS, NAMMCO, and NOAA to reassess the stock status of AWSD based on the findings presented in this study and acknowledge the range-wide connectivity of the species when implementing management strategies. Additionally, conducting further investigations of life history, abundance, and distribution alongside monitoring the extent and the impact of an-

thropogenic threats and climate change on the long-term survival of this species, should be prioritized as areas of future research.

Conclusion

We used a combination of high-resolution genomic and classical population genetic DNA markers to assess structure and diversity in AWSDs (*L. acutus*), across much of the species' range. We describe strong regional connectivity based on an absence of detectable population structure and low familiar relatedness, indicating species-wide panmixia. This result suggests the need for coordinated international management, alongside efforts to increase our understanding of the genetics, life history, and ecology of one of the most abundant cetacean species in North Atlantic waters. Focus should be given to both widening research and monitoring efforts on free-ranging individuals and an efficient exploitation of marine strandings as a data source to aid in addressing future research questions.

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Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of interest

None declared.

Author contributions

M.A.G.: conceptualization, methodology, formal analysis, visualization, investigation, writing—original draft, writing—review & editing, and data curation; E.H.: conceptualization, methodology, supervision, validation, and writing—review & editing; A.B.: conceptualization, project administration, resources, supervision, and writing—review & editing; C.L.: investigation and writing—review & editing; B.M., D.W., and N.D.: resources and writing—review & editing; E.R. and M.D.: resources; R.O.: conceptualization, funding acquisition, project administration, supervision, validation, and writing—review & editing.

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Data availability

Mitochondrial control region sequences are available on NCBI GenBank (OQ572550–OQ572557). Note that due to longer fragment size of the generated mtDNA sequences, we provide two more haplotypes here than presented in the study after trimming. Raw DarTseq reads can be accessed on the European Nucleotide Archive (PRJEB60155). All code for file processing and analyses is available on GitHub (https://github.com/MarcGose/AWSD_PopGen).

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