Agenda Item 4	Special Species Session: Atlantic White-Sided Dolphin Introduction and Conservation Status
Document Inf.4.1.a	**Phylogeography and Population Dynamics of the White-Sided Dolphin in the North Atlantic**
Action Requested	• Take note
Submitted by	Banguera-Hinestroza et al.

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RESEARCH ARTICLE

Phylogeography and population dynamics of the white-sided dolphin (*Lagenorhynchus acutus*) in the North Atlantic

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Abstract Highly mobile species in the marine environment may be expected to show little differentiation at the population level, but this is often not the case. Instead cryptic population structure is common, and effective conservation will require an understanding of how these patterns evolve. Here we present an assessment from both sides of the North Atlantic of differentiation among populations of a dolphin species that inhabits mainly pelagic waters, the Atlantic white-sided dolphin. We compare eleven putative populations in the western and eastern North Atlantic at mtDNA and microsatellite DNA loci and find reduced nucleotide diversity and signals for historical bottlenecks and post-bottleneck expansions in all regions. We calculate expansion times to have occurred during the early Holocene, following the last glacial maximum (LGM). We find evidence for connectivity among populations from either side of the North Atlantic, and differentiation between putative populations in the far northeast compared with all other areas sampled. Some data suggest the possibility of separate refugia during the LGM explaining this pattern, although ongoing ecological processes may also be a factor. We discuss the implications for developing effective programs of conservation and management in the context of ongoing anthropogenic impact.

Keywords Phylogeography · Population structure · North Sea · Population expansion

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Introduction

Panmixia is a reasonable expectation for highly mobile species distributed in the open ocean (or in pelagic offshore waters). There are few obvious boundaries to gene flow, and there are examples of panmixia or isolation by distance on a large geographic scale for various marine fish and invertebrate species (Garber et al. 2005; Knutsen et al. 2007; Palm et al. 2009; White et al. 2009, 2010). Connectivity in the marine environment is often promoted by current systems carrying gametes or larvae long distances, however the same systems can sometimes generate barriers to gene flow (e.g. Shaw et al. 2004; Knutsen et al. 2007). There are also examples of habitat characteristics correlating to population structure in fish species, though the degree of differentiation is often small, for example for black-spot bream (*Pagellus bogaraveo*; Stockley et al. 2005) and European flounder (*Platichthys flesus*; Hemmer-Hansen et al. 2007).

Marine mammal species often show population genetic structure, sometimes on a fine geographic scale, and in many cases this structure is cryptic (see review in Hoelzel 2009). For delphinid cetaceans, structure is typically most evident in species with a coastal distribution (e.g. Natoli et al. 2005; Banguera-Hinestroza et al. 2010; Moller et al. 2011), and there are sometimes oceanographic or geographic boundaries apparently isolating regional populations (e.g. Natoli et al. 2005). In other cases there is evidence that climatic cycles have influenced the establishment and dynamics of these populations (e.g. Hoelzel et al. 2007; Banguera-Hinestroza et al. 2010; Amaral et al. 2012). For pelagic species, the evidence for population structure can be much weaker (e.g. Natoli et al. 2006; Mirimin et al. 2009; Moura et al. 2013). In all cases population genetic data are essential for the development of effective conservation strategies, as well as understanding the mechanisms that generate structure, especially for species where there are no obvious boundaries to gene flow. Here we investigate the population genetics of a pelagic dolphin species, the Atlantic white-sided dolphin (*Lagenorhynchus acutus*, Gray 1828), typically found in temperate and sub-polar waters (Mikkelsen and Lund 1994; Couperus 1997; Reeves et al. 1999; Weinrich et al. 2001; Evans et al. 2003; Evans and Smeenk 2008), and with a distribution range restricted to the North Atlantic (from New England to West Greenland in the west, and from East Greenland, Iceland, British Isles, the North Sea and Norway in the east; Gaskin 1992; Evans and Smeenk 2008).

Little is known about population sizes, ecology, behaviour and life history of the Atlantic white-sided dolphin, with most studies being based on short-term data, or surveys targeting other species (e.g. Evans 1992; Northridge et al. 1997; Reeves et al. 1999; Hammond et al. 2002; Evans et al. 2003; Reid et al. 2003; Evans and Smeenk 2008; Hammond 2008; but see Waring et al. 2013 for some improved, regional census data). Information from sightings, strandings and incidental takes has suggested that *L. acutus* should be divided into three population stocks in the Western North Atlantic (Gulf of Maine, Gulf of St. Lawrence and Labrador Sea; Palka et al. 1997). However, this stock division remains controversial (Weinrich et al. 2001). Mikkelsen and Lund (1994) suggested the existence of a single population of this species across its geographic range, based on the lack of phenotypic differences among skulls of 228 specimens from the eastern and Western North Atlantic. In contrast to the proposal by Palka et al. (1997), these authors did not find evidence to subdivide populations into a northern and southern stock in either of the two areas studied, nor into western and eastern North Atlantic stocks. Here we use the term 'stock' in the context of management objectives for the protection of diversity among populations.

The distribution of this species coincides with regions of major fisheries in the eastern and western North Atlantic, and there is evidence for impact through by catch (Alling and Whitehead 1987; Reeves and Leatherwood 1994; Couperus 1997; Morizur et al. 1999; Reeves et al. 1999; Waring et al. 2006; Evans and Smeenk 2008). In addition, mass strandings (see Bogomolni et al. 2010) and direct exploitation have also been identified as threats for this species. For example, direct catches are common in the Faroe Islands, where takes in the traditional drive fisheries can number more than 500 dolphins in 1 year (Bloch and Mikkelsen 2009), and in southwest Greenland where the annual catch has been estimated at approximately 50 individuals (Reeves et al. 1999; Reeves and Leatherwood 1994). It is not known whether these harvests pose a threat to populations since, as indicated above, comprehensive population size estimates do not exist for most of the North Atlantic. Furthermore, little is known about their conservation status, in particular their effective population size, life history and conservation management stock boundaries.

Given this species' high mobility and pelagic distribution, it may be expected that it would show little evidence of population structure across the species range. However, various studies on other small cetacean species have suggested an influence of recent climatic cycles on the structure of re-expanding populations in the North Atlantic and North Sea (e.g. Tolley et al. 2001; Banguera-Hinestroza et al. 2010; Fontaine et al. 2010). Therefore, in this study we use genetic markers to test hypotheses about the pattern of connectivity for this species across the North Atlantic, and the potential for re-expansion following the last glacial maximum (LGM) having contributed to the evolution of white-sided dolphin population structure. In particular, we test the hypothesis that this species, adapted to pelagic habitat, will show panmixia across a broad geographic range. We also test the hypothesis that like other cetacean

species in the North Atlantic, there will be a signal for population expansion since the LGM, and that this may have contributed to current population structure.

Materials and methods

Sample collection

Atlantic white-sided dolphin tissue and teeth were collected from the western and eastern North Atlantic. Samples from the Eastern North Atlantic (N = 256) belong to different geographic locations in Western Ireland, Northwest British Isles, East Scotland, Shetland Isles, Northern North Atlantic (Faroe Islands and Iceland), Southern North Sea, Denmark, and Southern England. Samples from the Western North Atlantic (N = 88) belong to two putative modern populations (Maine and Massachusetts) and one nineteenth Century population from Massachusetts (all other samples are from recent collections; mostly from the 1990s or 2000s). Bone and teeth samples, as well as skin samples from living and stranded dolphins were obtained through cooperative agreements with a number of museums and institutions (see Table S3).

DNA extraction

Total genomic DNA from tissue samples was extracted following the procedure described by Hoelzel and Green (1998). Bone and teeth samples were cleaned with a 10 % solution of bleach for 2 h; and after being rinsed with water and placed in 95 % ethanol for 2 h, they were dried overnight at 37 °C and then placed under ultraviolet light for 20 min prior to extraction. Teeth or bones were ground using a Mikro-Dismembrator S (©Sartorius). They were then digested in 2 ml lysis solution (85 % EDTA (0.5 M, pH8 stock), 10 % Tris–HCl (1 M pH 8 stock), and 5 % SDS (1 %w/v stock) for 24 h at 55 °C. After digestion, the DNA was extracted using a Qiagen PCR purification kit, following the protocol recommended for cleaning PCR products. The samples were diluted in 0.1 mM Tris–EDTA buffer and placed at −20 °C until use. All extractions were conducted with disposable equipment and extraction and PCR controls were run to detect and minimise any sample contamination. Extractions were undertaken in an ancient DNA facility, separate from the modern lab.

Mitochondrial control region (mtDNA) amplification and sequencing

The mtDNA control hyper-variable region 1 (HVR1; 322 bp) was sequenced for a total of 344 individuals in the forward direction. Amplifications were conducted under the following cycle conditions: 94 °C 6 min followed by 35 cycles of 94 °C 30 s (45 cycles in teeth and bone samples), 54 °C 45 s and 72 °C 45 s. A 600 bp fragment was amplified when possible using universal primers MTCRF (5′-TTC CCC GGT CTT GTA AAC C-3′) and MTCR-R (5′-ATT TTC AGT GTC TTG CTT T-3′), from Hoelzel and Green (1998). This fragment did not amplify in bone and teeth samples; thus an internal reverse primer was used to amplify the smaller fragment (322 bp) (MACR 5′ CGGCATGGTGATTAAGCT), and all individuals were compared at this shorter sequence. After amplification, samples were purified using Qiagen PCR purification columns (Qiagen, Inc.) and were directly sequenced using an ABI 377 automated sequencer. A subset (57 %) of sequences was replicated by PCR and sequencing to ensure accuracy, and all sequencing was in the forward direction. Approximately 20 % of replicated sequences were replicated from new extractions. The sequences were aligned using the Clustal X programme (1.83) from Thompson et al. (1997) using default parameters, and visualised to confirm base calls using the programme Chromas Pro (www.technelysium.co.au).

mtDNA analysis

Regional samples

Samples were initially divided into eight geographic zones in the eastern North Atlantic: Western Ireland (WRL; N = 80), North West British Isles (NWBI; N = 35), East Scotland (ESC; N = 31), Shetland Isles (SHT; N = 20), Northern North Atlantic (NNA; N = 52) Southern North Sea (SNS; N = 15), Denmark (DMK; N = 14) and Southern England (SGL; N = 9). Samples from the Western North Atlantic were divided into three regional samples: Western ancient (WNAanc; N = 26), Western Massachusetts (WNAma; N = 29) and Western Maine (WNAmn; N = 33) (Figs. 1, 2). After population structure analyses (see results), the following samples were pooled: WRL and NWBI (with the combined sample being designated W-ENA; N = 115), DMK and SNS (combined sample designated 'North Sea'; N = 29), WNAma and WNAmn (designated WNA; N = 62) and ESC and SHT (designated E-ENA; N = 51). Samples from WNAanc and NNA were kept as separate populations. In addition, samples from Southern England (SGL) were included in the analysis but excluded from most interpretations due to the small number of samples available for this region. All population locations and pooled sample sets are illustrated in Figs. 1, 2. Samples that represent joint populations and samples of Western North Atlantic origin are mentioned hereafter with their acronyms.

Genetic diversity and population differentiation

The selection of the best-fit models of nucleotide substitution and estimated Ti:Tv ratio was carried out using jModelTest (Posada 2008). The best model was selected using the Akaike Information Criterion (AIC) as recommended by the authors (Posada and Buckley 2004). The extent of genetic variation in the control region was assessed by examining both haplotype (*h*) and nucleotide diversity (π), using Arlequin v 3.5.1.2 (Excoffier and Lischer 2010). The degree of genetic differentiation among geographic samples was determined using an Analysis of Molecular Variance (AMOVA) as implemented in Arlequin v 3.5.1.2 (Excoffier and Lischer 2010). The variance components of gene frequencies were partitioned between geographic regions (pooled groups, see above): among regional populations within groups; and within populations. The differentiation between populations was quantified using the F_{ST} index (based only on haplotype frequencies), the Φ_{ST} index (based on both genetic distances and haplotype frequencies) and the non-differentiation exact test, analogous to a Fisher exact test, which tests the hypothesis of a random distribution of different haplotypes among populations (Wright 1951; Excoffier et al. 1992; Raymond and Rousset 1995; Goudet et al. 1996). The statistical significance of fixation statistics was tested using a non-parametric permutation approach with 10,000 permutations, and 100,000 Markov steps in the exact test. Given that transversions and deletions could be of evolutionary importance, analyses were run giving these changes twice the weight of transitions, and compared against the actual Ti:Tv ratio (20:1) and no weighting (all transitions). All weightings produced the same results. The power available to detect structure was tested using the program PowSim (Ryman and Palm 2006) as described for organelles (mtDNA) in Larsson et al. (2009). An Ne of 1,000 was set and the generations (t) of drift adjusted to test different levels of F_{ST}. The power was determined as the proportion of significant outcomes based on the Fisher Exact test. A median joining network was generated using the software Network version 4.5.0.0 (Bandelt et al. 1999).

Mismatch distribution and neutrality test

The distribution of the number of observed differences between pairs of DNA sequences (mismatch distribution; Rogers and Harpending 1992) was used as an assessment of demographic history of the population, using the program Arlequin v 3.5.1.2 (Excoffier and Lischer 2010). The calculations were carried out following the principles explained by Schneider and Excoffier (1999) and using a coalescent algorithm modified from Hudson (1990). The hypothesis that the observed data fit the sudden expansion model was tested using the sum of square deviations (SSD) (Schneider and Excoffier 1999) and the raggedness index (Harpending 1994). The confidence intervals for these parameters are obtained by a parametric bootstrap approach that assumes that the data are distributed according to the sudden expansion model.

The coalescence time of expansion in years (t) was calculated using the relationship $\tau = 2\upsilon t$, where τ represents the mode of the mismatch distribution (in units of evolutionary time) and υ is the mutation rate for the sequence used ($\mu = 5 \times 10^{-7}$; Ho et al. 2007). The υ value was calculated as suggested by Rogers and Harpending (1992), using the formula $\upsilon = \mu k$, where μ is the mutation rate per nucleotide and k is the number of nucleotides evaluated.

Fu's test (Fu 1997) and Tajima's test (Tajima 1989) were used to evaluate the demographic history of *L. acutus* populations. The significance of Tajima's D was determined by generating 1,000 random samples under the assumption of selective neutrality with a coalescent simulation algorithm (Hudson 1990). Both tests were evaluated using Arlequin v 3.5.1.2 (Excoffier and Lischer 2010). Mismatch distributions were run with 1,000 replicates for the parametric bootstrap using DNAsp v 5.10.00 (Librado and Rozas 2009).

Microsatellite amplification and analysis

In order to determine genetic variability and differentiation for biparental gene flow among geographic samples, four regions: Shetland Isles (SHT; N = 14), East Scotland (ESC; N = 20), North West British Isles (NWBI; N = 17) and Western Ireland (WRL; N = 25), were evaluated and compared using 10 microsatellite cetacean-specific loci (see Table S1 for a list and citations). A subset of the tooth samples from WNA (N = 21) were included in order to test differentiation between both sides of the North Atlantic using five loci (Table S1). Suitable materials were not available for the remaining sample regions. A reduced number of loci were screened due to the difficulty with amplifying microsatellite DNA loci from the tooth samples. A proportion of samples (10 %) were replicated 2–4 times to ensure accurate genotyping, and any ambiguous genotypes were discarded. The PCR reactions were run using 20–50 ng of DNA (10 µl for teeth samples). The PCR conditions for D08, D22, GT136, FCB4, Igf1, KWM2a and texvet5 were: denaturation at 95 °C for 5 min, 35 cycles at 94 °C for 45 s, 1 min 30 s at locus-specific annealing temperature (Table S1), extension at 72 °C for 1 min 30 s. PCR conditions for Ev37 and Ev94 were as described in Valsecchi and Amos (1996). PCR conditions for TexVet 7:95 °C for 5 min, 35 cycles at 94 °C for 40 s, 1 min 30 s at 59 °C and 1 min 40 s at

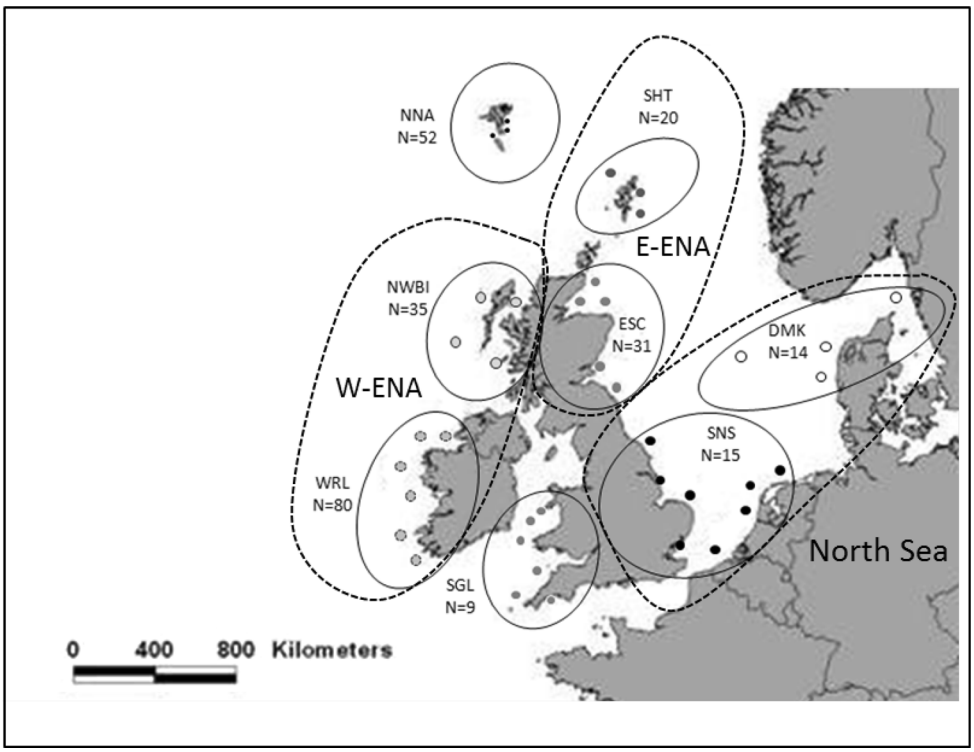

Fig. 1 Eastern North Atlantic regional samples, showing both local population sample sites (*solid circles*) and combined sample sets (*dashed circles*) for analyses. *Dots* indicate sampling locations

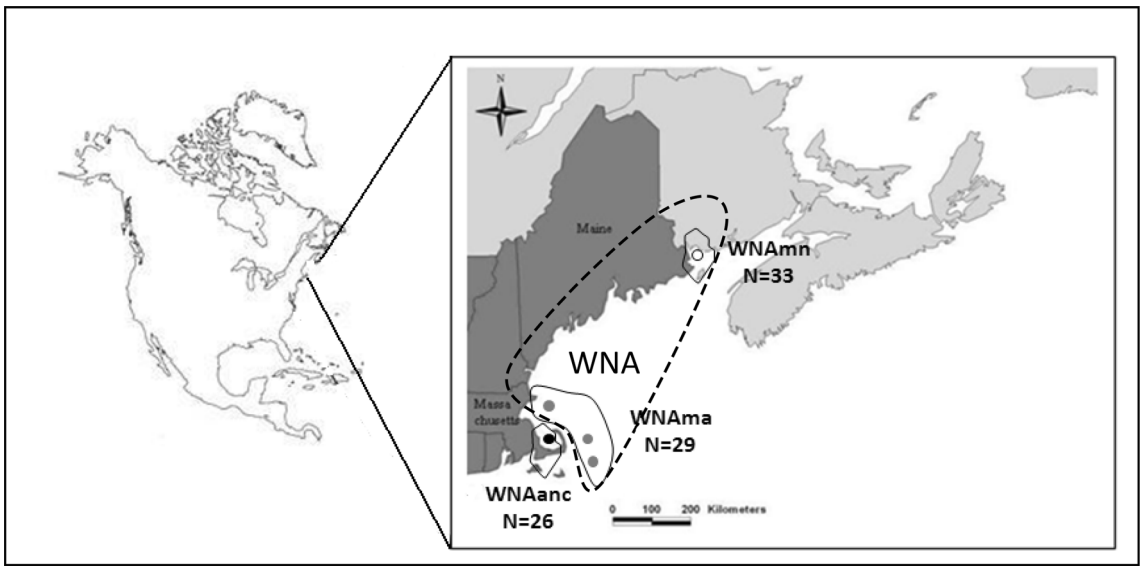

Fig. 2 Western North Atlantic regional samples showing local (*solid circles*) and combined (*dashed circles*) sample sets. *Dots* indicate sampling locations

72 °C. PCR conditions for Gt011: 95 °C for 3 min, 35 cycles at 94 °C for 1 min, 1 min 30 s at 59 °C and 10 s at 72 °C.

After amplification, microsatellite loci were run on polyacrylamide gels using a 377 ABI automated sequencer and analyzed using ABI GenescanTM and Genotyper TM with Rox used as the size standard. To identify and correct genotyping errors (i.e. to check evidence for scoring error due to stuttering, large allele dropout or evidence for null alleles), the program MicroChecker (Van Oosterhout et al. 2004) was used. Microsatellite variation was examined by estimating the number of alleles per locus, gene diversity and allelic richness using the programme FSTAT 2.9.3 (Goudet 2001). Regional differences in frequencies and

deviation from the Hardy–Weinberg equilibrium were tested using the GENEPOP 1.2 programme (Raymond & Rousset 1995) and Arlequin 3.5.1.2 (Excoffier and Lischer 2010). Linkage disequilibrium to test the null hypothesis of independence between genotypes was tested using FSTAT 2.9.3 (Goudet 2001). Population differentiation was assessed using the fixation index (F_{ST}) approach of Weir and Cockerham (1984) implemented in Arlequin. The M-ratio statistic was used to test for signals for population bottlenecks (Garza and Williamson 2001, run in Arlequin using default parameters), chosen in preference to alternatives based on the outcome of various simulation studies (e.g. Williamson-Natesan 2005; Peery et al. 2012). Type 1 errors are corrected using the Boferroni method.

Results

MtDNA analysis

Genetic variation at the mtDNA control region

Sixty-four haplotypes (accession numbers KJ456520–KJ456583) among the 344 samples were found for the 322 bp fragment among all geographic regions (eastern and Western North Atlantic) defined by 44 polymorphic sites, 26 of which were parsimony informative. Replicate samples revealed no errors. Amongst the eight geographic regions in the eastern North Atlantic (see above), 55 haplotypes were found with unique haplotypes in the Northern North Atlantic (7), Southern North Sea (4), Denmark (1), East Scotland (3), NW British Isles (5) and Western Ireland (15). In the Western North Atlantic, a total of 24 haplotypes were identified, with 8 unique haplotypes for this region (see illustration in the network tree shown in Figure S1). Over all samples, haplotypic (gene) diversity ($h = 0.927 \pm 0.007$; Table 1) was high, but nucleotide diversity values were relatively low ($\pi = 0.00891 \pm 0.00028$). Western North Atlantic ancient samples were excluded from these calculations to avoid bias in the analyses given that they belong to a population from the early 19th century.

Differentiation among populations

The initial analyses, performed by regions using F_{ST}, and Φ_{ST}, showed few significant differences among the initial eight sampling regions (Table 2). We therefore pooled areas that were not significantly differentiated, but represented contiguous areas separated from other similar areas by distance or natural barriers (see Figs. 1, 2). In the North Sea northern and southern sampling groups were retained reflecting ecological and genetic divisions seen for other cetacean species (e.g. de Luna Lopez et al. 2012). East Scotland (ESC) and the Shetland Isles (SHT) each showed significant differentiation compared with a number of other regions, but not with each other (see Table 2). The sample size for southern England (SGL) was too small (N = 9) for strong inference and there was no clear group with which it should be pooled, and so it was left on its own. The northern North Atlantic (NNA) sample was differentiated from both the E-ENA and the North Sea samples, and therefore retained as a separate population (Table 3; Fig. 1).

F_{ST} Comparisons based on pooled regions showed that E-ENA samples (Fig. 1) are significantly differentiated from NNA, W-ENA, and WNA (Table 3, Figs. 1, 2). Differentiation between E-ENA and both NNA and WNA was supported by the Exact test, which also suggested some degree of differentiation between North Sea samples and samples from NNA and E-ENA (Table 3). No differentiation was seen across the North Atlantic (e.g. comparing WNA against W-ENA; Table 3). The power analysis indicated that an F_{ST} of 0.008 or larger could have been detected with a confidence of 95 %, given the data available. An Analysis of Molecular Variance (AMOVA) using conventional F-Statistics from haplotype frequencies showed that 98.98 % of the variance could be explained as a result of the differences within populations: $F_{SC} = 0.00335$ ($P = 0.023$); $F_{ST} = 0.01019$ ($P = 0.024$); $F_{CT} = 0.00686$ ($P = 0.009$).

Mismatch distribution analysis and neutrality tests

The mismatch distributions show a clear unimodal shape in most populations that were analyzed (Fig. 3). The variance (SSD) and the small, non-significant values of the raggedness index (r) suggested that the curves did not differ significantly from that expected under a model of sudden expansion. The exception was the Shetland Isles, where the raggedness index was higher than in other populations and significant (0.135, $P = 0.022$), rejecting the hypothesis of sudden expansion in this region (Table 4).

The sudden expansion in most *L. acutus* populations was also corroborated by the negative and significant values of Tajima's D, with the exception of WNAanc (0.748, $P > 0.8020$) and Shetland Isles (0.228, $P > 0.622$; Table 4) where values were positive and not significant. Fu's statistics showed large negative and highly significant values in all populations, except for the WNA anc (-1.713, $P > 0.197$) and Shetland Isles ($Fs = -1.181$, $P > 0.27$; Table 4), suggesting different demographic histories for these regions. However, when combining samples from the Shetland Isles and East Scotland (E-ENA), the mismatch distribution graph was unimodal (Fig. 3), values of Raggedness index and SSD were small and not significant (0.00578, $P > 0.13$; 0.0349, $P > 0.281$ respectively), and Tajima's D and Fu's statistic were negative and significant (-0.668, $P > 0.0423$; -8.391, $P > 0.00001$ respectively). The expansion time in *L. acutus* populations, calculated from the parameter τ from the

Table 1 Genetic diversity estimates at mtDNA in *L. acutus*

Populations	Sample size	Polimorphic sites	Number of haplotypes	*h*: Haplotype diversity	π: Nucleotide diversity
NNA	52	20	21	0.9186 ± 0.0195	0.0087 ± 0.0052
WNAma	29	14	14	0.8990 ± 0.0360	0.0094 ± 0.0056
WNAmn	33	20	17	0.9280 ± 0.0266	0.0092 ± 0.0055
WNA (WNAma + WNAmn)	62	23	22	0.9159 ± 0.0199	0.0093 ± 0.0055
WNAanc	26	10	9	0.8862 ± 0.0362	0.0100 ± 0.0059
SNS	15	15	12	0.9619 ± 0.0399	0.0125 ± 0.0074
DMK	14	13	12	0.9780 ± 0.0345	0.0116 ± 0.0070
North Sea (SNS + DMK)	29	20	19	0.9655 ± 0.0189	0.0119 ± 0.0069
ESC	31	18	17	0.9462 ± 0.0210	0.0098 ± 0.0058
SHT	20	9	8	0.8684 ± 0.0410	0.0085 ± 0.0053
E-ENA (ESC + SHT)	51	19	19	0.9286 ± 0.0165	0.0094 ± 0.0055
NWBI	35	13	17	0.9092 ± 0.0329	0.0083 ± 0.0050
WRL	80	28	33	0.9329 ± 0.0149	0.0097 ± 0.0056
W-ENA (NWBI + WRL)	115	31	41	0.9263 ± 0.0139	0.0092 ± 0.0054
SGL	9	9	8	0.9722 ± 0.0640	0.0089 ± 0.0059
Overall	344	44	64	0.9270 ± 0.0070[a]	0.00891 ± 0.0003

Populations names are as follow: *NNA* Northern North Atlantic (Faroe Isles plus Iceland); *NWBI* Northwest British Isles; *WRL* West Ireland; *SGL* South England; *WNAma* Western North Atlantic, Massachussets; *WNAmn* Western North Atlantic, Maine; *WNAanc* Western North Atlantic ancient; *SNS* Southern North Sea; *DMK* Denmark; *ESC* East Scotland; *SHT* Shetland Isles

[a] Over all samples, the genetic diversity and nucleotide diversity values were computed excluding samples from Western Ancient origin

mismatch distributions (Table 4), ranged from ~14,000 to ~9,000 years ago, using a mutation rate of 5×10^7 (Ho et al. 2007). These estimates are consistent with a range expansion after the LGM in the Pleistocene (19,000–14,000 YBP; Pedersen 1983).

Microsatellite data

Genetic variation and differentiation at microsatellite loci

None of the 10 loci showed genotyping errors based on MicroChecker analysis (including sample sets restricted to tooth samples), and replicated samples did not reveal genotyping errors. The genotypic independence between each pair of loci was confirmed using the linkage disequilibrium test. After Bonferroni correction, two loci (EV94 and D08) showed a significant deviation from the Hardy–Weinberg equilibrium expectation in one population (Western Ireland; Table S2). All loci were retained because there was no indication that these deviations biased results (no significant deviation between Western Ireland and other putative populations; see below). The average gene diversity over ten loci (N = 76) was: 0.728 ± 0.387. An average of 10.10 ± 4.228 alleles were found. The average of genetic diversity over loci for Shetland Isles was 0.722 ± 0.397, for East Scotland 0.662 ± 0.355, for NW British Isles 0.747 ± 0.401, and for Western Ireland 0.744 ± 0.424. The Garza & Williamson statistics ranged between 0.424 ± 0.126 and 0.472 ± 0.111. F_{ST} values showed small but significant differentiation only between the Shetland Isles and NW British Isles (0.0158, $P = 0.047$; Table 5). For comparisons against the WNA sample for F_{ST} at 5 loci (with or without EV94, which showed heterozygote deficiency in WNA; Table S1) there were no significant values (ranging from 0.010 to 0.012). Low power is clearly a potential issue, given relatively small sample sizes and few loci.

Discussion

Genetic variability in Atlantic white-sided dolphins

A total of 344 mtDNA control region sequences were obtained from *L. acutus* from the Western and Eastern North Atlantic, and a subset of 102 samples was evaluated with microsatellite loci. Microsatellite gene diversity (0.728 ± 0.387) and the mtDNA haplotype diversity found in this species (overall 0.927 ± 0.007) were similar to values reported for other delphinids (e.g., Pichler and Baker 2000; Cassens et al. 2003; Harlin et al. 2003; Hayano et al. 2004; Natoli et al. 2006; Quérouil et al. 2007), though comparability for microsatellite DNA depends on the set of loci investigated. However, nucleotide diversity was low compared to haplotype diversity, ranging from 0.0087 ± 0.0052 to 0.0119 ± 0.0069. Similar levels of nucleotide diversity have been reported for cetacean populations worldwide (e.g. Bérubé et al. 1998, Pichler and Baker 2000; Parsons et al. 2002; Natoli et al. 2006).

Table 2 F_{ST} (below diagonal) and Φ_{ST} (above diagonal) comparisons among population samples

Regional Samples	NNA	NWBI	WRL	SGL	WNAma	WNAmn	WNAanc	SNS	DMK	ESC	SHT
NNA		−0.01	−0.0077	−0.0307	−0.0081	−0.0154	0.0068	−0.0024	−0.0103	0.0024	**0.051 (0.0198)**
NWBI	−0.0051		−0.0061	−0.0178	−0.0055	−0.0119	0.0051	−0.0086	−0.0205	0.0057	**0.0529 (0.0312)**
WRL	−0.0019	0.0013		−0.0299	−0.0019	−0.0091	0.0105	−0.0079	−0.0112	−0.0032	0.0324
SGL	−0.0267	−0.0122	−0.0313		−0.05	−0.0263	−0.062	−0.063	−0.0584	0.0002	0.0501
WNAma	−0.0012	0.0079	0.0079	−0.0322		−0.0038	−0.0132	−0.0316	−0.0128	0.0248	0.0482
WNAmn	0.0024	0.0009	−0.0019	−0.0207	0.0031		0.0098	0.0028	−0.0221	−0.0108	**0.0467 (0.0384)**
WNAanc	0.0102	0.025	0.0123	−0.0426	0	0.0146		−0.0131	−0.0284	**0.0415 (0.0486)**	0.0518
SNS	0.0156	0.0209	0.0124	−0.0359	−0.0134	0.0222	0.014		−0.0267	0.0142	0.035
DMK	0.0026	0.003	0.0023	−0.0326	0.0015	−0.0112	0.0068	−0.0083		−0.0093	0.0405
ESC	0.0134	**0.02 (0.050)**	0.0099	−0.0205	**0.0321 (0.0125)**	0.0127	**0.0529 (0.0007)**	0.0166	−0.0031		0.0396
SHT	**0.0358 (0.0197)**	0.0242	**0.0232 (0.0443)**	−0.0066	0.0344	**0.0336 (0.0355)**	**0.0573 (0.0123)**	0.0344	0.0261	0.0274	

Fst values and Φ_{ST} values were calculated using 10,000 permutations. Values in bold are significant at the 0.05 level after Bonferroni correction. *Populations*: *NNA* Northern North Atlantic (Faroe Isles plus Iceland), *NWBI* Northwest British Isles; *WRL* West Ireland; *SGL* South England; *WNAma* Western North Atlantic, Massachussets; *WNAmn* Western North Atlantic, Maine; *WNAanc* Western North Atlantic ancient; *SNS* Southern North Sea; *DMK* Denmark; *ESC* East Scotland; *SHT* Shetland isles

In general, a pattern of high haplotypic diversity and low nucleotide diversity is consistent with population expansion, which creates an excess of haplotypes differing by one or a few mutations (Rogers and Harpending 1992). Various authors have noted an association between signals for expansion and past climatic events (e.g., Pleistocene glaciations) that suggest bottlenecked populations in glacial refugia (see Wares 2002; Hewitt 2000, 2004; Banguera-Hinestroza et al. 2010). A rapid expansion from refugial populations may have involved several bottlenecks, with progressive loss of allelic diversity among populations in the postglacial colonized regions (see review in Hewitt 2000). In our study, the possibility of a post-bottleneck population expansion was corroborated by the Tajima's D statistics, the Fu's statistics, and the mismatch distribution analyses in most populations, indicating a likely reduction in population sizes and subsequent expansion.

The fact that much of the diversity in the network phylogeny (Figure S1) is derived from a few dominant haplotypes is also consistent with an expansion signal. Although the signal was not as strong for the Shetland sample, it became stronger when the small, undifferentiated eastern Scotland and the Shetlands population samples were combined. The timing of expansion events based on our analyses would be consistent with expansion from refugia following the LGM (expansion time estimates ranged from 9,000 to 14,000 YBP). Evidence for this was also found for the congener *L. albirostris* in the North Atlantic (Banguera-Hinestroza et al. 2010). Signatures for population bottlenecks were also found for the sample sets analysed for microsatellite DNA loci, with M-ratio values ranging from 0.42 to 0.46 (compared to the proposed cutoff of below 0.67 for a bottleneck signal; Garza and Williamson 2001).

Population structure

Western North Atlantic versus Eastern North Atlantic

No differentiation was found (within the power limits of our analysis) between the Westernmost part of the Eastern North Atlantic and the Western North Atlantic: W-ENA versus WNA. These results agree with aspects of the results reported by Mikkelsen and Lund (1994) who found no craniometrical differences among samples on either side of the North Atlantic. The absence of differentiation between these regions could be explained by the large dispersal capabilities of *L. acutus* suggested by the observation of large aggregations of individuals in the mid-Atlantic (e.g. Selzer and Payne 1988). This could prevent differentiation due to ongoing gene flow across populations, as has been suggested in other marine organisms with high dispersal

Table 3 F_{ST} values (below diagonal) and Non-differentiation exact P values (above diagonal) for grouped population comparisons at mtDNA

	NNA	W-ENA	WNA	WNAanc	E-ENA	North Sea
N	52	115	62	26	51	29
NNA		0.744 ± 0.027	0.197 ± 0.021	0.188 ± 0.013	**0.012 ± 0.003**	**0.044 ± 0.005**
W-ENA	−0.0032		0.301 ± 0.023	0.487 ± 0.013	0.281 ± 0.019	0.153 ± 0.013
WNA	−0.0001	0.0022		0.416 ± 0.009	**0.002 ± 0.001**	0.177 ± 0.012
WNAanc	0.0102	0.0156	0.0068		**0.0002 ± 0.0002**	0.188 ± 0.009
E-ENA	**0.0155**	**0.0103**	**0.0191**	**0.0473**		**0.043 ± 0.004**
	(0.033)	**(0.043)**	**(0.012)**	**(0.001)**		
North Sea	0.0105	0.0102	0.0014	0.0110	0.0111	

F_{ST} values were calculated using 10,000 permutations and non-differentiation exact P values were performed using 100,000 markov steps. Values in bold are significant at level 0.05 after Bonferroni correction. *Populations*: *NNA* Northern North Atlantic; *W-ENA* NW British isles plus Western Ireland; *SGL* South England; *WNA* Western North Atlantic; *WNAanc* Western North Atlantic ancient; *E-ENA* Shetland isles plus East Scotland; *North Sea* Southern North Sea plus Denmark

capacities (Bremer et al. 2005; Ely et al. 2005, White et al. 2010).

In contrast to the absence of differentiation among open Atlantic samples, some degree of differentiation was found between Atlantic populations (WNA, W-ENA and NNA) and putative populations in the easternmost part of the North Atlantic (Shetland Isles and North Sea) (see Tables 2, 3, 4, 5). Differentiation between E-ENA versus NNA and E-ENA versus WNA was supported based on mtDNA data by F_{ST} and the exact test; whereas differentiation between E-ENA and W-ENA was only supported by F_{ST}. Differentiation between the North Sea (Denmark plus Southern North Sea) versus NNA and North Sea vetsus E-ENA was only supported by the exact test. When analyzing individual regions, both Φ_{ST} and F_{ST} showed evidence of differentiation between Shetland and NNA (see Table 2); Φ_{ST} also showed differentiation between Shetland and NW British isles, but this differentiation was not supported by F_{ST}. It was supported by the comparison of these sites based on 10 microsatellite DNA loci, although sample sizes were small (Table 5). There was no indication that the ancient WNA sample was differentiated from other WNS samples, suggesting spatial and temporal continuity, given our level of resolution.

On balance it was apparent that there was some level of differentiation between dolphins sampled east and north of Scotland and samples collected further west, which had also been seen for bottlenose dolphin populations in this region (*Tursiops truncatus*; Parsons et al. 2002; Nichols et al. 2007). However, this is unexpected for *L. acutus* due to the fact that they mostly inhabit the shelf edge entering the northern and central North Sea mainly in late summer (July–September, see Evans et al. 2003). Although sightings data do not suggest a resident population in the North Sea, their seasonal presence could indicate a coherent migratory stock, which would still be consistent with the genetic data. More information on distribution, abundance and movement patterns will be needed to help resolve this question.

One possible explanation for differentiation between a population in the North Sea and the rest of the North Atlantic could be the differential effect of glaciated epochs in different regions. For example, it has been suggested that during the LGM the ice sheet covered much of the North Sea, with the exception of the southern regions (see Fig. 1, in Siegert and Dowdeswell 2004), which could have been the only available habitat for dolphin species in the eastern North Atlantic and resulted in a refugial population separate from populations further west.

Conclusions

The balance of evidence indicates that there is an association between reduced variation and extinction risk (Frankham 2005). However, after strong bottleneck events, the survival of populations may depend on non-genetic factors and their capacity to promote recovery in a post-bottleneck phase (e.g. Weber et al. 2000). Following population reductions in the past (likely during glacial epochs, as suggested previously for the congener *L. albirostris* and other cetacean species in the North Atlantic; see Banguera-Hinestroza et al. 2010 and references therein), *L. acutus* evidently recovered quickly. The data suggest connectivity across the North Atlantic, although this may reflect a shared refugial population and little time for differentiation post expansion. At the same time, there is differentiation between the northeast and the rest of the Atlantic. Although the sample sets differed, data for *L. albirostris* also suggested a post-glacial expansion and isolation of a population in the northeastern Atlantic (in this case, a sample off Norway was isolated from samples from the UK and the Netherlands; Banguera-Hinestroza et al. 2010). Similar signals for expansion in the North Atlantic (Tolley et al.

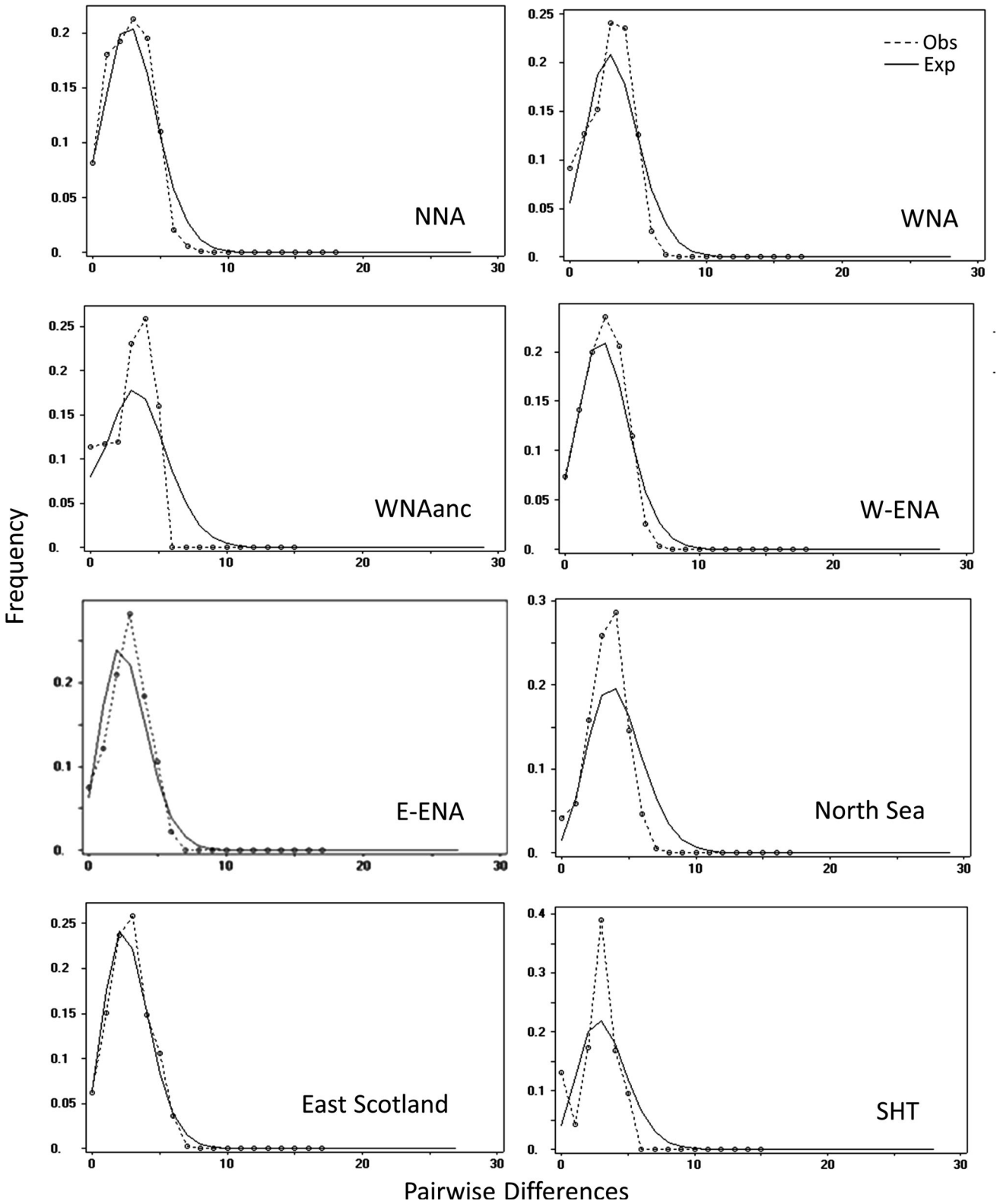

Fig. 3 Mismatch distributions in putative populations as labelled (*c.f.* Figs. 1, 2)

Table 4 Parameters of mismatch distribution for a model of sudden expansion in *L. acutus*, expansion time and neutrality tests

Populations	NNA	WNAma	WNAmn	WNAanc	SNS	DMK	ESC	SHT	NWB	WRL	SGL	Mean	SD
Sample size	52	29	33	26	15	14	31	20	35	80	9	31	20
Statistics													
τ	3.1934	3.6367	3.3965	4.0664	4.6406	3.9805	3.2637	3.3125	2.8125	3.4414	3.0293	3.5249	0.5252
τ 5 %	1.5371	1.8008	1.7832	1.8789	3.0117	2.3906	1.9141	1.9023	1.3770	1.9492	1.4082	1.9048	0.4637
τ 95 %	4.6172	5.0742	4.6426	6.3242	6.0586	5.3613	4.1231	4.4473	4.0273	4.3477	4.6250	4.8771	0.7553
SSD	0.0035	0.0111	0.0068	0.0152	0.0200	0.0053	0.0017	0.0453	0.0010	0.0021	0.0334	0.0132	0.0145
SSD *P* value	0.5250	0.1600	0.2520	0.2490	0.1260	0.6210	0.6430	**0.0190**	0.8670	0.4600	0.2350	0.3779	0.2626
Raggedness index	0.0238	0.0370	0.0311	0.0418	0.0927	0.0326	0.0279	0.1352	0.0222	0.0217	0.1505	0.0560	0.0473
Raggedness *P* value	0.6780	0.4280	0.5110	0.4380	0.1080	0.6850	0.6030	**0.0220**	0.8310	0.6610	0.2010	0.4696	0.2613
Expansion time (T)	9917	11294	10548	12629	14412	12362	10136	10287	8734	10688	9408	–	–
Neutrality tests													
Tajima's D	−1.1187	−0.4602	−1.3757	0.7147	−0.5444	−0.6423	−0.8929	0.2283	−0.6275	−1.5408	−0.6645	−0.6295	0.6539
Tajima's D *P* value	**0.0130**	0.0544	**0.0033**	0.2489	**0.0256**	**0.0222**	**0.0191**	0.1437	**0.0420**	**0.0021**	**0.0094**	0.0531	0.0763
Fu's FS test													
FS	−11.9858	−5.6320	−9.0767	−0.8224	−5.9777	−7.2182	−9.0291	−1.1814	−9.5985	−25.5469	−4.5500	−8.2381	6.6944
FS *P* value	**0.00001**	**0.00001**	**0.00001**	0.10950	**0.00040**	**0.00001**	**0.00001**	0.05990	**0.00001**	**0.00001**	**0.00050**	**0.01548**	0.03598

Table 5 F_{st} values for microsatellite loci between ENA regional samples

	Shetland Islands (SHT) (N = 14)	East Scotland (ESC)	NW British Isles (NWBI)
East Scotland (N = 20)	0.0068		
NW British Isles (N = 17)	**0.0158 (0.047)**	0.0054	
Western Ireland (N = 25)	0.0097	0.0069	0.0091

Values were computed using 10 microsatellites loci and 1,000 permutations, values in bold were significant at 0.05 level after Bonferroni correction

2001) and structuring in the eastern North Atlantic (de Luna Lopez et al. 2012) have been described for the harbor porpoise (*Phocoena phocoena*).

The implications for conservation are that populations of *L. acutus* have reduced mtDNA nucleotide diversity throughout its distribution range (likely due to historical demographic events), suggesting possible vulnerability to exploitation (e.g. in bycatch, direct takes and habitat degradation). Further, the northeastern region of the North Atlantic merits separate management, given evidence for isolation of the regional population there (possibly due to a separate refugia being located in that part of the ocean during the LGM) and ongoing impact from the drive fishery in the Faroes (see Introduction). Importantly, this is another cetacean species showing a similar pattern, suggesting the potential for transferable inference about conservation needs for small cetaceans in these regions, and at least the need to consider these factors with further research in the future.

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References

Alling AK, Whitehead HP (1987) A preliminary study of the status of white-beaked dolphins, *Lagenorhynchus albirostris*, and other small cetaceans off the coast of Labrador. Can Field Nat 1012:131–135

Amaral AR, Beheregaray LB, Bilgmann K, Freitas L, Robertson KM, Sequeira M, Stockin KA, Coelho MM, Moller LM (2012) Influences of past climate changes on historical population structure and demography of a cosmopolitan marine predator, the common dolphin (genus *Delphinus*). Mol Ecol 21:4854–4871

Bandelt HJ, Forster P, Röhl A (1999) Median joining networks for inferring intraespecific phylogenies. Mol Biol Evol 16:37–48

Banguera-Hinestroza E, Bjørge A, Reid RJ, Jepson P, Hoelzel AR (2010) The influence of glacial epochs and habitat dependence on the diversity and phylogeography of a coastal dolphin species: *Lagenorhynchus albirostris*. Conserv Genet 11:1823–1836

Bérubé M, Aguilar A, Dendanto D, Larsen F, Notarbartolo di Sciara G, Sears R, Sigurjónsson J, Urban R, Palsbøll PJ (1998) Population genetic structure of North Atlantic, Mediterranean Sea and Sea of Cortez fin whales, *Balaenoptera physalus* Linnaeus 1758): analysis of mitochondrial and nuclear loci. Mol Ecol 7:585–599

Bloch D, Mikkelsen B (2009) Catch history and distribution of white-sided dolphin (*Lagenorhynchus acutus*) of the Faroe Islands. Fródskaparrit, 57, pp 190–198

Bogomolni AL, Pugliares KR, Patchett K, Herzig SM, Harry CT, LaRocque JM, Touhey KM, Moore MJ (2010) Mortality trends of stranded marine mammals on Cape Cod and southeastern Massachusetts between 2000–2006. Dis Aquat Org 88:143–155

Bremer JRA, Mejuto J, Gomez-Marquez J, Boan F, Carpintero P, Rodriguez JM, Vinas J, Greig TW, Ely B (2005) Hierarchical analyses of genetic variation of samples from breeding and feeding grounds confirm the genetic partitioning of northwest Atlantic and South Atlantic populations of swordfish (*Xiphias gladius* L.). J Exp Mar Biol Ecol 327:167–182

Cassens I, Van Waerebeek K, Best PB, Crespo EA, Reyes J, Milinkovitch MC (2003) The phylogeography of dusky dolphins (*Lagenorhynchus obscurus*): a critical examination of network methods and rooting procedures. Mol Ecol 12:1781–1792

Couperus AS (1997) Interactions between Dutch Midwater Trawl and Atlantic White-sidedDolphins (*Lagenorhynchus acutus*) Southwest of Ireland. J Northwest Atl Fish Sci 22:209–218

De Luna Lopez CJ, Goodman SJ, Thatcher O, Jepson PD, Andersen L, Tolley K, Hoelzel AR (2012) Phenotypic and genetic divergence among harbour porpoise populations associated with habitat regions in the North Sea and adjacent seas. J Evol Biol 25(4):674

Ely B, Viñas J, Bremer Alvarado JR, Black D, Lucas L, Covello K, Labrie AV, Thelen E (2005) Consequences of the historical demography on the global population structure of two highly migratory cosmopolitan marine fishes: the yellowfin tuna (*Thunnus albacares*) and the skipjack tuna (*Katsuwonus pelamis*). BMC Evol Biol 5:19

Evans PGH (1992) Status review of cetaceans in British and Irish waters. UK Department of the Environment, London

Evans PGH, Smeenk C (2008) Atlantic White-sided Dolphin *Leucopleurus acutus*. In: Harris S, Yalden DW (eds) Mammals of the British Isles. Handbook, 4th edn. The Mammal Society, Southampton, pp 727–731

Evans PGH, Anderwald P, Baines ME (2003) UK Cetacean status review. Report to English Nature and the Countryside Council for Wales. Sea Watch Foundation, Oxford

Excoffier L, Lischer H (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol Ecol Res 10:564–567

Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131:479–491

Fontaine MC, Tolley KA, Michaux JR, Birkun AJR, Ferreira M, Jauniaux T, Llavona A, Öztürk B, Öztürk AA, Ridoux V, Rogan E, Sequeira M, Bouquegneau JM, Baird JS (2010) Genetic and historic evidence for climate-driven population fragmentation in a top cetacean predator: the harbour porpoises in European water. Proc Royal Soc B 277:2829–2837

Frankham R (2005) Genetics and extinction. Biol Conserv 126:131–140

Fu YX (1997) Statistical neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147:915–925

Garber AF, Tringali MD, Franks JS (2005) Population genetic and phylogeographic structure of wahoo, *Acanthocybium solandri*, from the Western central Atlantic and central Pacific Oceans. Mar Biol 147:205–214

Garza JC, Williamson EG (2001) Detection of reduction in population size using data from microsatellite loci. Mol Ecol 10:305–318

Gaskin DE (1992) Status of the Atlantic white-sided dolphin, *Lagenorhynchus acutus*, in Canada. Can Field Nat 106:64–72

Goudet J (2001) fstat (version 2.9.3): A program to estimate and test gene diversities and fixation indices. Available from http://www.unil.ch/izea/softwares/fstat.html

Goudet J, Raymond M, de Meeüs T, Rousset F (1996) Testing differentiation in diploid populations. Genetics 144:1933–1940

Hammond PS (2008) Small cetaceans in the European Atlantic and North Sea (SCANS II). Final report to the European Commission under contract LIFE04NAT/GB/000245

Hammond PS, Berggren P, Benke H, Borchers DL, Collet A, Heide-Jorgensen MP, Heimlich S, Hiby AR, Leopold MF, Oien N (2002) Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent water. J Appl Ecol 39:361–376

Harlin AD, Markowitz T, Baker CS, Würsig B, Honeycutt RL (2003) Genetic structure, diversity, and historical demography of New Zealand's dusky dolphin (*Lagenorhynchus obscurus*). J Mamm 84:702–717

Harpending RC (1994) Signature of ancient population growth in a low-resolution mitochondrial DNA mismatch distribution. Hum Biol 66:591–600

Hayano H, Yoshioka M, Tanaka M, Amano M (2004) Population differentiation in the pacific white-sided Dolphin *Lagenorhynchus obliquidens* inferred from mitochondrial DNA and microsatellite analyses. Zool Sci 21:989–999

Hemmer-Hansen J, Nielsen EE, Gronkjaer P, Loeschcke V (2007) Evolutionary mechanisms shaping the genetic population structure of marine fishes; lessons from the European flounder (*Platichthys flesus* L.). Mol Ecol 16:3104–3118

Hewitt GM (2000) The genetic legacy of the quaternary ice ages. Nature 405:907–913

Ho SYW, Kolokotronis SO, Allaby RG (2007) Elevated substitution rates estimated from ancient DNA sequences. Biol Lett 18:1–5

Hoelzel AR (2009) Evolution of population structure in marine mammals. In: Bertorelle G, Bruford MW, Hauffe HC (eds) Population genetics for animal conservation. Cambridge University Press, Cambridge

Hoelzel AR, Green A (1998) PCR protocols and population analysis by direct DNA sequencing and PCR-based fingerprinting. In: Hoelzel AR (ed) Molecular genetic analysis of population, a practical approach, 2nd edn. Oxford University Press, Oxford, pp 159–189

Hoelzel AR, Hey J, Dahlheim ME, Nicholson C, Burkanov V, Black N (2007) Evolution of population structure in a highly social top predator, the killer whale. Mol Biol Evol 24:1407–1415

Hudson RR (1990) Gene genealogies and the coalescent process. Oxf Surv Evol Biol 7:1–44

Knutsen H, Jorde PE, Albert OT, Hoelzel AR, Stenseth NC (2007) Population genetic structure in the North Atlantic Greenland halibut: influenced by oceanic current systems? Can J Fish Aquat Sci 64:857–866

Larsson LC, Charlier J, Laikre L, Ryman N (2009) Statistical power for detecting genetic divergence–organelle versus nuclear markers. Conserv Gen 10:1255–1264

Librado P, Rozas J (2009) DnaSP v. 5, a software for comprehensive analyses of DNA polymorphism data. Bioinformatics 25:1451–1452

Mikkelsen AMH, Lund A (1994) Intraespecific variation in the dolphins *Lagenorhynchus albirostris* and *L. acutus* (Mammalia, cetacean) in metrical and nonmetrical skull characters, with remarks on occurrence. J Zool 234:289–299

Mirimin L, Westgate A, Rogan E, Rosel P, Read A, Coughlan J, Cross T (2009) Population structure of short-beaked common dolphins (*Delphinus delphis*) in the North Atlantic Ocean as revealed by mitochondrial and nuclear genetic markers. Mar Biol 156:821–834

Moller L, Valdez FP, Allen S, Bilgemann K, Corrigan S, Beheregaray LB (2011) Fine-scale genetic structure in short-beaked common dolphins (*Delphinus delphis*) along the East Australian current. Mar Biol 158:113–126

Morizur Y, Berrow SD, Tregenza NJ, Couperus AS, Pouvreau S (1999) Incidental catches of marine mammals in pelagic trawl fisheries of the Northeast Atlantic. Fish Res 41:297–307

Moura AE, Natoli A, Rogan E, Hoelzel AR (2013) Atypical panmixia in a European dolphin species (*Delphinus delphis*); implications for the evolution of diversity across oceanic boundaries. J Evol Biol 40:341–354

Natoli A, Birkin A, Aquilar A, Lopez A, Hoelzel AR (2005) Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). Proc Royal Soc B 272:1217–1226

Natoli A, Cañadas A, Peddemors VM, Aguilar C, Vaquero C, Fernandez-Piqueras P, Hoelzel AR (2006) Phylogeography and alpha taxonomy of the common dolphin (*Delphinus* sp.). J Evol Biol 19:943–954

Nichols C, Herman J, Gaggiotti OE, Dobney KM, Parsons K, Hoelzel AR (2007) Genetic isolation of a now extinct population of bottlenose dolphins (*Tursiops truncatus*). Proc Royal Soc B 247:1611–1616

Northridge SP, Tasker ML, Webb A, Camphuysen K, Leopold M (1997) White-beaked *Lagenorhynchus albirostris* and Atlantic white-sided dolphin *L. acutus* distributions in Northwest European and U.S. North Atlantic waters. Rep Int Whal Comm 47:797–805

Palka D, Read A, Potter C (1997) Summary of knowledge of white-sided dolphins (*Lagenorhynchus acutus*) from the U.S. and Canadian North Atlantic waters. Rep Int Whal Comm 47:729–734

Palm S, Dannewitz J, Prestegaard T, Wickstrom H (2009) Panmixia in European eel revisited: no genetic difference between maturing adults from southern and northern Europe. Heredity 103:82–89

Parsons KM, Noble LR, Reid RJ, Thompson PM (2002) Mitochondrial genetic diversity and population structuring of UK bottlenose dolphins (*Tursiops truncatus*): is the NE Scotland population demographically and geographically isolated? Biol Conserv 108:175–182

Pedersen T (1983) Increased productivity in the eastern equatorial Pacific during the last glacial maximum (19,000 to 14,000 yr B.P.). Geology 1:16–19

Peery MZ, Kirby R, Reid BN, Stoelting R, Doucet-Beer E, Robinson S, Vasquez-Carrillo C, Pauli JN, Pallsboll PJ (2012) Reliability of genetic bottleneck tests for detecting recent population declines. Mol Ecol 21:3403–3418

Pichler FB, Baker CS (2000) Loss of genetic diversity in the endemic Hector's dolphin due to fisheries-related mortality. Proc R Soc Lond Ser B Biol Sci 267:97–102

Posada D (2008) jModelTest: phylogenetic model averaging. Mol Biol Evol 25:1253–1256

Posada D, Buckley TR (2004) Model selection and model averaging in phylogenetics: advantages of the AIC and Bayesian approaches over likelihood ratio tests. Syst Biol 53:793–808

Quérouil S, Silva MA, Freitas L, Prieto R, Magalhães S, Dinis A, Alves F, Matos JA, Mendonça D, Hammond PS, Santos RS (2007) High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. Conserv Genet 8:1405–1419

Raymond M, Rousset F (1995) An exact test for population differentiation. Evolution 49:1280–1283

Reeves RR, Leatherwood S (1994) Dolphins, porpoises, and whales. 1994–1998 Action Plan for the conservation of cetaceans

Reeves RR, Smeenk C, Brownell L, Kinze CC (1999) Atlantic white-sided dolphin *Lagenorhynchus acutus* (Gray, 1828). In: Ridgway SH, Harrison SR (eds) Handbook of marine mammals, vol 6., The second book of dolphins and porpoisesAcademic Press, San Diego, pp 31–56

Reid JB, Evans PGH, Northridge SP (2003) Atlas of cetacean distribution in north-west European waters. Joint Nature Conservation Committee, Peterborough

Rogers AR, Harpending H (1992) Population growth makes waves in the distribution of pairwise genetic differences. Mol Biol Evol 9:552–569

Ryman N, Palm S (2006) PowSim: a computer program for assessing statistical power when testing for genetic differentiation. Mol Ecol 6:600–602

Schneider S, Excoffier L (1999) Estimation of past demographic parameters from the distribution of pairwise differences when the mutation rates vary among sites: application to human mitochondrial DNA. Genetics 152:1079–1089

Selzer LA, Payne PM (1988) The distribution of white-sided (*Lagenorhynchus acutus*) and common dolphins (*Delphinus delphis*) vs environmental features of the continental-shelf of the northeastern United States. Mar Mamm Sci 4:141–153

Shaw PW, Arkhipkin AI, Al-Khairulla H (2004) Genetic structuring of Patagonian toothfish populations in the Southwest Atlantic Ocean: the effect of the Antarctic Polar Front and deep-water troughs as barriers to genetic exchange. Mol Ecol 13:3293–3303

Siegert MJ, Dowdeswell JA (2004) Numerical reconstructions of the Eurasian ice sheet and climate during the Late Weichselian. Quatern Sci Rev 23:1273–1283

Stockley B, Menezes G, Pinho MR, Rogers AD (2005) Genetic population structure in the black-spot sea bream (*Pagellus bogaraveo* Brunnich, 1768) from the NE Atlantic. Mar Biol 146:793–804

Tajima F (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585–595

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res 25:4876–4882

Tolley KA, Vikingsson GA, Rosel PE (2001) Mitochondrial DNA sequence variation and phylogeographic patterns in harbour porpoises (*Phocoena phocoena*) from the North Atlantic. Conserv Gen 2:349–361

Valsecchi E, Amos W (1996) Microsatellite markers for the study of cetacean populations. Mol Ecol 5:151–156

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) Micro-Checker: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4:535–538

Wares JP (2002) Community genetics in the Northwestern Atlantic intertidal. Mol Ecol 11:1131–1144

Waring GT, Josephson E, Fairfield CP, Maze-Foley K (eds) (2006) U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments—2005. NOAA Tech Memo

Waring GT, Josephson E, Maze-Foley K, Rosel PE (2013) U.S Atlantic and Gulf of Mexico marine mammal stock assessments—2012. NOAA Tech Memo, vol 2. NMFS-NE-223. NMFS NEFSC. Woods Hole, MA

Weber DS, Stewart BS, Lehman N (2000) Genetic consequences of a severe population bottleneck in the Guadalupe Fur Seal (*Arctocephalus townsendi*). J Hered 95:144–153

Weinrich MT, Belt CR, Morin D (2001) Behavior and ecology of Atlantic white-sided dolphin (*Lagenorhynchus acutus*) in coastal New England waters. Mar Mamm Sci 17:231–248

Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population structure. Evolution 38:1358–1370

White TA, Stefanni S, Stamford J, Hoelzel AR (2009) Unexpected panmixia in a long-lived, deep-sea fish with well-defined spawning habitat and relatively low fecundity. Mol Ecol 18:2563–2573

White TA, Fotherby HA, Stephens PA, Hoelzel AR (2010) Genetic panmixia and demographic dependence across the North Atlantic in the deep-sea fish, blue hake (*Antimora rostrata*). Heredity 106:690–699

Williamson-Natesan EG (2005) Comparison of methods for detecting bottlenecks from microsatellite loci. Conserv Gen 6:551–562

Wright S (1951) The genetic structure of populations. Ann Eugen 15:323–354