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Post-glacial colonization of northern coastal habitat by bottlenose dolphins: A marine leading-edge expansion?

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Abstract

Oscillations in the Earth's temperature and the subsequent retreating and advancing of ice-sheets around the polar regions are thought to have played an important role in shaping the distribution and genetic structuring of contemporary high-latitude populations. After the Last Glacial Maximum (LGM), retreating of the ice-sheets would have enabled early colonizers to rapidly occupy suitable niches to the exclusion of other conspecifics, thereby reducing genetic diversity at the leading-edge. Bottlenose dolphins (genus *Tursiops*) form distinct coastal and pelagic ecotypes, with finer scale genetic structuring observed within each ecotype. We reconstruct the post-glacial colonization of the Northeast Atlantic (NEA) by bottlenose dolphins using habitat modelling and phylogenetics. The AquaMaps model hindcasted suitable habitat for the LGM in the Atlantic lower latitude waters and parts of the Mediterranean Sea. The time-calibrated phylogeny, constructed with 86 complete mitochondrial genomes including 30 generated for this study and created using a multi-species coalescent model, suggests that the expansion to the available coastal habitat in the NEA happened via founder events starting ~15,000 years ago (95% highest posterior density interval: 4,900–26,400). The founders of the two distinct coastal NEA populations comprised as few as two maternal lineages that originated from the pelagic population. The low effective population size and genetic diversity estimated for the shared ancestral coastal population subsequent to divergence from the pelagic source population are consistent with leading-edge expansion. These findings highlight the legacy of the Late Pleistocene glacial cycles on the genetic structuring and diversity of contemporary populations.

Keywords: Last Glacial Maximum (LGM), multi-species coalescent, time-dependency, phylogenetics, genetic diversity, habitat modelling

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Introduction

During the Late Quaternary period (1 Ma to present) the Earth's climate was governed by a series of glacial and interglacial events and temperature fluctuations that occurred at approximately 100,000-year intervals (Shackleton, 2000). These glacial cycles are thought to have played an important role in shaping the current distribution and genetic structuring of species and populations. In the Northern Hemisphere, this is more pronounced at high latitudes where the presence of ice sheets and Arctic temperatures during cold stadial periods restricted the available habitat to warmer refugia for many temperate-adapted species (Hewitt, 2000). The distribution of temperate-adapted species at high latitudes is thought to have been characterized by cyclical range contractions and expansions throughout the Pleistocene (Hewitt, 2000), and present-day populations represent lineages descended from relict populations that survived in glacial refugia (Hofreiter & Barnes, 2010). However, the capacity to adapt to environmental change varies among species and populations through their dispersal ability, genetic diversity and generation time (Stewart *et al.*, 2010; Montgomery *et al.*, 2014; Younger *et al.*, 2016) and has likely affected their present-day distribution.

Hewitt (1999, 2000) proposed that colonization of terrestrial species during the warm interglacial periods typically occurred via long-range dispersal events, or 'leading-edge range expansions'. During these events a few individuals from the source population, carrying a subset of the genetic diversity, first colonized and then expanded their range to fill emerging geographic and ecological niches leading to the exclusion of secondary waves of colonizers and thereby reducing genetic variability at this leading-edge. Unlike most terrestrial mammal species, marine mammals have a relatively low cost of movement (Tucker, 1975; Williams *et al.*, 1992; Williams, 1999) and few geographic barriers to dispersal, so the leading-edge colonization model may, or may not, be realistic for such highly mobile organisms that are able to move thousands of kilometers within a few weeks (Gabriele *et al.*, 1996; Mate *et al.*, 1997). High mobility certainly makes them capable of undertaking long-distance dispersal events, but at the same time, also increases the potential to retain ongoing gene flow and migration between the leading-edge and source populations. Compared to terrestrial species, little is known about the post-glacial colonization history of Europe's marine fauna, but during recent years a growing number of studies have explored the dynamics of postglacial range expansion in marine taxa (e.g. de Bruyn *et al.*, 2009; Fontaine *et al.*, 2010, 2014;

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Catchen *et al.*, 2013; Foote *et al.*, 2013). Genetic analyses of carbon-dated sub-fossils indicate that temperate climate adapted species such as gray whales *Eschrichtius robustus* (Lilljeborg, 1861) and North Atlantic right whales *Eubalaena glacialis* (Müller, 1776) replaced cold-adapted species such as bowhead whales *Balaena mysticetus* (Linneaus, 1758) in mid-latitude European waters during the Late Pleistocene-Early Holocene transition (Foote *et al.*, 2013; Alter *et al.*, 2015). However, the refugial distribution during the Last Glacial Maximum (LGM) of the source populations for these re-colonizing temperate marine species is largely unknown.

Here, a multi-species coalescent model was used together with information on species and population structure to reconstruct the post-glacial colonization in a highly mobile marine genus *Tursiops*. Specifically, the aim was to determine the timing of the colonization into the northeastern Atlantic coastal habitats and to investigate whether the colonization occurred via leading-edge expansion. The genus *Tursiops* currently consists of two separate species recognized by the International Union for the Conservation of Nature, *T. truncatus* (Montagu, 1821; common bottlenose dolphin) and *T. aduncus* (Ehrenberg, 1833; Indo-Pacific bottlenose dolphin), although *T. australis* (Burrunan dolphin) inhabiting the coastal waters in southern Australia has been proposed as a separate species (Charlton-Robb *et al.*, 2011). For simplicity, we refer to the latter as *T. australis* throughout this paper but acknowledge the unofficial status of this putative species. Species in the *Tursiops* genus are found in coastal inshore waters, continental shelf regions and open ocean environments (Wells & Scott, 2009) in tropical and temperate waters (Leatherwood & Reeves, 1989). Throughout much of their range, they exhibit a hierarchical population structure, with the greatest genetic divergence found between pelagic and coastal populations (Hersh & Duffield, 1990; Curry & Smith, 1998; Hoelzel *et al.*, 1998; Natoli *et al.*, 2005; Tezanos-Pinto *et al.*, 2008; Louis *et al.*, 2014b; a; Lowther-Thieleking *et al.*, 2015; Nykänen *et al.*, 2018). The broad-scale population structuring between coastal and pelagic ecotypes in the Northeast Atlantic (NEA) (Louis *et al.*, 2014b) likely reflects colonization of emerging or available inshore habitats after the LGM from a pelagic source population followed by divergence in allopatry (Moura *et al.*, 2013; Louis *et al.*, 2014a). It has been suggested that the colonization of coastal habitats in the NEA was possibly achieved via a founder event by a small number of individuals (Louis *et al.*, 2014a). However, the possible role of leading-edge colonization has not been fully investigated in this genus by quantifying historic population sizes. Therefore, to better understand the climatic, temporal and spatial context of the evolutionary processes that gave

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rise to the present-day diversity and habitat use of bottlenose dolphins in the NEA, mitogenomic data were analyzed in combination with habitat mapping, using newly available tools that can robustly infer ancestral effective population sizes and therefore give insights to colonization processes.

Methods

Models of suitable habitat

Following the methods in Foote *et al.* (2013), Alter *et al.* (2015) and Morin *et al.* (2015), the AquaMaps modelling approach (Ready *et al.*, 2010; Kaschner *et al.*, 2011) was used to predict the distribution of suitable habitat for common bottlenose dolphins during the present, for the year 2100 (under the Institut Pierre Simon Laplace climate scenario SRES A2), and for the LGM (~20,000 ya). AquaMaps is a bioclimatic model that combines large sets of occurrence data (e.g. from visual observations) with available expert knowledge on species preference and tolerance to different environmental parameters and ultimately generates large-scale predictions of the probability of occurrence for different marine species. This way the preferred habitat of a species can be estimated based on a predefined set of environmental parameters including water depth, sea surface temperature, salinity, primary production, sea ice concentration and proximity to land, and projected into geographic space as relative probability of occurrence. For the purpose of this study, a slightly modified version of the original AquaMaps model (which is available on www.aquamaps.org) was used; specifically, primary production was excluded from the model, as there are no available data for this parameter for the Pliocene or Pleistocene. Current environmental conditions were assumed to be representative of the entire Holocene as the variability in conditions during this time period has been small compared to the differences between glacial cycles (Folland *et al.*, 2002). AquaMaps has been previously used to hindcast suitable habitat predictions for bowhead whales, gray whales and killer whales, *Orcinus orca* (Linnaeus, 1758), during the LGM (Foote *et al.*, 2013; Alter *et al.*, 2015; Morin *et al.*, 2015) by using mean annual environmental conditions during the LGM based on the GLAMAP project data set (Schäfer-Neth & Paul, 2003).

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Sample collection

Tissue samples from twelve individuals from *T. truncatus* were obtained by biopsy sampling free-ranging animals (see Krützen *et al.*, 2002) in coastal waters of Ireland and France in 2005–2012. Additionally, skin samples were collected from 21 individuals that stranded along the coast of Ireland, France and the UK in 1991–2010 (Fig. 1). Samples were specifically selected for sequencing based on previous genetic assignment to distinct ecotypes/populations using microsatellites, supported by significant F_{ST} values (Islas-Villanueva, 2010; Mirimin *et al.*, 2011; Louis *et al.*, 2014b) and the lack of evidence for recent migration between the populations (Louis *et al.*, 2014b). For consistency, we refer to individuals not assigned to a coastal population as belonging to a 'pelagic' ecotype. However, we acknowledge that little is known about the ecology of these individuals, and they may inhabit both neritic and oceanic waters. In addition to the 30 samples successfully sequenced for the study, 57 mitochondrial haplotypes from the genus *Tursiops* from other regions of the world, along with 17 delphinid sequences, were downloaded from GenBank (Appendix S1, Electronic Supplementary Material).

DNA extraction, amplification and sequencing

DNA was extracted from 33 tissue samples using the Qiagen DNeasy (Qiagen DNeasy, Valencia, CA, USA) kit following the manufacturer's guidelines. DNA yield was quantified using a Qubit (Life Technologies) and ranged between 10 and 300 ng⁄µL for all samples. The DNA samples were then sheared to fragments of ~150-200 bp using a Diagenode Bioruptor NGS run with 20 cycles of 30 seconds on, and 30 seconds off.

To generate mitochondrial genome sequences we employed a simple shotgun sequencing method (see Tilak *et al.*, 2015). Illumina sequencing libraries were built on the sheared DNA extracts using NEBNext (Ipswich, MA, USA) DNA Sample Prep Master Mix Set 1 following Meyer and Kircher (2010). Libraries were subsequently index amplified for 15 cycles using Phusion High-Fidelity Master Mix (Finnzymes) in 50-µL reactions following the manufacturer guidelines. The libraries were then purified using a MinElute PCR purification kit (Qiagen, Hilden, Germany). Concentrations of amplified libraries were initially checked using a Qubit (Life Technologies) and fragment size distribution was visualized on agarose gel, before a 1/10 diluted aliquot was run on Agilent Bioanalyser 2100 (Palo Alto, CA, USA) to determine molarity and concentration and facilitate equimolar pooling of index amplified libraries. The index amplified libraries were then sequenced in sub-partitions of single

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channels on an Illumina HiSeq 2500 ultra-high-throughput sequencing platform using single read (SR) 100-bp chemistry.

Conversion of Illumina's *.bcl files to fastq, and demultiplexing were performed using Illumina's CASAVA (version 1.8.2) software allowing for no mismatch in the 6-nucleotide indices used for barcoding. Sequencing reads within the generated fastq files were processed with ADAPTER-REMOVAL (Lindgreen 2012) to trim residual adapter sequence contamination and to remove adapter dimer sequences as well as low-quality stretches at 3' ends (i.e. consecutive stretches of N's and of bases with a quality score of 2 or lower). Reads that were ≤30 bp following trimming were discarded. Filtered reads with average phred-scores ≥30 were then mapped to a reference *T. truncatus* mitogenome sequence (KF570351.1) using BWA version 0.5.9 (Li & Durbin, 2009), requiring a mapping quality of Q ≥30 for all bases. The reference mitochondrial sequence was modified as per Morin *et al.* (2015) to improve assembly coverage at the 'ends' of the linearized mitogenome by adding 40-bp from each end to the opposite end (so that reads could map across the artificial break point of the linearized sequence). The influence of potential NUMTs was excluded given the absence of stop codons or frame shifts in the aligned protein encoding genes, and the lack of regions of excessive coverage due to the mapping of both mt and nuDNA. Clonal reads were collapsed using the rmdup program of the SAMTOOLS (version 0.1.18) suite (Li *et al.*, 2009). Consensus mitogenome sequences were then reconstructed using bam files, which were assembled and visualised in GENEIOUS (Biomatters Ltd.), allowing indels and unique variants to be visually verified in the BAM files, and only including nucleotide positions with a read depth of ≥3× coverage; ambiguous bases were assigned as Ns.

Time-calibrated phylogeny of delphinids and the genus Tursiops

There were insufficient data for the reconstruction of complete mitochondrial genomes for three sequenced samples, which were therefore excluded from further analyses. The remaining 30 whole mitochondrial *T. truncatus* genomes were used in the subsequent analyses. The inference of time-calibrated phylogenies followed a two-step methodology following Morin *et al.* (2015) with the purpose of the first step (delphinid phylogeny) to estimate a calibration point (divergence of the two most evolutionarily distant *Tursiops* spp. haplotypes) for the second step (*Tursiops* spp. phylogeny).

The 30 whole mitochondrial *T. truncatus* genomes sequenced for this study were first aligned with 56 sequences from the genus *Tursiops* and a rough-toothed dolphin (*Steno bredanensis*)

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sequence downloaded from GenBank (see Appendix S1 for sequence accession numbers) that was used as an outgroup using the MUSCLE algorithm in MEGA 6 (Tamura *et al.*, 2007). A topology tree in MRBAYES (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) was then built with these sequences after initial model selection for the best substitution scheme in JMODELTEST2 (Posada, 2008; Darriba *et al.*, 2012), and the resulting consensus tree was inspected to find the two most divergent *Tursiops* haplotypes (SABD1, representing a haplotype of *T. australis* obtained from South Australia, and SA99 representing a haplotype of *T. aduncus* collected from South Africa (see Moura *et al.*, 2013). The thirteen protein coding genes of the mitochondrial genome from these two most divergent *Tursiops* sequences were then aligned with the additional 18 delphinid sequences downloaded from GenBank (Appendix S1). We used the package *ClockstaR* (Duchêne *et al.*, 2014) in R 3.3.3 (R Core Team, 2016) to investigate whether the different mitochondrial genes had different mutation rates or whether a single rate could be applied in further time-calibrated models.

The 'greedy' search in PARTITIONFINDER (v1.1.0) (Lanfear *et al.*, 2012) was used to find the best partitioning scheme for each gene, and a time-calibrated phylogenetic tree was built in BEAST2 (Drummond *et al.*, 2012) with three different data partitions for nucleotide substitution models (Appendix S2). We used a single clock model based on the *ClockstaR* results and estimated a single tree due to the non-recombining properties of mtDNA to find the time to most recent common ancestor (TMRCA) between the two most divergent *Tursiops* haplotypes. The TMRCA of Delphinidae (mean = 10.08 Myr, SD = 1.413, (McGowen *et al.*, 2009) was used to calibrate the root of the tree and a Calibrated Yule prior was used for the branching rate. Both uncorrelated log-normal relaxed clock (Drummond *et al.*, 2006) and strict clock models were tested with 40,000,000 Markov Chain Monte Carlo (MCMC) steps, 25% pre-burn-in, and a sampling frequency of 4,000. Each model was run twice and the convergence of chains and the Effective Sample Size (ESS) values relating to the model parameters were checked in TRACER (Rambaut *et al.*, 2014). After verifying convergence, LOGCOMBINER and TREEANNOTATOR (Drummond *et al.*, 2012) were used to combine and summarize the trees, respectively. Model selection between the two clock models was done by inspecting the ucldStdev parameter in the relaxed clock model; a standard deviation close to zero (<0.1) in this parameter indicates negligible variation in the substitution rates across branches and a better fit of the strict clock model (Drummond & Bouckaert, 2015).

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We tested for potential saturation (multiple substitutions) of the third codon positions by plotting the uncorrected pairwise genetic distances and model-corrected (Tamura-Nei substitution model, Tamura & Nei, 1993) genetic distances in R. To investigate the potential effect of incomplete purifying selection, we compared the node TMRCA estimates and clock rates derived using all codon positions (as described above) to a time-calibrated phylogeny created using only the third codon positions, as most mutations that occur in third codon positions are silent and therefore code for the same amino acid (Lagerkvist, 1978). This makes them less likely to be directly targeted by purifying selection (but does not account for purifying selection upon a linked site), thereby maintaining a more constant substitution rate over evolutionary time. The approach of using only the third codon positions has been recently used in a study resolving killer whale (*Orcinus orca*) mitochondrial lineages (Morin *et al.*, 2015).

The best nucleotide partitioning scheme for the coalescent analysis of the genus *Tursiops* was determined for the data set, consisting of thirteen protein coding gene regions of the 30 mitochondrial genomes sequenced for this study supplemented by 56 *Tursiops* haplotypes downloaded from GenBank (Appendix S1, Electronic Supplementary Material), using PARTITIONFINDER (v1.1.0) (Lanfear *et al.*, 2012) (Appendix S2, Electronic Supplementary Material). These samples/haplotypes from *T. truncatus*, *T. aduncus* and *T. australis* had been determined to have originated from coastal or pelagic regions in different parts of the world in previous studies and had been delineated into separate populations or ecotypes (Fig. 1; Appendix S1, Electronic Supplementary Material). This information on population structure was used in this study together with mitochondrial gene regions to create a time-calibrated phylogeny for the genus *Tursiops* and to estimate the divergence times for the different populations of *T. truncatus* in the North Atlantic.

As the multi-species coalescent (MSC) model has been found not only to delimit species but to identify genetic structuring between putative populations (Sukumaran & Knowles, 2017), this approach was chosen to construct the time-calibrated phylogeny using StarBEAST2 (Ogilvie *et al.*, 2017), an extension of BEAST2 (Drummond *et al.*, 2012). This method is thought to provide accurate inferences of species tree topologies, divergence times, and substitution rates even in the presence of incomplete lineage sorting, i.e., when individual gene trees do not correspond well with the species tree (Ogilvie *et al.*, 2017). For this reason, information on population structure obtained from previous studies on nuclear microsatellite markers were included in the MSC model. In order to estimate historical effective population

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sizes (N_e) for the populations sequenced for this study, the MSC model was run with the population model 'Linear with Constant Root Populations' assuming that population sizes change over time but keeping the size of the root (the ancestor of all species/populations) constant. The scaled population sizes for pelagic Northeast Atlantic, Coastal North and Coastal South produced by the StarBEAST2 models were adjusted by the average generation time of 21 years estimated for *T. truncatus* and *T. aduncus* (Taylor *et al*., 2007) to convert the estimates to population sizes. As with the delphinid phylogeny, to investigate the possible effect of incomplete purifying selection, StarBEAST2 was run with two different models; a model including all codon positions and a second model including only the third codon positions. Both models were run with an uncorrelated log-normal relaxed clock (Drummond *et al.*, 2006) and a strict clock and with 200,000,000 MCMC steps, 10% burn-in and a sampling frequency of 20,000. Based on the results of *ClockstaR* analysis (Duchêne *et al.*, 2014) on delphinids, a single clock model was used for all the data partitions. We applied a constraint on the root age obtained in the delphinid phylogeny (split of the two most divergent *Tursiops* haplotypes; 3.662Myr (95% highest posterior density interval, HPDI: 2.567–4.725) with the all codon model, 3.692 Myr (95% HPDI: 2.567–4.153) with the third codon model) to calibrate the trees. The convergence of chains and model performance was inspected in TRACER (Rambaut *et al*., 2014) after running each model twice, and LOGCOMBINER and TREEANNOTATOR (Drummond *et al.*, 2012) were used to combine the log- and tree-files and summarize the trees, respectively. The resulting summary trees were plotted using *phytools* (Revell, 2012) in R.

Using DnaSP 5.0 (Librado & Rozas, 2009), we calculated the number of segregating sites (*k*) and four different indices of historical population demographic changes (bottlenecks or expansions); Tajima's D (Tajima, 1989) , Fu and Li's D* and F* (Fu & Li, 1993) and Ramos-Onsins & Rozas' R2 (Ramos-Onsins & Rozas, 2002), for the pelagic, the Coastal North and the Coastal South populations. The examination of deviation from the neutral theory model at equilibrium between mutation and genetic drift by these indices was based on 10,000 coalescent simulations. Expectations of these statistics are ~zero in a constant-size population, whereas significant negative or positive values can indicate a sudden expansion or a recent population bottleneck, respectively. In addition, differences in nucleotide and haplotype diversity (π_{nuc} and π_{hap}, respectively) were compared between pelagic and the Coastal North and Coastal South populations with the "genetic_diversity_diffs" function (Alexander *et al.*, 2016) implemented in R and using 10,000 re-sampling permutations, in

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order to test whether the observed differences in diversity between the populations were greater than expected by chance. A haplotype network of the whole mtDNA sequences (16,390 bp) and including all the North Atlantic *T. Tursiops* samples was created in popART (Leigh & Bryant, 2015) using the median-joining network (Bandelt *et al.*, 1999).

Results

Models of suitable habitat

According to the AquaMaps model, the core suitable habitat for common bottlenose dolphins during the LGM ranged from ~42°N (approximately the latitude of the state of Connecticut) in the Northwest Atlantic southwards along the coast to lower latitudes (Fig. 2, Appendix S3). In the Northeast Atlantic, their coastal range was restricted to approximately 40°N, corresponding to the south of the Iberian Peninsula, and to an area around the Alboran Sea in the Mediterranean. In addition, suitable habitat was hindcasted to cover an area in the pelagic North Atlantic around the Mid-Atlantic ridge and around the islands on both sides of the Atlantic. Note that AquaMaps hindcasted suitable habitat also in the Black Sea, however, this remained closed and thus inaccessible for the dolphins until after 10 kya (Kerey *et al.*, 2004).

DNA sequencing

A total of 292×10^6 sequencing reads were generated from the samples; >1 million reads per individual for 28 of the 33 individuals included on the sequencing lane. Following QC filtering, removal of duplicate reads, mapping and only including nucleotide positions with a read depth of ≥3× coverage, complete mitochondrial genomes were assembled for 30 individuals with a mean sequence coverage ranging from 10× to >100×. Control region sequences were compared with those generated for the same individuals by Sanger sequencing in previously published studies (Islas-Villanueva, 2010; Mirimin *et al.*, 2011; Louis *et al.*, 2014b), in some cases the same individual had been previously sequenced independently by all three studies. In all cases our high-throughput sequencing generated data agreed 100% with the Sanger sequence data. Twenty new haplotypes from the samples sequenced for this study were identified (Appendix S1), which are deposited in GenBank (KT601188-KT601207).

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Time-calibrated delphinid phylogeny

The approximately linear relationship between the uncorrected and model-corrected genetic distances indicated no evidence of saturation of the third codon position of the protein coding genes (Appendix S4). Low standard deviation (<0.1) of the clock rate parameter (ucldStdev) in both delphinid models, the all codon model and the third codon model, run with an uncorrelated log-normal relaxed clock indicated low variation in substitution rates between lineages; therefore, the models run with a strict clock were considered to be a better fit to the data. Average substitution rate for the strict clock all codon model was estimated as 6.663×10^{-3} substitutions/site/Myr (95% HPDI: $4.872 \times 10^{-3} – 8.865 \times 10^{-3}$), and for the third codon model as 0.017 substitutions/site/Myr (95% HPDI: 0.012 – 0.022). Both models produced similar topology and node age estimates for the clade including the *Tursiops* and *Stenella* species, *Sousa chinensis*, *Steno bredanensis* and *Delphinus capensis* (Appendix S5). However, *Lagenorhynchus albirostris* and *Cephalorhynchus heavisidii* were placed in different clades in the trees depending on the model used and the models also estimated the divergence of killer whales (*Orcinus orca*) differently. The placement of these species has been uncertain in previous studies (LeDuc *et al.*, 1999; Caballero *et al.*, 2008; McGowen *et al.*, 2009; Steeman *et al.*, 2009; Vilstrup *et al.*, 2011) and is thought to reflect rapid radiation in the Delphinidae family (Vilstrup *et al.*, 2011). We compared the time to most recent common ancestor (TMRCA) estimates for the common nodes derived using the two models and found them to be significantly correlated (Pearson's $r^2 = 0.99$, $P < 0.001$, Appendix S6) with a slope of 1.01, implying that incomplete purifying selection was not an issue in the delphinid phylogeny. The TMRCA of the two most divergent *Tursiops* samples was estimated as 3.662 Myr (95% HPDI: 2.567 – 4.725) with the all codon model and as 3.692 Myr (95% HPDI: 2.567 – 4.772) with the third codon only model. The Effective Sample Size (ESS) values for the different parameters were all >500 in the third codon only model (most of them >2000), whereas in the all codon model they were >200 (most of them >2000), except for one parameter for the gamma shape and one parameter for the proportion of invariant sites, which were both >150 (Appendix S7).

Time-calibrated Tursiops *phylogeny*

Very low standard deviation (<0.01 in both all codon and third codon only models) in the substitution rates estimated with the uncorrelated log-normal relaxed clock indicated negligible variation in substitution rates between lineages; therefore, in StarBEAST2, a strict

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clock was used to estimate the time-calibrated phylogeny of the genus *Tursiops*. The ESS values for the parameters in both models were all >300 (most of them >6000), indicating no sign of autocorrelation between samples and a good convergence of chains (Appendix S8, Electronic Supplementary Material). Both models resulted in identical species/population topologies and similar node age estimates and posterior probabilities (Appendix S9, Electronic Supplementary Material). Similar to the Delphinid phylogeny, the node ages were significantly correlated with a slope of 1.01 (Pearson's $r^2 > 0.99$, $P < 0.001$, Appendix S10), indicating no evidence of incomplete purifying selection affecting the *Tursiops* tree.

The summary consensus species tree, inferred using the third codon only model and showing only the NEA and Mediterranean and Black Sea *T. truncatus* populations (Fig. 3), indicates that the branch including haplotypes from the Mediterranean and Black Seas split from the NEA branch ~ 35,900 years ago (95% HPDI: 11,200–60,500). The coastal NEA populations, on the other hand, diverged from the pelagic population around 14,800 years ago (95% HPDI: 4,900–26,400) with a further more recent divergence of the northernmost coastal population (Coastal North) occurring ~7,200 years ago (95% HPDI: 0–14,200). However, the node posterior probabilities of the pelagic and coastal NEA populations are quite low (Fig. 3), likely due to incomplete lineage sorting. Indeed, incomplete lineage sorting, especially of the coastal North Atlantic *T. truncatus* sequences, is evident in the consensus gene tree consisting of all samples from the genus *Tursiops* (green tips in the tree, Appendix S12, Electronic Supplementary Material), and is accompanied by older node coalescence times compared to the time-calibrated species tree (Fig. 3). The consensus gene tree also indicates that the coastal bottlenose dolphin population currently occupying the northern parts of the NEA (i.e. Coastal North) originates from at least two separate mitochondrial lineages.

The summary consensus species tree depicting the effective population sizes (N_e) through Late Pleistocene–Holocene (Fig. 3, Appendix S11) indicates that, unlike the pelagic population, which is estimated to have retained a relatively stable effective size throughout the Late Pleistocene and Holocene, all of the present-day coastal populations, and especially the Black Sea and the Coastal North populations, are inferred to have undergone a genetic bottleneck around 7,000–8,000 years ago followed by expansion towards the present day (Fig. 3, Appendix S11). The significantly lower nucleotide (π_{nuc}) and haplotype diversities (π_{hap}) in the Coastal North population compared to the pelagic population, and the significantly lower π_{nuc} in the Coastal South population compared to the Pelagic East Atlantic (all $P < 0.05$, based on 10,000 permutations) are further indications of ancestral population

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bottlenecks in the coastal populations, as are the reduced number of segregating sites (*k*) (see Table 1). Conversely, the non-significant values of Tajima's *D*, Fu and Li's D* and F* and Ramos-Onsins & Rozas' R2, albeit the first three indicators being negative for the Coastal South population (Table 1), fail to provide support for our inference of post-glacial demographic expansion from a small founder population and indicate that there is no significant excess of low frequency variants in the Coastal North and Coastal South populations. This could be an artefact of lack of power to detect significance, or it could be due to a violation of the assumption of panmixia inherent in these statistics. For example, the Coastal North population consists of demes that are interconnected by limited and varying gene flow (Louis *et al.*, 2014b; Nykänen *et al.*, 2018). This could increase the number of rare variants, but it could also inflate intermediate variants; for example, variants that are at high frequency in one or two demes would be identified as intermediate frequency variants in our sample set. The possible unaccounted population structuring, in turn, would inflate the effective population sizes, which could help explain the unrealistically high recent time N_e values estimated for the coastal populations. Furthermore, the fact that the divergence of the coastal populations from the pelagic population was estimated to have occurred already ~15,000 years ago, could mean that the rare variants expected to arise in a population after a bottleneck or founder event have had sufficient time to drift to extinction or intermediate frequency.

The haplotype network shows the two source lineages of the haplotypes shared among different NEA coastal populations (Fig. 4). One of the haplotypes is shared between six individuals from two different populations, five from the Coastal North and one from the Coastal South, and another haplotype is private to the Coastal North population and is shared by five individuals. Thus, 71% of the Coastal North individuals sampled in this study shared just these two haplotypes; the remainder have haplotypes recently derived from these ancestral lineages. This is consistent with the demographic expansion of the Coastal North population from just two founding lineages and a probable ancestral origin in the pelagic population. Similarly, the Coastal South population may have originated from only one or two pelagic founding lineages; however, sequencing more samples from this population will be required to determine this with certainty. Nevertheless, it is likely that the pelagic population gave rise to coastal lineages with current populations located in the NEA as well as in the Mediterranean and Black seas.

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Discussion

Our analyses indicate that bottlenose dolphins have colonized the northernmost range of their distribution through a leading-edge expansion, in which the early colonists have expanded to fill the available coastal niches, to the exclusion of others. Due to its strict maternal inheritance the mitochondrial genome tracks only the matrilineal population history, a very stochastic coalescent process, and generally has less power to detect ancestral demographic changes than estimates based on analyses of multiple nuclear markers (Ho & Shapiro, 2011). For this reason, a multi-species coalescent (MSC) model that utilized information on population structure from previous studies on biparentally inherited nuclear DNA markers (microsatellites) was used to infer divergence times of distinct species and populations of bottlenose dolphins. Incomplete lineage sorting and rapid radiation among delphinids (e.g. McGowen *et al.*, 2009; Amaral *et al.*, 2012; Moura *et al.*, 2013; Louis *et al.*, 2014b; Morin *et al.*, 2015; Foote & Morin, 2016) can complicate the estimation of the timing of speciation events and population divergence in the genus *Tursiops* over phylogenetic time-scales (Moura *et al.*, 2013). One advantage of using MSC model, such as StarBEAST2 (Ogilvie *et al.*, 2017), compared to traditional methods which assume that evolutionary histories of gene trees match the evolutionary history of the species tree, is that the branch lengths and divergence times are not overestimated (Ogilvie *et al.*, 2017). Another advantage of StarBEAST2 is the possibility to infer historical effective population sizes while accounting for population structuring, as this structuring combined with uneven sampling can lead to bias in N_e estimates inferred with traditionally used Bayesian Skyline methods (Heller *et al.*, 2013) that assume panmixia. Additionally, time-dependency of increasing mutation rate towards the present caused by incomplete purifying selection – the time lag between the appearance of a mutation and its removal due to purifying selection - has the potential to further bias divergence time estimates (e.g. Ho *et al.*, 2005; Ho *et al.*, 2011). The use of sites under strong selective constraint extends terminal branches potentially leading to overestimation of older node ages (Ho *et al.*, 2011; He *et al.*, 2019). In this study, based on the comparison of time-calibrated phylogenies inferred using all codon positions and only the third codons, we found no evidence of incomplete purifying selection affecting the divergence time estimates in the delphinid family or in the phylogeny consisting of *Tursiops* spp. sequences and haplotypes. However, this may have been an artefact of the small number of common nodes (N=8) included in the comparison or the relatively young node ages of the branches consisting of *T. truncatus* samples, and the issue of time-dependency in *Tursiops*

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phylogenies should be re-examined with more samples collected from various populations. Nevertheless, third codon positions are thought to be less constrained by purifying selection compared to first and second codon positions, and they are therefore expected to evolve in a more clock-like fashion, accumulating mutations at a more constant rate and thus minimizing the effect of time-dependence (Ho *et al.*, 2011).

The average substitution rate for the third codon positions across all branches for the samples from the genus *Tursiops* was estimated as 0.017 substitutions/site/Myr. This estimate corresponds well with previously estimated rates of 0.024 for third codon positions for cetaceans (Ho & Lanfear, 2010) and 0.021 substitutions/site/Myr for bottlenose dolphin mitogenome-wide rates (Moura *et al.*, 2013). Similarly, the estimated divergence date for the second youngest node for the genus *Tursiops* in this study, represented by the divergence between Mediterranean and Black Sea bottlenose dolphins (around 7,900 years ago), is concordant with that derived previously by Moura *et al.* (2013), and is consistent with the geological timeframe of the opening of the Bosphorus Strait as well as the climatic context linking to the LGM. In contrast, the average root age for the genus *Tursiops* in this study was estimated as 3.7 Myr, which is considerably older than 1.1 Myr estimated by Moura *et al.* (2013). Possible reasons for this incongruence may be a result of the different modelling strategies applied to different parts of the mitogenome (mtDNA protein coding regions were used in this study whilst Moura *et al.* (2013) used the whole mtDNA sequence). However, a more likely reason is the fact that these authors used a relatively narrow prior for their biogeographical calibration (Uniform prior of 0.003–0.01, supplementary table S5 in Moura *et al.* (2013) that overpowered the fossil calibrations with much wider priors, and this ultimately resulted in poor convergence of the older node age posterior estimates based on low (<100) ESS values (supplementary table S6 in Moura *et al.* (2013)).

Pleistocene climatic oscillations are thought to have played a major role in shaping species distribution and divergence and in promoting speciation (Avise *et al.*, 1998). The divergence of the Northwest Atlantic coastal population from other Atlantic *T. truncatus* populations around 600,000 years ago coincides with the end of a cooler period during the mid-Pleistocene when the SST started to gradually rise again up to ~10°C in the Northern Hemisphere (Clark *et al.*, 2006). Consistent with previous studies (Natoli *et al.*, 2005; Moura *et al.*, 2013; Louis *et al.*, 2014a), the phylogenetic tree estimated in this study for the genus *Tursiops* (Fig. 3) suggests that the colonization of coastal habitats in the NEA occurred from

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a pelagic source population. According to our results, this happened via an ancestor that occupied lower latitude Atlantic waters. The AquaMaps model also indicated that bottlenose dolphins may have inhabited parts of the Mediterranean Sea during the LGM, as some areas were highlighted as suitable habitat (Fig. 2b). Even if the northern parts of the Mediterranean Sea (e.g. Tyrrhenian Sea) were too cold or otherwise unsuitable for the bottlenose dolphins during the LGM, a refugial population may have existed in the areas around the warmer Alboran Sea, with models of SST showing consistently warmer annual temperatures above 10°C for this area throughout the last ice age (Cacho *et al.*, 2001). Similar refugia at lower latitudes have been documented, for example, with Atlantic salmon, *Salmo salar* (Consuegra *et al.*, 2002; Finnegan *et al.*, 2013) and European eel, *Anguilla anguilla* (Kettle *et al.*, 2011). Suitable habitat for bottlenose dolphins during the LGM was also hindcasted with AquaMaps in the Black Sea. However, the land bridge between the Black Sea and the Mediterranean collapsed only ~10,000 years ago (Kerey *et al.*, 2004). Moreover, an accumulation of species found in the Black Sea sediment that are indicative of marine, rather than brackish, conditions was dated to 7,000–6,400 yr (the Kalamitian transgression (Yanko-Hombach *et al.*, 2007)). This makes the Black Sea an unlikely habitat for bottlenose dolphins until ~7,000 years ago at the earliest, and the divergence time between the eastern Mediterranean and Black Sea populations estimated as ca. 7,900 ya in this study fits quite well within this timeframe.

Temperature changes after the LGM have likely also played a role in the colonization of the northern parts of the NEA. The post-LGM divergence of the coastal populations in the NEA from the pelagic ~15,000 years ago coincides with the rising temperatures in the lower latitudes of the North Atlantic Ocean. The subsequent recent split of the Coastal North population from its southern counterpart currently occupying lower latitude European waters was estimated to have occurred around 8,000 years ago, and the timing of the split is supported by two *T. truncatus* subfossils found in the Dutch Southern Bight and radio-carbon aged to 7,390 and 8,135 yrs, respectively (Post, 2005). It thus appears that these cladogenetic events are correlated with periods of temperature changes, with warmer temperatures leading to an increase in sea-level in coastal areas and the subsequent release of available habitat. Further, it is also likely that suitable coastal habitat became available gradually in the NEA coastal areas after the LGM and the onset of the warmer Holocene leading to sequential colonization and divergence.

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According to Hewitt (1999, 2000), the colonization of suitable niches in high latitudes would occur rapidly via long-range dispersal events. Being highly mobile, cetaceans are capable of undertaking long distance movements on relatively short time-scales (Forcada, 2009; O'Brien *et al.*, 2009; Robinson *et al.*, 2012). Coupled with this potential for long-range dispersal, the fact that bottlenose dolphins form small local resident populations in coastal European waters (e.g. Ingram & Rogan, 2002; Cheney *et al.*, 2013; Louis *et al.*, 2015), makes post-glacial leading-edge colonization of the northern NEA a likely dispersal scenario. The demographic contraction and subsequent expansion observed in the coastal populations of this study, as well as the significantly reduced nucleotide and haplotype diversities, suggest that bottlenose dolphins indeed expanded their range northwards to coastal areas via founder events during leading-edge expansion. A similar founder event has recently been suggested to give rise to the present-day resident-type killer whale communities in the Russian Pacific (Filatova *et al.*, 2018), and rapid demographic expansions after the LGM have been documented across other marine taxa (e.g. Klimova *et al.*, 2014; Jenkins *et al.*, 2018).

Our results indicate that the colonization and expansion to fill the available coastal habitat around the British Isles happened via serial founder events after the LGM by a small leading-edge founder group, that comprised as few as two maternal lineages, from the source pelagic population. This finding is supported by previous publications of larger datasets of 136 mitochondrial control region sequences from coastal populations around the British Isles, which comprise the same two mitochondrial haplogroups (Mirimin *et al.*, 2011; Louis *et al.*, 2014b). The inferred process of post-glacial expansion into emerging habitat reflects the model inferred by Hoelzel *et al.*, (2007) for colonization of the coastal regions of the North Pacific and the formation of structure in killer whales. This process may thus reflect a commonality in the demographic history of high latitude social odontocetes. More broadly, serial founder events by a small subset of the parent population, leading to sequential loss of genetic diversity, have been linked to the phylogeographic history in a number of species, including modern humans (*Homo sapiens*) during the migration out of Africa (DeGiorgio *et al.*, 2009; Deshpande *et al.*, 2009; Henn *et al.*, 2012). Still today the greatest nuclear and haplotype diversity among modern humans is found in Africa (reviewed in Campbell & Tishkoff, 2008), and it is generally accepted that Africa was the source of all current modern human populations. Similarly, we identify a loss of genetic diversity in bottlenose dolphins at the northern edge of their coastal range relative to that found in the large pelagic population (e.g. Quérouil *et al.*, 2007; Mirimin *et al.*, 2011; Louis *et al.*, 2014b).

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In summary, our results suggest that the present day geographic and genetic structuring of bottlenose dolphins in the North Atlantic were shaped by the climatic cycles of the Late Quaternary, and the most northerly coastal population represents a leading-edge expansion by two founding mitochondrial lineages. We estimate these lineages originated from a diverse pelagic source population, and then rapidly spread throughout and retained the available coastal territory and associated resources around the British Isles. However, the responses to climate change are likely to vary even among mobile species depending on their tolerance to environmental conditions and the derived habitat preference (Foote et al., 2013; Sydeman et al., 2015). Although it seems likely that the amount of available suitable habitat for bottlenose dolphins will increase and expand northwards in the next hundred years with the ongoing warming of the oceans (Appendix S13, Electronic Supplementary Material), the complexity of ecosystems that bottlenose dolphins live in, combined with a range of social behaviors that they exhibit, makes predicting the consequences of the climate change to populations an extremely difficult task.

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Supporting information

Supporting information (Appendices S1-S13) have been uploaded as part of the Electronic Supplementary Material.

Data availability

The datasets supporting this article have been uploaded in dryad at doi:10.5061/dryad.XXXX.

References

Alexander, A., Steel, D., Hoekzema, K., Mesnick, S.L., Engelhaupt, D., Kerr, I., *et al.* 2016. What influences the worldwide genetic structure of sperm whales (*Physeter macrocephalus*)? *Mol. Ecol.* **25**: 2754–2772.

Alter, S.E., Meyer, M., Post, K., Czechowski, P., Gravlund, P., Gaines, C., *et al.* 2015. Climate impacts on transocean dispersal and habitat in gray whales from the Pleistocene to 2100. *Mol. Ecol.* **24**: 1510–1522.

Amaral, A.R., Beheregaray, L.B., Bilgmann, K., Freitas, L., Robertson, K.M., Sequeira, M., *et al.* 2012. Influences of past climatic changes on historical population structure and

Accepted Manuscript

Downloaded from https://academic.oup.com/jhered/advance-article-abstract/doi/10.1093/jhered/esz039/5520132 by University College Cork user on 27 June 2019

demography of a cosmopolitan marine predator, the common dolphin (genus *Delphinus*). *Mol. Ecol.* **21**: 4854–4871.

Avise, J.C. & others. 1998. Pleistocene phylogeographic effects on avian populations and the speciation process. *Proc. R. Soc. Lond. B Biol. Sci.* **265**: 457–463.

Bandelt, H., Forster, P. & Röhl, A. 1999. Median-joining networks for inferring intraspecific phylogenies. Mol. Biol. Evol. **16**: 37–48.

Caballero, S., Jackson, J., Mignucci-Giannoni, A.A., Barrios-Garrido, H., Beltrán-Pedreros, S., Montiel-Villalobos, M.A.G., *et al.* 2008. Molecular systematics of South American dolphins Sotalia: sister taxa determination and phylogenetic relationships, with insights into a multi-locus phylogeny of the Delphinidae. *Mol. Phylogenet. Evol.* **46**: 252–268.

Cacho, I., Grimalt, J.O., Canals, M., Sbaffi, L., Shackleton, N.J., Schönfeld, J., *et al.* 2001. Variability of the western Mediterranean Sea surface temperature during the last 25,000 years and its connection with the Northern Hemisphere climatic changes. *Paleoceanography* **16**: 40–52.

Campbell, M.C. & Tishkoff, S.A. 2008. African Genetic Diversity: Implications for Human Demographic History, Modern Human Origins, and Complex Disease Mapping. *Annu. Rev. Genomics Hum. Genet.* **9**: 403–433.

Catchen, J., Bassham, S., Wilson, T., Currey, M., O'Brien, C., Yeates, Q., *et al.* 2013. The population structure and recent colonization history of Oregon threespine stickleback determined using restriction-site associated DNA-sequencing. *Mol. Ecol.* **22**: 2864–2883.

Charlton-Robb, K., Gershwin, L., Thompson, R., Austin, J., Owen, K. & McKechnie, S. 2011. A New Dolphin Species, the Burrunan Dolphin *Tursiops australis* sp. nov., Endemic to Southern Australian Coastal Waters. *PLoS ONE* **6**: e24047.

Cheney, B., Thompson, P.M., Ingram, S.N., Hammond, P.S., Stevick, P.T., Durban, J.W., *et al.* 2013. Integrating multiple data sources to assess the distribution and abundance of bottlenose dolphins *Tursiops truncatus* in Scottish waters: Abundance of bottlenose dolphins around Scotland. *Mammal Rev.* **43**: 71–88.

Accepted Manuscript

Downloaded from https://academic.oup.com/jhered/advance-article-abstract/doi/10.1093/jhered/esz039/5520132 by University College Cork user on 27 June 2019

Clark, P.U., Archer, D., Pollard, D., Blum, J.D., Rial, J.A., Brovkin, V., *et al.* 2006. The middle Pleistocene transition: characteristics, mechanisms, and implications for long-term changes in atmospheric pCO2. *Quat. Sci. Rev.* **25**: 3150–3184.

Consuegra, S., García de Leániz, C., Serdio, A., González Morales, M., Straus, L.G., Knox, D., *et al.* 2002. Mitochondrial DNA variation in Pleistocene and modern Atlantic salmon from the Iberian glacial refugium. *Mol. Ecol.* **11**: 2037–2048.

Curry, B.E. & Smith, J. 1998. Phylogeographic structure of the bottlenose dolphin (*Tursiops truncatus*): stock identification and implications for management. In: *Molecular genetics of marine mammals* (A. E. Dizon, S. J. Chivers, & W. F. Perrin, eds), pp. 227–247. The Society for Marine Mammalogy, Lawrence, KS.

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nat. Methods* **9**: 772–772.

de Bruyn, M., Hall, B.L., Chauke, L.F., Baroni, C., Koch, P.L. & Hoelzel, A.R. 2009. Rapid Response of a Marine Mammal Species to Holocene Climate and Habitat Change. *PLoS Genet.* **5**: e1000554.

DeGiorgio, M., Jakobsson, M. & Rosenberg, N.A. 2009. Explaining worldwide patterns of human genetic variation using a coalescent-based serial founder model of migration outward from Africa. *Proc. Natl. Acad. Sci.* **106**: 16057–16062.

Deshpande, O., Batzoglou, S., Feldman, M.W. & Luca Cavalli-Sforza, L. 2009. A serial founder effect model for human settlement out of Africa. *Proc. R. Soc. B Biol. Sci.* **276**: 291–300.

Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. 2006. Relaxed Phylogenetics and Dating with Confidence. *PLoS Biol.* **4**: e88.

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. 2012. Bayesian Phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* **29**: 1969–1973.

Drummond, A.J. & Bouckaert, R.R. 2015. *Bayesian evolutionary analysis with BEAST*. Cambridge University Press.

Accepted Manuscript

Downloaded from https://academic.oup.com/jhered/advance-article-abstract/doi/10.1093/jhered/esz039/5520132 by University College Cork user on 27 June 2019

Duchêne, S., Molak, M. & Ho, S.Y.W. 2014. ClockstaR: choosing the number of relaxed-clock models in molecular phylogenetic analysis. *Bioinformatics* **30**: 1017–1019.

Filatova, O.A., Borisova, E.A., Meschersky, I.G., Logacheva, M.D., Kuzkina, N.V., Shpak, O.V., *et al.* 2018. Colonizing the Wild West: Low Diversity of Complete Mitochondrial Genomes in Western North Pacific Killer Whales Suggests a Founder Effect. *J. Hered.*, doi: 10.1093/jhered/esy037.

Finnegan, A.K., Griffiths, A.M., King, R.A., Machado-Schiaffino, G., Porcher, J.P., Garcia-Vazquez, E., *et al.* 2013. Use of multiple markers demonstrates a cryptic western refugium and postglacial colonisation routes of Atlantic salmon (Salmo salar L.) in northwest Europe. *Heredity* **111**: 34–43.

Folland, C.K., Karl, T.R. & Salinger, M.J. 2002. Observed climate variability and change. *Weather* **57**: 269–278.

Fontaine, M.C., Roland, K., Calves, I., Austerlitz, F., Palstra, F.P., Tolley, K.A., *et al.* 2014. Postglacial climate changes and rise of three ecotypes of harbour porpoises, *Phocoena phocoena*, in western Palearctic waters. *Mol. Ecol.* **23**: 3306–3321.

Fontaine, M.C., Tolley, K.A., Michaux, J.R., Birkun, A., Ferreira, M., Jauniaux, T., *et al.* 2010. Genetic and historic evidence for climate-driven population fragmentation in a top cetacean predator: the harbour porpoises in European water. *Proc. R. Soc. B Biol. Sci.* **277**: 2829–2837.

Foote, A.D., Kaschner, K., Schultze, S.E., Garilao, C., Ho, S.Y.W., Post, K., *et al.* 2013. Ancient DNA reveals that bowhead whale lineages survived Late Pleistocene climate change and habitat shifts. *Nat. Commun.* **4**: 1677.

Foote, A.D. & Morin, P.A. 2016. Genome-wide SNP data suggest complex ancestry of sympatric North Pacific killer whale ecotypes. *Heredity*.

Forcada, J. 2009. Distribution. In: *Encyclopedia of Marine Mammals* (W. F. Perrin, B. Wursig, & J. G. M. Thewissen, eds), pp. 316–321. Academic Press, San Diego, CA.

Fu, Y.X. & Li, W.H. 1993. Statistical tests of neutrality of mutations. *Genetics* **133**: 693–709.

Accepted Manuscript

Downloaded from https://academic.oup.com/jhered/advance-article-abstract/doi/10.1093/jhered/esz039/5520132 by University College Cork user on 27 June 2019

Gabriele, C.M., Straley, J.M., Herman, L.M. & Coleman, R.J. 1996. Fastest documented migration of a North Pacific humpback whale. *Mar. Mammal Sci.* **12**: 457–464.

Hamming, R.W. 1950. Error Detecting and Error Correcting Codes. *Bell Syst. Tech. J.* **29**: 147–160.

He, C., Liang, D. & Zhang, P. 2019. Evaluating the Impact of Purifying Selection on Species-level Molecular Dating. *bioRxiv* 622209.

Heller, R., Chikhi, L. & Siegismund, H.R. 2013. The Confounding Effect of Population Structure on Bayesian Skyline Plot Inferences of Demographic History. *PLoS ONE* **8**: e62992.

Henn, B.M., Cavalli-Sforza, L.L. & Feldman, M.W. 2012. The great human expansion. *Proc. Natl. Acad. Sci.* **109**: 17758–17764.

Hersh, S.L. & Duffield, D.A. 1990. Distinction between northwest Atlantic offshore and coastal bottlenose dolphins based on hemoglobin profile and morphometry. In: *The Bottlenose Dolphin*, pp. 129–139. Academic Press, San Diego, CA.

Hewitt, G. 2000. The genetic legacy of the Quaternary ice ages. *Nature* **405**: 907–913.

Hewitt, G.M. 1999. Post-glacial re-colonization of European biota. *Biol. J. Linn. Soc.* **68**: 87–112.

Ho, S.Y.W., Phillips, M.J., Cooper, A. & Drummond, A.J. 2005. Time Dependency of Molecular Rate Estimates and Systematic Overestimation of Recent Divergence Times. *Mol. Biol. Evol.* **22**: 1561–1568.

Ho, S.Y.W. & Lanfear, R. 2010. Improved characterisation of among-lineage rate variation in cetacean mitogenomes using codon-partitioned relaxed clocks. *Mitochondrial DNA* **21**: 138–146.

Ho, S.Y.W., Lanfear, R., Bromham, L., Phillips, M.J., Soubrier, J., Rodrigo, A.G., *et al.* 2011. Time-dependent rates of molecular evolution: Time-dependent rates of molecular evolution. *Mol. Ecol.* **20**: 3087–3101.

Accepted Manuscript

Downloaded from https://academic.oup.com/jhered/advance-article-abstract/doi/10.1093/jhered/esz039/5520132 by University College Cork user on 27 June 2019

Ho, S.Y.W. & Shapiro, B. 2011. Skyline-plot methods for estimating demographic history from nucleotide sequences: Invited technical review. *Mol. Ecol. Resour.* **11**: 423–434.

Hoelzel, A.R., Hey, J., Dahlheim, M.E., 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.

Hoelzel, A.R., Potter, C.W. & Best, P.B. 1998. Genetic differentiation between parapatric 'nearshore'and 'offshore'populations of the bottlenose dolphin. *Proc. R. Soc. Lond. B Biol. Sci.* **265**: 1177–1183.

Hofreiter, M. & Barnes, I. 2010. Diversity lost: are all Holarctic large mammal species just relict populations? *J. Biol.* **9**: 1.

Huelsenbeck, J.P. & Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinforma. Oxf. Engl.* **17**: 754–755.

Ingram, S.N. & Rogan, E. 2002. Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. *Mar. Ecol. Prog. Ser.* **244**: 247–255.

Islas-Villanueva, V. 2010. Genetic Characterisation and Social Structure of the East Scotland Population of Bottlenose Dolphins (*Tursiops truncatus*). University of St Andrews, St Andrews, Scotland.

Jenkins, T.L., Castilho, R. & Stevens, J.R. 2018. Meta-analysis of northeast Atlantic marine taxa shows contrasting phylogeographic patterns following post-LGM expansions. *PeerJ* **6**: e5684.

Kaschner, K., Tittensor, D.P., Ready, J., Gerrodette, T. & Worm, B. 2011. Current and Future Patterns of Global Marine Mammal Biodiversity. *PLoS ONE* **6**: e19653.

Kerey, I.E., Meriç, E., Tunoğlu, C., Kelling, G., Brenner, R.L. & Doğan, A.U. 2004. Black Sea–Marmara Sea Quaternary connections: new data from the Bosphorus, İstanbul, Turkey. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **204**: 277–295.

Kettle, A.J., Morales-Muñiz, A., Roselló-Izquierdo, E., Heinrich, D. & Vøllestad, L.A. 2011. Refugia of marine fish in the northeast Atlantic during the last glacial maximum:

Accepted Manuscript

Downloaded from https://academic.oup.com/jhered/advance-article-abstract/doi/10.1093/jhered/esz039/5520132 by University College Cork user on 27 June 2019

concordant assessment from archaeozoology and palaeotemperature reconstructions. *Clim. Past* **7**: 181–201.

Klimova, A., Phillips, C.D., Fietz, K., Olsen, M.T., Harwood, J., Amos, W., *et al.* 2014. Global population structure and demographic history of the grey seal. *Mol. Ecol.* **23**: 3999–4017.

Krützen, M., Barré, L.M., Möller, L.M., Heithaus, M.R., Simms, C. & Sherwin, W.B. 2002. A biopsy system for small cetaceans: Darting success and wound healing in *Tursiops* spp. *Mar. Mammal Sci.* **18**: 863–878.

Lagerkvist, U. 1978. "Two out of three": an alternative method for codon reading. *Proc. Natl. Acad. Sci. U. S. A.* **75**: 1759–1762.

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. 2012. PartitionFinder: Combined Selection of Partitioning Schemes and Substitution Models for Phylogenetic Analyses. *Mol. Biol. Evol.* **29**: 1695–1701.

Leatherwood, S. & Reeves, R. 1989. *The bottlenose dolphin*. Academic Press, San Diego, CA.

LeDuc, R.G., Perrin, W.F. & Dizon, A.E. 1999. Phylogenetic relationships among the delphinid cetaceans based on full cytochrome b sequences. *Mar. Mammal Sci.* **15**: 619–648.

Leigh, J.W. & Bryant, D. 2015. PopART: Full-feature software for haplotype network construction. *Methods Ecol Evol* **6**: 1110–1116.

Librado, P. & Rozas, J. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* **25**: 1451–1452.

Li, H. & Durbin, R. 2009. Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics* **25**: 1754–1760.

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., *et al.* 2009. The Sequence Alignment/Map format and SAMtools. *Bioinformatics* **25**: 2078–2079.

Lindgreen, S. 2012. AdapterRemoval: easy cleaning of next-generation sequencing reads. *BMC Res. Notes* **5**: 1.

Accepted Manuscript

Downloaded from https://academic.oup.com/jhered/advance-article-abstract/doi/10.1093/jhered/esz039/5520132 by University College Cork user on 27 June 2019

Louis, M., Fontaine, M.C., Spitz, J., Schlund, E., Dabin, W., Deaville, R., *et al.* 2014a. Ecological opportunities and specializations shaped genetic divergence in a highly mobile marine top predator. *Proc. R. Soc. B Biol. Sci.* **281**: 20141558–20141558.

Louis, M., Gally, F., Barbraud, C., Béesau, J., Tixier, P., Simon-Bouhet, B., *et al.* 2015. Social structure and abundance of coastal bottlenose dolphins, *Tursiops truncatus*, in the Normano-Breton gulf, English Channel. *J. Mammal.* **96**: 481–493.

Louis, M., Viricel, A., Lucas, T., Peltier, H., Alfonsi, E., Berrow, S., *et al.* 2014b. Habitat-driven population structure of bottlenose dolphins, *Tursiops truncatus*, in the North-East Atlantic. *Mol. Ecol.* **23**: 857–874.

Lowther-Thieleking, J.L., Archer, F.I., Lang, A.R. & Weller, D.W. 2015. Genetic differentiation among coastal and offshore common bottlenose dolphins, *Tursiops truncatus*, in the eastern North Pacific Ocean. *Mar. Mammal Sci.* **31**: 1–20.

Mate, B.R., Nieukirk, S.L. & Kraus, S.D. 1997. Satellite-Monitored Movements of the Northern Right Whale. *J. Wildl. Manag.* **61**: 1393.

McGowen, M.R., Spaulding, M. & Gatesy, J. 2009. Divergence date estimation and a comprehensive molecular tree of extant cetaceans. *Mol. Phylogenet. Evol.* **53**: 891–906.

Meyer, M. & Kircher, M. 2010. Illumina Sequencing Library Preparation for Highly Multiplexed Target Capture and Sequencing. *Cold Spring Harb. Protoc.* **2010**: pdb.prot5448-pdb.prot5448.

Mirimin, L., Miller, R., Dillane, E., Berrow, S.D., Ingram, S., Cross, T.F., *et al.* 2011. Fine-scale population genetic structuring of bottlenose dolphins in Irish coastal waters: Population genetic structure of bottlenose dolphins. *Anim. Conserv.* **14**: 342–353.

Montgomery, W.I., Provan, J., McCabe, A.M. & Yalden, D.W. 2014. Origin of British and Irish mammals: disparate post-glacial colonisation and species introductions. *Quat. Sci. Rev.* **98**: 144–165.

Morin, P.A., Parsons, K.M., Archer, F.I., Ávila-Arcos, M.C., Barrett-Lennard, L.G., Dalla Rosa, L., *et al.* 2015. Geographic and temporal dynamics of a global radiation and diversification in the killer whale. *Mol. Ecol.* **24**: 3964–3979.

Accepted Manuscript

Downloaded from https://academic.oup.com/jhered/advance-article-abstract/doi/10.1093/jhered/esz039/5520132 by University College Cork user on 27 June 2019

Moura, A.E., Nielsen, S.C.A., Vilstrup, J.T., Moreno-Mayar, J.V., Gilbert, M.T.P., Gray, H.W.I., *et al.* 2013. Recent Diversification of a Marine Genus (*Tursiops* spp.) Tracks Habitat Preference and Environmental Change. *Syst. Biol.* **62**: 865–877.

Natoli, A., Birkun, A., Aguilar, A., Lopez, A. & Hoelzel, A.R. 2005. Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). *Proc. R. Soc. B Biol. Sci.* **272**: 1217–1226.

Nykänen, M., Dillane, E., Englund, A., Foote, A.D., Ingram, S.N., Louis, M., *et al.* 2018. Quantifying dispersal between marine protected areas by a highly mobile species, the bottlenose dolphin, *Tursiops truncatus*. *Ecol. Evol.*, doi: 10.1002/ece3.4343.

O'Brien, J., Berrow, S., Ryan, C., McGrath, D., O'Connor, I., Giovanna, P., *et al.* 2009. A note on long-distance matches of bottlenose dolphins (*Tursiops truncatus*) around the Irish coast using photo-identification. *J. Cetacean Res. Manag.*

Ogilvie, H.A., Bouckaert, R.R. & Drummond, A.J. 2017. StarBEAST2 Brings Faster Species Tree Inference and Accurate Estimates of Substitution Rates. *Mol. Biol. Evol.* **34**: 2101–2114.

Paradis, E. 2010. pegas: an R package for population genetics with an integrated-modular approach. *Bioinformatics* **26**: 419–420.

Posada, D. 2008. jModelTest: Phylogenetic Model Averaging. *Mol. Biol. Evol.* **25**: 1253–1256.

Post, K. 2005. A Weichselian marine mammal assemblage from the southern North Sea. *DEINSEA* **11**: 21–27.

Quérouil, S., Silva, M.A., Freitas, L., Prieto, R., Magalhães, S., Dinis, A., *et al.* 2007. High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. *Conserv. Genet.* **8**: 1405–1419.

R Core Team. 2016. *R: A language and environment for statistical computing. R Foundation for Statistical Computing*. Vienna, Austria.

Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. 2014. *Tracer v1.6*.

Accepted Manuscript

Downloaded from https://academic.oup.com/jhered/advance-article-abstract/doi/10.1093/jhered/esz039/5520132 by University College Cork user on 27 June 2019

Ramos-Onsins, S.E. & Rozas, J. 2002. Statistical properties of new neutrality tests against population growth. *Mol. Biol. Evol.* **19**: 2092–2100.

Ready, J., Kaschner, K., South, A.B., Eastwood, P.D., Rees, T., Rius, J., *et al.* 2010. Predicting the distributions of marine organisms at the global scale. *Ecol. Model.* **221**: 467–478.

Revell, L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other things): phytools: R package. *Methods Ecol. Evol.* **3**: 217–223.

Ronquist, F. & Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.

Robinson, K.P., O'Brien, J., Berrow, S., Cheney, B., Costa, M., Elsfield, S.M., *et al.* 2012. Discrete or not so discrete: Long distance movements by coastal bottlenose dolphins in UK and Irish waters. *J. Cetacean Res. Manag.*

Schäfer-Neth, C. & Paul, A. 2003. The Atlantic Ocean at the Last Glacial Maximum: 1. Objective Mapping of the GLAMAP Sea-Surface Conditions. In: *The South Atlantic in the Late Quaternary* (G. Wefer, S. Mulitza, & V. Ratmeyer, eds), pp. 531–548. Springer Berlin Heidelberg, Berlin, Heidelberg.

Shackleton, N.J. 2000. The 100,000-year ice-age cycle identified and found to lag temperature, carbon dioxide, and orbital eccentricity. *Science* **289**: 1897–1902.

Steeman, M.E., Hebsgaard, M.B., Fordyce, R.E., Ho, S.Y.W., Rabosky, D.L., Nielsen, R., *et al.* 2009. Radiation of Extant Cetaceans Driven by Restructuring of the Oceans. *Syst. Biol.* **58**: 573–585.

Stewart, J.R., Lister, A.M., Barnes, I. & Dalen, L. 2010. Refugia revisited: individualistic responses of species in space and time. *Proc. R. Soc. B Biol. Sci.* **277**: 661–671.

Sukumaran, J. & Knowles, L.L. 2017. Multispecies coalescent delimits structure, not species. *Proc. Natl. Acad. Sci.* **114**: 1607–1612.

Sydeman, W.J., Poloczanska, E., Reed, T.E. & Thompson, S.A. 2015. Climate change and marine vertebrates. *Science* **350**: 772–777.

Accepted Manuscript

Downloaded from https://academic.oup.com/jhered/advance-article-abstract/doi/10.1093/jhered/esz039/5520132 by University College Cork user on 27 June 2019

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

Tamura, K., Dudley, J., Nei, M. & Kumar, S. 2007. MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) Software Version 4.0. *Mol. Biol. Evol.* **24**: 1596–1599.

Tamura, K. & Nei, M. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Mol. Biol. Evol.* **10**: 512–526.

Taylor, B.K., Chivers, S., Larese, J., & Perrin, W. 2007. Generation length and percent mature estimates for IUCN assessments of cetaceans. NOAA, NMFS, Southwest Fisheries Science Center Administrative Report LJ-07-01.

Tezanos-Pinto, G., Baker, C.S., Russell, K., Martien, K., Baird, R.W., Hutt, A., *et al.* 2008. A Worldwide Perspective on the Population Structure and Genetic Diversity of Bottlenose Dolphins (*Tursiops truncatus*) in New Zealand. *J. Hered.* **100**: 11–24.

Tilak, M.-K., Justy, F., Debiais-Thibaud, M., Botero-Castro, F., Delsuc, F. & Douzery, E.J.P. 2015. A cost-effective straightforward protocol for shotgun Illumina libraries designed to assemble complete mitogenomes from non-model species. *Conserv. Genet. Resour.* **7**: 37–40.

Tucker, V.A. 1975. The energetic cost of moving about: walking and running are extremely inefficient forms of locomotion. Much greater efficiency is achieved by birds, fish—and bicyclists. *Am. Sci.* **63**: 413–419.

Vilstrup, J.T., Ho, S.Y., Foote, A.D., Morin, P.A., Kreb, D., Krützen, M., *et al.* 2011. Mitogenomic phylogenetic analyses of the Delphinidae with an emphasis on the Globicephalinae. *BMC Evol. Biol.* **11**: 1.

Wells, R. & Scott, M.D. 2009. Common bottlenose dolphin (*Tursiops truncatus*). In: *Encyclopedia of Marine Mammals. Second Edition* (W. Perrin, B. Wursig, & J. Thewissen, eds), pp. 249–255. Elsevier, San Diego, California.

Williams, T.M. 1999. The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **354**: 193–201.

Accepted Manuscript

Downloaded from https://academic.oup.com/jhered/advance-article-abstract/doi/10.1093/jhered/esz039/5520132 by University College Cork user on 27 June 2019

Williams, T.M., Friedl, W.A., Fong, M.L., Yamada, R.M., Sedivy, P. & Haun, J.E. 1992. Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. *Nature* **355**: 821–823.

Yanko-Hombach, V., Gilbert, A.S. & Dolukhanov, P. 2007. Controversy over the great flood hypotheses in the Black Sea in light of geological, paleontological, and archaeological evidence. *Quat. Int.* **167–168**: 91–113.

Younger, J.L., van den Hoff, J., Wienecke, B., Hindell, M. & Miller, K.J. 2016. Contrasting responses to a climate regime change by sympatric, ice-dependent predators. *BMC Evol. Biol.* **16**.

Table and figure captions

Table 1. Summary statistics of genetic diversity and the site frequency spectra used to infer recent population expansion/contraction in Northeast Atlantic bottlenose dolphin populations. Only the sequences generated for this study (N=30) have been included in the analyses.

Figure 1. (a) *Tursiops* spp. haplotypes retrieved from GenBank and the approximate sampling location of the species/populations they represent; SABD – *T. australis* (South Australia, N=7), SA – *T. aduncus* (South Africa, N=10), IPTA – *T. aduncus* (Southeast Australia, N=10), WNAC – *T. truncatus* (coastal Northwest Atlantic, N=9), EMED – *T. truncatus* (Eastern Mediterranean Sea, N=10), BSEA – *T. truncatus ponticus* (Black Sea, N=10). (b) the biopsy/stranding locations of the 30 new *T. truncatus* samples sequenced for this study with the populations represented by the different symbols; PEA – *T. truncatus*, pelagic (Northeast Atlantic, N=11), CS – *T. truncatus*, Coastal South (Northeast Atlantic, N=5), CN – *T. truncatus*, Coastal North (Northeast Atlantic, N=14). Note that some of the sample locations overlap in map (b). The area in map (b) is marked with the rectangle in map (a). See online version for full color.

Figure 2. AquaMaps suitable habitat map for *T. truncatus* for (a) the present day, and (b) the Last Glacial Maximum in the North Atlantic. White to red colors represent least to most suitable habitat, respectively, and land is shown in light gray. Dark green color in Fig. (b) represents areas with permanent ice sheet and light green color areas with >50% sea ice concentration. The predictions for the entire world are given in Appendix S3.

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Figure 3. Time-calibrated phylogenetic tree depicting the effective population size *(N_e)* over time, shown only for the Northeast Atlantic *T. truncatus* populations and estimated with StarBEAST2 model 'Linear with Constant Root Populations', using only the third codon positions from 13 mitochondrial genes. The numbers in rectangles are node posterior probabilities, numbers below nodes median node ages, and the bars represent 95% HPDI in node TMRCA. The width of the line depicts N_e with the values given in Appendix S11. The tips represent current populations/species and their sampling locations, see Fig. 1. The full *Tursiops* species trees are shown in Appendix S9, Electronic Supplementary Material.

Figure 4. Median-joining haplotype network of North Atlantic (including Mediterranean and Black Seas) *T. truncatus* based on 16,390 bp mtDNA sequence constructed in PopART. Haplotypes (circles) have been assigned a color based on population assignment in previous studies and their sampling locations (see Fig. 1). The size of the circle represents the frequency of occurrence of each haplotype and the number inside it the number of individuals. Mutational steps between haplotypes are indicated by hatch marks and small black circles are missing haplotypes. See online version for full color.

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Tables and figures

Table 1. Summary statistics of genetic diversity and the site frequency spectra used to infer recent population expansion/contraction in Northeast Atlantic bottlenose dolphin populations. Only the sequences generated for this study (N=30) have been included in the analyses.

Population	*k*	π_{nuc}	π_{hap}	Tajima's *D*	Fu and Li's *D**	Fu and Li's *F**	Ramos-Onsins & Rozas' R_2
Pelagic (PEA, n=11)	247	0.0044†	1.000††	-0.722	-0.325	-0.552	0.111
Coastal North (CN, n=14)	66	0.0021	0.780	2.641	1.461	2.253	0.245
Coastal South (CS, n=5)	64	0.0016	0.900	-1.119	-0.321	-0.613	0.330

k = number of segregating sites, i.e. polymorphisms

π_{nuc}/π_{hap} = nucleotide/haplotype diversity

* an outgroup (*Steno bredanensis*) was used in the calculations of the indices

† = significant difference atα=0.05 level was detected between the pelagic and both of the coastal populations

†† = significant difference atα=0.05 level was detected between the pelagic and the Coastal North population

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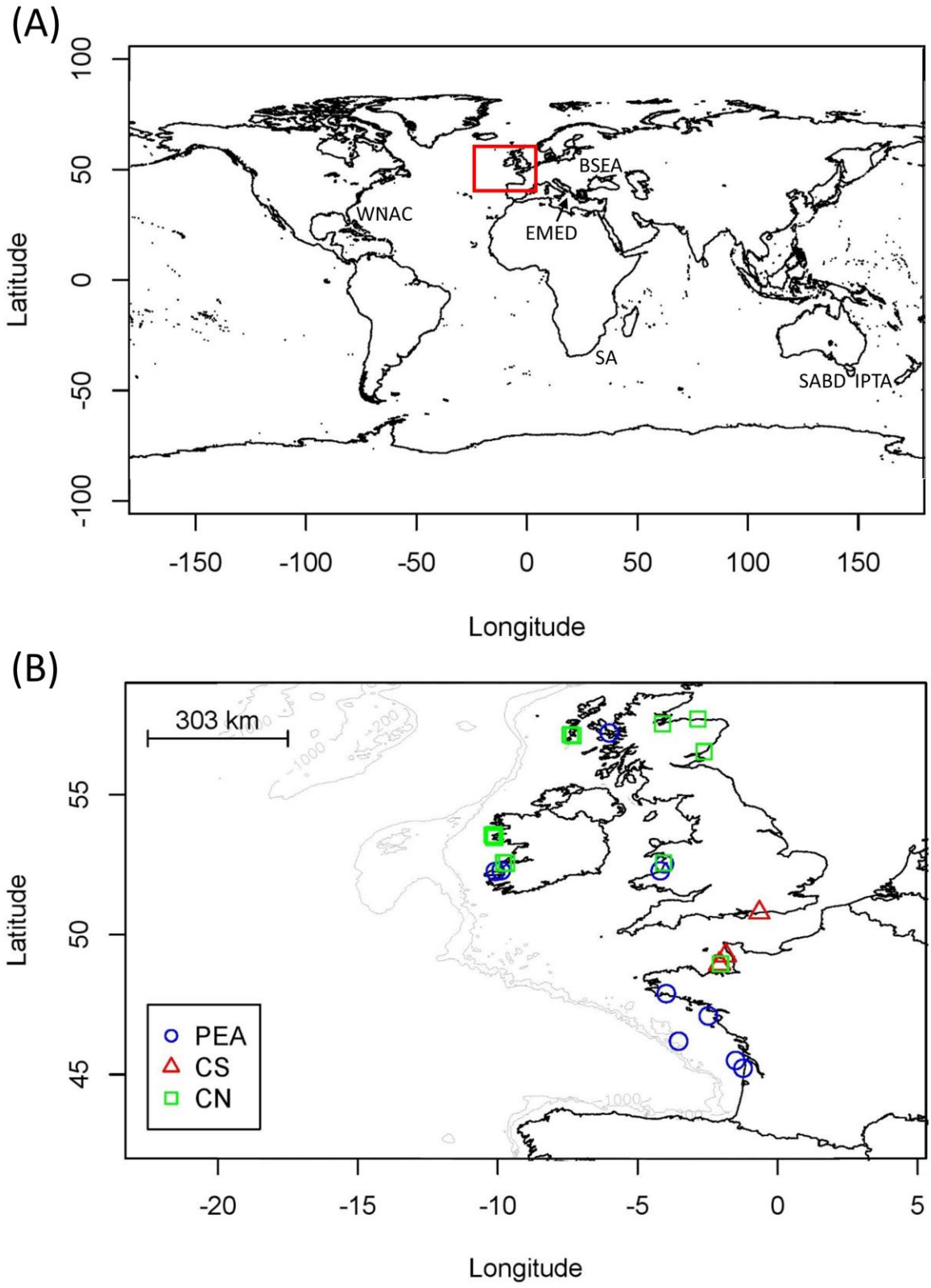


Figure 1

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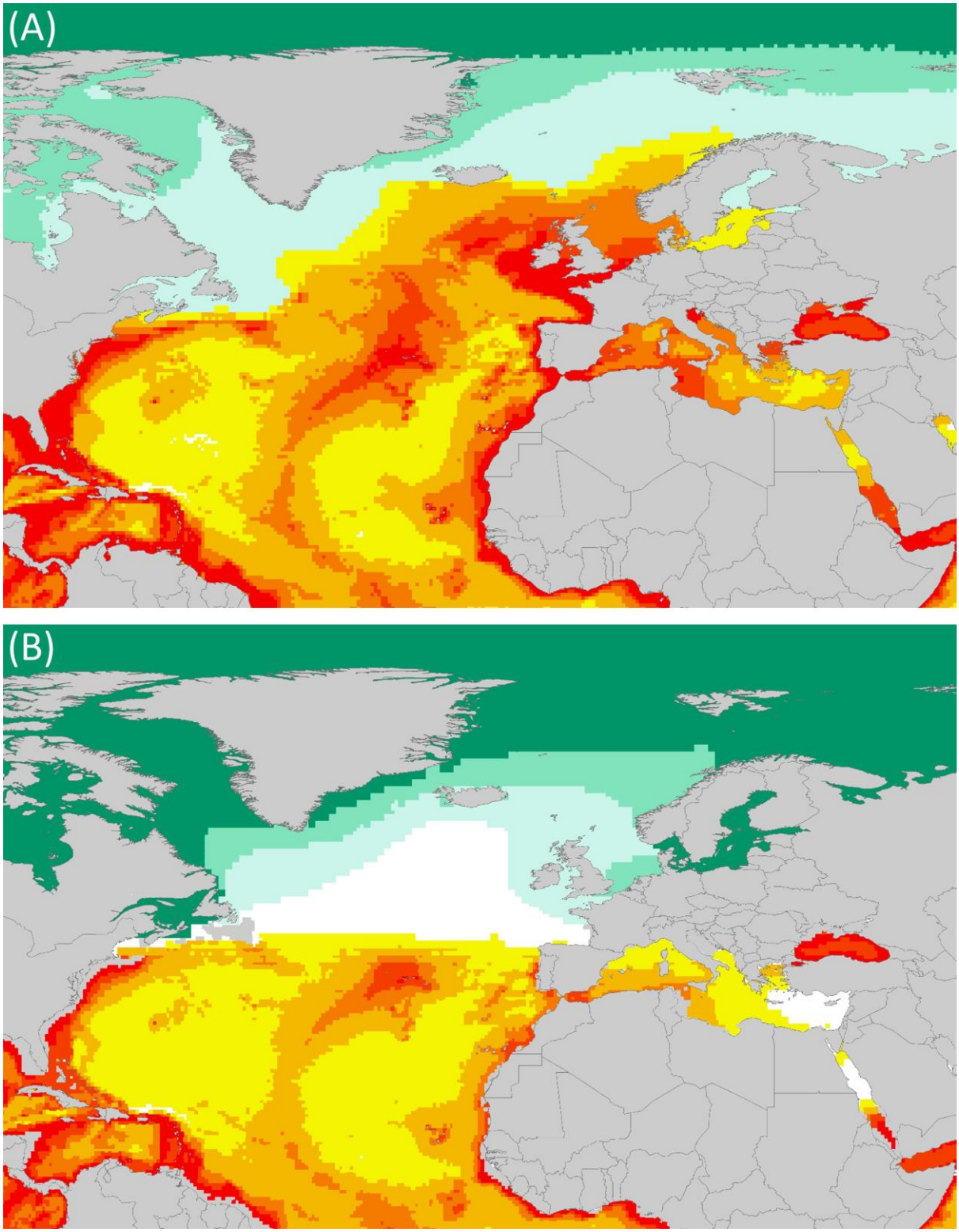


Figure 2

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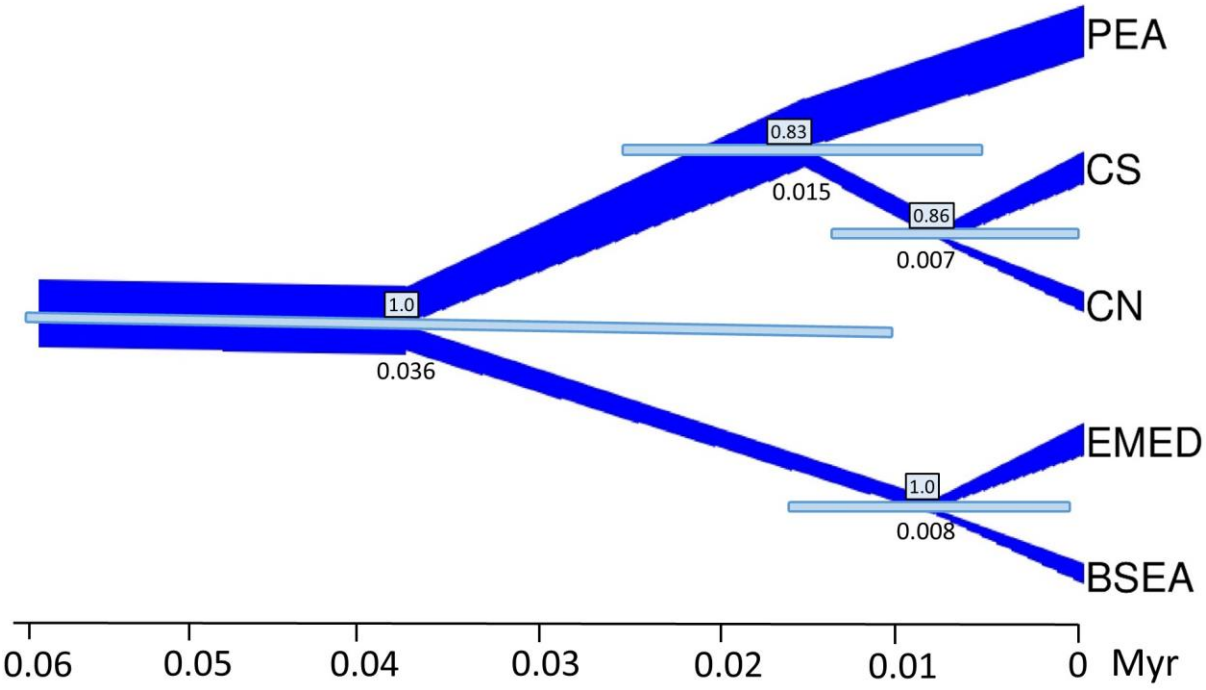


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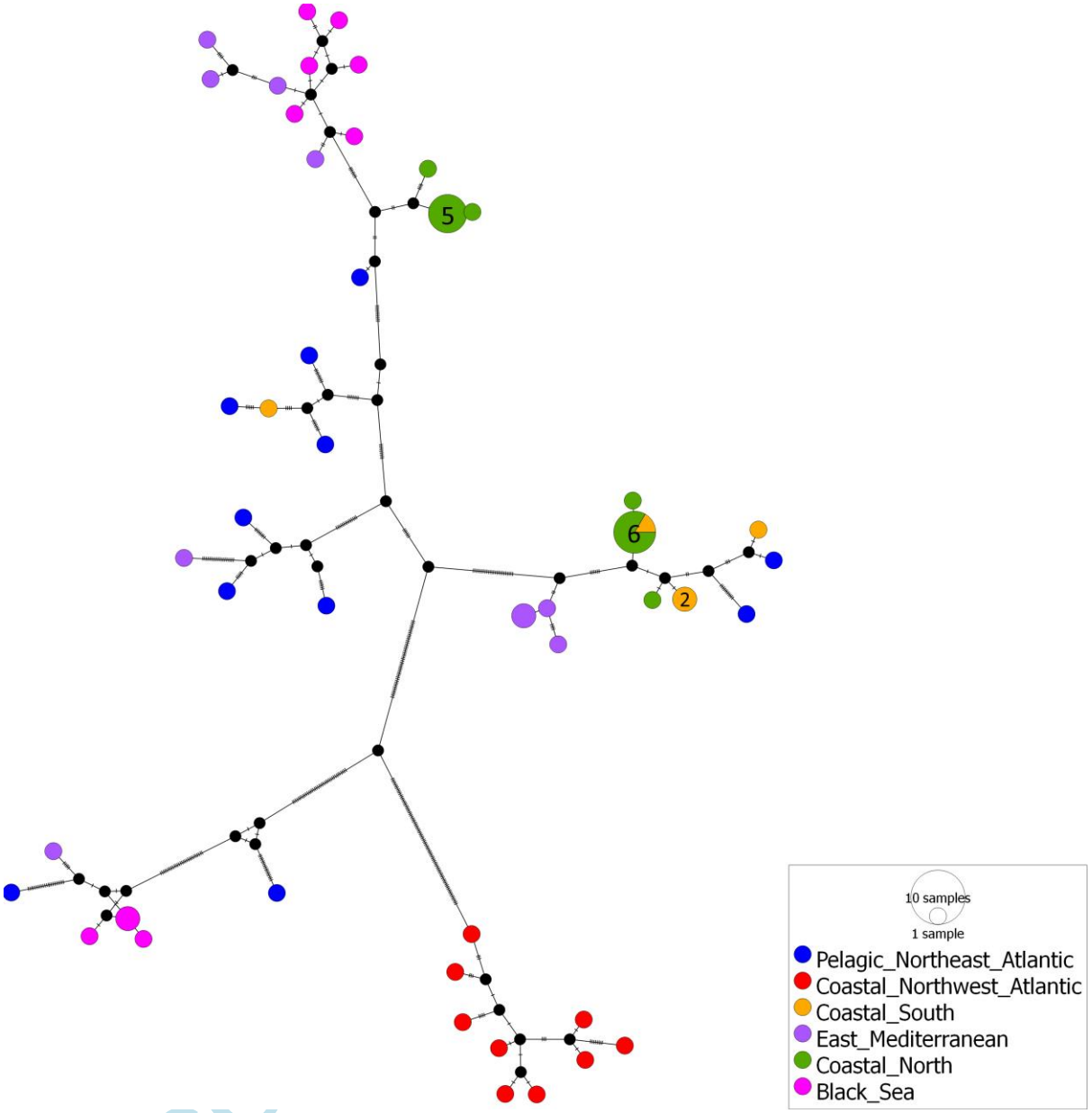


Figure 4

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