MOLECULAR ECOLOGY

Climate impacts on transocean dispersal and habitat in gray whales from the Pleistocene to 2100

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Abstract

Arctic animals face dramatic habitat alteration due to ongoing climate change. Understanding how such species have responded to past glacial cycles can help us forecast their response to today's changing climate. Gray whales are among those marine species likely to be strongly affected by Arctic climate change, but a thorough analysis of past climate impacts on this species has been complicated by lack of information about an extinct population in the Atlantic. While little is known about the history of Atlantic gray whales or their relationship to the extant Pacific population, the extirpation of the Atlantic population during historical times has been attributed to whaling. We used a combination of ancient and modern DNA, radiocarbon dating and predictive habitat modelling to better understand the distribution of gray whales during the Pleistocene and Holocene. Our results reveal that dispersal between the Pacific and Atlantic was climate dependent and occurred both during the Pleistocene prior to the last glacial period and the early Holocene immediately following the opening of the Bering Strait. Genetic diversity in the Atlantic declined over an extended interval that predates the period of intensive commercial whaling, indicating this decline may have been precipitated by Holocene climate or other ecological causes. These first genetic data for Atlantic gray whales, particularly when combined with predictive habitat models for the year 2100, suggest that two recent sightings of gray whales in the Atlantic may represent the beginning of the expansion of this species' habitat beyond its currently realized range.

Keywords: ancient DNA, climate change, last glacial maximum, marine mammal

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Introduction

Climate change is causing dramatic shifts in distribution and habitat availability across a broad range of taxa and ecosystems, particularly those in high northern latitudes (Parmesan 2006; Burrows *et al.* 2011; Hazen *et al.* 2013). As boreal species adjust their distributions to correspond to physiological tolerances and other factors, range changes are being documented across diverse taxa, including marine fishes, invertebrates and mammals (e.g. Moore *et al.* 2003; Perry *et al.* 2005; Mecklenburg *et al.* 2007; Mueter & Litzow 2008). An additional likely consequence of warming in the Arctic is large-scale marine faunal exchange between ocean basins due to drastic declines in Arctic sea-ice barriers (Vermeij & Roopnarine 2008). However, predicting the response to climate change of long-lived, migratory species, including many marine mammals, remains extremely challenging (Hazen *et al.* 2013). Distribution and dispersal patterns in such species depend on a complex set of factors including prey availability, behavioural imprinting and history of exploitation, raising the question of how quickly range adjustments can occur.

Ancient DNA data isolated from the remains of individuals that lived within the last hundred thousand or so years have been used to infer the impacts of climate on population dynamics and distribution in a number of long-lived taxa, including marine mammals (De Bruyn *et al.* 2009; Edwards *et al.* 2011; Alter *et al.* 2012a; Foote *et al.* 2013). However, unlike for many terrestrial species (Shapiro *et al.* 2004; Lorenzen *et al.* 2011), inferences for marine species have been limited due to challenges of sample availability across broad geographic scales. Despite the fact that fossil preservation in marine environments can be superior to that of terrestrial environments due to protection from UV radiation and high temperatures, sample collection has thus far been limited to relatively few areas (Foote *et al.* 2012). Here, we overcome some of the challenges of marine fossil availability by combining ancient DNA data with predictive habitat modelling based on observed species distributions. This approach has great potential for achieving a more comprehensive understanding of the role of climate in shaping range patterns, in particular for marine species that inhabit rapidly changing polar and subpolar habitats.

Among marine species, gray whales (*Eschrichtius robustus*) represent an important example of climate-related distribution shifts. These migratory baleen whales spend approximately half of the year in Arctic and sub-Arctic regions, where climate change is rapidly reshaping ecosystems, and a northward shift in feeding range, among other population changes, has been attributed to climate impacts on benthic habitats (Moore *et al.* 2003; Moore 2008). Today, gray whales survive in geographically separate eastern and western populations in the North Pacific Ocean, with subtle genetic structure observed both between these populations (LeDuc *et al.* 2002) and among feeding (Lang *et al.* 2014) and breeding (Alter *et al.* 2009) groups in the eastern Pacific. However, radiometric dating of subfossil remains shows that gray whales were also present in the Atlantic Ocean during the Holocene (Bryant 1995) and Pleistocene (Noakes *et al.* 2013). Among baleen whale populations, gray whales stand out as the only species to have gone extinct in an entire ocean basin during historical times. Until two very recent sightings, the first off the coasts of Israel and Spain in 2010 (Scheinin *et al.* 2011) and the second off the coast of Namibia in 2013 (Paterson 2013), and no gray whales had been sighted in the Atlantic Ocean since at least the mid-nineteenth century (Mead & Mitchell 1984). These more recent sightings have been interpreted as extralimital movements from the eastern Pacific population and are not believed to reflect a newly established or relict Atlantic population (e.g. Scheinin *et al.* 2011). However, these unusual occurrences, similar to others documented recently in other marine mammals (Heide-Jorgensen *et al.* 2012), may be of importance in understanding new patterns of increased trans-Arctic faunal exchange due to loss of Arctic sea ice.

Prior to our study, only 21 fossil and subfossil gray whale specimens had been reported from the Atlantic Ocean: eleven from the western Atlantic (Mead & Mitchell 1984; Noakes *et al.* 2013) and ten from the eastern Atlantic (Bryant 1995; Macé 2003). The most recent of these was dated to ~1675 AD (Mead & Mitchell 1984). Written information about Atlantic gray whales is also relatively scarce; in a review of historical whaling literature, Mead & Mitchell (1984) determined that only three whaling accounts from the North Atlantic reliably describe gray whales. Despite this scarcity of written and fossil information, Mead and Mitchell concluded that gray whales were once common in the Atlantic. Although they do not directly attribute the decline of Atlantic gray whales to historical-era whaling, this idea has persisted in the literature (e.g. Bryant 1995; Pompa *et al.* 2011).

Little is known about the evolutionary relationship between Pacific gray whales and the extinct population of Atlantic gray whales. Both the fossil and subfossil records of gray whales are relatively sparse. The oldest fossils classified as *Eschrichtius* were discovered in Hokkaido, Japan (Ichishima *et al.* 2006), suggesting modern gray whales evolved in the Pacific, although the fossil record indicates that members of the family

Eschrichtiidae spanned both ocean basins (Deméré *et al.* 2005; Bisconti & Varola 2006; Bisconti 2008). However, it remains unknown whether the Atlantic and Pacific gray whale populations evolved as isolated populations over long evolutionary time, as is the case for most other baleen whales found in both the Atlantic and Pacific (e.g. Baker *et al.* 1993; Rosenbaum *et al.* 2000), or whether migration between the two populations occurred with some frequency.

Like that of other polar and subpolar marine mammals, the biogeographic history of Atlantic and Pacific gray whales was probably shaped by climate shifts during the Pleistocene ice ages, which would have affected both the availability of dispersal routes and the distribution of benthic habitat. Gray whales typically spend part of each year feeding on shallow shelf habitat in high-latitude waters, but are not well adapted for moving through consolidated or heavy sea ice (Moore *et al.* 2003). Because of the massive ice sheets that occupied most of the continental shelves bordering the Arctic Ocean during the last glacial period, large-scale migration through the Arctic Ocean is thought to have last been possible during the previous interglacial period (MIS 5e, 130–115 thousand years [ka] ago; (Darby *et al.* 2006)). Moreover, during roughly the last 10–70 ka, the closure of the Bering Strait due to low epistatic sea level would have prevented migration via an Arctic route (Hu *et al.* 2010). Changes in the extent of sea ice and global sea levels would have also altered the distribution of benthic habitats. Gray whales use a modified mode of suction-feeding to forage on benthic invertebrates along shallow continental shelves, although they are also capable of generalized filter feeding in the water column. During the last glacial maximum (LGM, 26.5–19 ka ago; Clark *et al.* 2009), extensive sea ice covered much of the potential habitat in the high-latitude North Atlantic, and it is unclear whether gray whales persisted in the Atlantic through this period or recolonized the Atlantic from the Pacific following the end of the LGM.

To investigate the population history of the Atlantic population in the context of climate change and to determine the frequency and timing of gene flow between Pacific and Atlantic gray whale populations, we combined phylogenetic reconstruction of ancient and modern mitochondrial DNA sequences and predictive habitat modelling. We compared mitochondrial DNA isolated from 33 Atlantic gray whale subfossils, including 24 newly reported specimens, with DNA sequences from modern and ancient Pacific gray whales. We also used an environmental envelope modelling approach (AquaMaps, Ready *et al.* 2010) to predict gray whale distributions for three time points: the present, the LGM and the year 2100. Our results provide new insights into the impacts of long-term climate changes on transoceanic dispersal and habitat distribution of gray whales and demonstrate the broader utility of combining ancient DNA data with predictive habitat modelling to forecast the effects of climate change on marine fauna.

Methods

Genetic data collection

We extracted DNA from 33 Atlantic gray whale subfossils, including nine of the 21 Atlantic gray whale subfossils that had been identified previously and 24 vertebrae that were dredged from the North Sea between 1995 and 2007. We used between 50 and 3000 mg of bone powder from each individual, along with one negative control (no bone powder) per every seven samples. We performed DNA extraction in a dedicated ancient DNA clean laboratory using the extraction technique described by Rohland & Hofreiter (2007). Briefly, bone powder was digested overnight at room temperature in a simple extraction buffer (0.45 M EDTA, pH 8.0 and 0.25 mg/mL proteinase K) and DNA was extracted using a silica suspension in the presence of a binding buffer. We reconstructed a 510-bp region of the mitochondrial control region by amplifying multiple overlapping fragments in 60-cycle singleplex PCRs using AmpliTaq Gold polymerase (Applied Biosystems) or in multiplex PCR as described by Römpler *et al.* (2006). Using various combinations of PCR primers (available from the authors on request), we first attempted to amplify long fragments (~350 bp) and, if unsuccessful, successively reduced amplicon size to ~100 bp to increase the chance of successful amplification from samples with poor DNA preservation. To control for potential contamination, we used at least one negative PCR control (water) and one negative extraction control as template with each primer pair every time a PCR was set up. Amplification products were visualized on 2% agarose gels, and the absence of contamination was inferred from the absence of target-sized bands in the negative controls.

Most of the PCR products were sequenced using a cloning and Sanger sequencing strategy as described by Rohland *et al.* (2007). We sequenced the remaining PCR products on the Genome Sequencer FLX system (Roche/454), using sample barcoding and pooling (Meyer *et al.* 2008). We obtained at least three clones or 454 sequences for each PCR product and built a consensus sequence based on majority rule. To exclude errors arising from miscoding modifications in ancient DNA, we determined each position twice by independent PCR amplification and sequencing. We observed no

consistent differences other than C/T or G/A changes, which are expected to occur as a result of cytosine deamination in ancient DNA (Hofreiter *et al.* 2001). If consensus sequences conflicted at any position, we further replicated amplification and sequencing to reveal the real state. Atlantic gray whale haplotypes were deposited in NCBI (see Table S1, Supporting information).

We collected previously published mitochondrial control region sequences from modern and ancient (Holocene) gray whales from the eastern and western Pacific Ocean (LeDuc *et al.* 2002; Alter *et al.* 2012b) from the NCBI database. We aligned modern and ancient sequences using CLUSTAL X (Larkin *et al.* 2007) and trimmed the resulting alignment to 511 bp.

Radiocarbon dating

Most ^{14}C dates were obtained using accelerator mass spectrometry (AMS) measurements from three laboratories: Groningen (GrA), Kiel (KIA) and Oxford (OxA). For seven samples, ^{14}C dates (radiometrically dated) were obtained from the literature (Mead & Mitchell 1984; Bryant 1995). One sample was dated by radiometry in Groningen (GrN).

We extracted bone collagen according to an improved version of the protocol developed by Longin (1971). Briefly, extracted collagen is combusted into purified CO_2. This is used as counting gas in proportional counters for radiometry (GrN). For AMS, the CO_2 is converted into graphite, which is used in the ion source of the AMS (GrA, KIA and OxA). The three laboratories have similar AMS machines, based on a 2.5 MV tandetron accelerator manufactured by High Voltage Engineering Europa (Amersfoort, the Netherlands; e.g. Van der Plicht & Hogg 2006). For both radiometry and AMS, the $^{14}C/^{12}C$ ratios are measured. The ^{14}C ages are reported by convention in BP, that is relative to the ^{14}C radioactivity of the oxalic acid standard, including correction for isotopic fractionation by means of the stable isotope ratio $^{13}C/^{12}C$ to $^{13}\delta = -25‰$ (details provided by Mook & Streurman 1983; Tables 1 and S1). The observed values all fall within the range of marine mammal bone collagen. These values are not available for the data taken from the literature (Mead & Mitchell 1984; Bryant 1995).

Radiocarbon dates for marine organisms show an offset from atmospheric/terrestrial organisms, the so-called reservoir effect. This effect occurs when the carbon that is incorporated into a sample during life is not in equilibrium with the contemporary atmosphere. This gives the sample an apparent radiocarbon age which is older than that of a contemporary terrestrial sample. For the Northern Atlantic, this is generally taken as

400 years on the ^{14}C timescale (e.g. Reimer *et al.* 2013). The ^{14}C dates from our samples shown in Table 1 are given as conventional years BP; that is, no reservoir effect has been subtracted. The values taken from Bryant (1995) were corrected for this effect; therefore, we have added 400 years to their values, in order to be able to work with numbers on the same scale. It is not known whether the values from the study by Mead & Mitchell (1984) were corrected for the reservoir effect, so we left these dates as published in BP (i.e. we assume they were not reservoir-corrected). In addition, because the ^{14}C dates are reported on a defined timescale (BP), the ^{14}C dates need calibration to obtain calendar ages. The internationally accepted calibration curves are IntCal13 and Marine13 for terrestrial and marine samples, respectively (Reimer *et al.* 2013). Calibrated dates are shown in Table 1, reported in calBP, which is defined as calendar age relative to 1950 AD (e.g. Van der Plicht & Hogg 2006). All uncertainties in the table are given at 1-sigma confidence level. All numbers are rounded to the nearest 5 or 10, depending on significance.

Genetic data analysis

We estimated the evolutionary relationships among individuals in the complete data set using the Bayesian phylogenetic inference package BEAST v1.8 (Drummond & Rambaut 2007). We used the HKY + G model of nucleotide substitution determined in prior studies (Alter & Palumbi 2009), a model that incorporates gamma-distributed variation in rates across sites, with the ages (calibrated radiocarbon dates or stratigraphically assigned ages) of ancient and historical specimens incorporated as prior information. For six specimens with infinite radiocarbon dates (SP1415, SP1417, SP1455, SP1461, SP1818 and SP1822), we sampled the age as described by Shapiro *et al.* (2011) from a lognormal distribution with a mean of 9.76 and standard deviation of 0.47, so that 95% of sampled values were contained within the interval 48–85 ka ago. The interval for this prior, which is not strict but rather concentrates density of sampling within this range, was determined based on radiocarbon dates of marine mammal samples and stratigraphic data from the North Sea (e.g. Hijma & Cohen 2011), as well as upper limits on the survival of ancient DNA.

Given the shallow temporal depth of the data set, it was not appropriate to calibrate the molecular clock using a (fossil) calibration at the root of the tree (Ho *et al.* 2008). Serially sampled sequences provide an alternate means to calibrate the molecular clock and may be more appropriate for within-population data (Ho *et al.* 2008). To assess whether our data set contained sufficient temporal signal to calibrate the molecular clock,

Table 1 Sample information for all Atlantic gray whales used in this study. Additional sample details are available in online supporting information (Table S1)

Sample no.	Collection no./citation	Type (skeletal element)	Collection locality	Collection date	Age calBP (1-sigma)
SP1058	NMR999100001877[*]	Mandible, juv.	North Sea, the Netherlands	2001	1150–1270
SP1059	n/a	n/a	North Sea, the Netherlands	n/a	1350–1500
SP1345	NMR999100001783[*]	Mandible, juv.	North Sea, the Netherlands	1997	1350–1500
SP1347	NMR999100001780[*]	Cervical vertebra	North Sea, the Netherlands	2003	2650–2730
SP1369	n/a	Vertebra	North Sea, the Netherlands	n/a	>48 000
SP1415	NMR999100001938[*]	Large vertebra	North Sea, the Netherlands	2005	>48 000
SP1417	NMR999100001781[*]	Half atlas, juv.	North Sea, the Netherlands	2003	42 500–43 300
SP1446	Leiden NML 13130[†]	Skull	North Sea, the Netherlands	1879	9470–9550
SP1447	Leiden NML 630[†]	Skull	North Sea, the Netherlands	1916	1600–1800
SP1448	Leiden NML 20350[†]	Skull	North Sea, the Netherlands	1935	4760–4850
SP1449	NMR9990-00082[*]	Skull	North Sea, the Netherlands	n/a	4950–5250
SP1450	Brabant CollNr42002	Skull	North Sea, the Netherlands	1954	3830–3960
SP1453	NMR999100001790[*]	Thoracic vertebra juv.	North Sea, the Netherlands	1994	960–1120
SP1454	NMR999100001785[*]	Lumbar vertebra	North Sea, the Netherlands	1995	4230–4420
SP1455	NMR999100001788[*]	Axis	North Sea, the Netherlands	1996	>48 000
SP1460	NMR999100001789[*]	Axis	North Sea, the Netherlands	2005	1820–1950
SP1461	NMR999100001786[*]	Caudal vertebra	North Sea, the Netherlands	2005	>50 000
SP1462	NMR999100001791[*]	Lumbar vertebra	North Sea, the Netherlands	2005	3480–3630
SP1463	NMR999100001784[*]	Radius	North Sea, the Netherlands	2005	10 000–10 180
SP1643	NMR999100002102[*]	Thoracic vertebra	North Sea, the Netherlands	2005	5280–5430
SP1645	NMR999100001999[*]	ulna	North Sea, the Netherlands	2005	6620–6700
SP1745	Vo1, CollVonk/Texel	n/a	North Sea, the Netherlands	n/a	5320–5470
SP1746	Vo2, CollVonk/Texel	n/a	North Sea, the Netherlands	n/a	3470–3620
SP1818	NMR999100001998[*]	ulna	North Sea, the Netherlands	n/a	40 200–41 400
SP1821	NMR999100001994[*]	mandible	North Sea, the Netherlands	n/a	1680–1800
SP1822	NMR999100001996[*]	Thoracic vertebra	North Sea, the Netherlands	n/a	42 400–43 600
SP1941	NMR999100003115[*]	Mandible	North Sea, the Netherlands	2007	3930–4070
SP2058	n/a	n/a	North Sea, the Netherlands	n/a	4020–4270
SP2205	USNM 187448[‡]	Left mandible	USA	1850s	<250[§]
SP2211	USNM 244465[‡]	Left mandible	USA	1970s	440–500[§]
SP2213	USNM 256749[‡]	Squamosal	USA	1978	(n/a)[§]
SP2455	UK, Torquay	Vertebra	Cornwall, UK	1865	150–650[¶]
SP2456	Flower, 1872	Partial skeleton	Cornwall, UK	1829	1050–1550[¶]

[*]Natuurhistorisch Museum, Rotterdam.
[†]National Natural History Museum Naturalis, Leiden.
[‡]Smithsonian National Museum of Natural History, Washington D.C.
[§]Dating reference: Mead & Mitchell (1984).
[¶]Dating reference: Bryant (1995).

we performed tip-swapping analysis as described by Ho et al. (2011). We ran 20 BEAST analyses as above, but with age assignments randomly shuffled and reassigned to each sequence. The 95% confidence limits of the evolutionary rate estimated for the data set with the correct ages assigned to each sample fell outside the 95% confidence limits for all 20 of the age-shuffled data sets, indicating strong support for a temporal signal in the real data set.

To infer the most appropriate coalescent prior, we ran BEAST analyses using both the Bayesian skyline plot (Drummond et al. 2005) and a constant population size prior and performed Bayes factor analyses using path sampling and stepping stone approaches as implemented in BEAST (Baele et al. 2012). The Bayes factor tests resulted in decisive preference for using the constant population size model rather than the more complicated coalescent model.

For each BEAST analysis, we ran two independent MCMC chains for 60 million iterations each, drawing samples from the posterior every 6000 iterations. We checked for adequate exploration of parameter space and convergence of the MCMC chains using TRACER v1.6 (http://tree.bio.ed.ac.uk/software/tracer/). We discarded the first 10% of the sampled states as burn-in and combined the latter for subsequent data processing. We created a maximum clade credibility tree with treeAnnotator, which is distributed as part of the BEAST package. The xml file is available from the authors on request.

We estimated haplotype diversity (Hd), the genetic diversity parameters Watterson's Θ and nucleotide diversity (π), and Tajima's D for all sampling locations using DNASP v.5 (Rozas *et al.* 2003). We measured genetic differentiation between sample sets using F_{ST} using the program ARLEQUIN v. 3.1 (Excoffier *et al.* 2005). The software IMA (Hey & Nielsen 2007) was used to estimate probability density functions for effective female population size ($N_{e(f)}$). We restricted the analysis to Holocene Atlantic sequences and all modern Pacific sequences (excluding the Atlantic samples with AMS dates ~40 kyr or older). After multiple test runs to ensure mixing, a burn-in of 100 000 steps was used, followed by 50 million iterations.

We used the conservative double-test method (Thomas *et al.* 2002) to test for a significant difference in Atlantic haplotype diversity between the early/mid-Holocene and late Holocene. Because approximately half of the Holocene samples were younger than 3000 years and half were older, we considered the difference in Hd between sequences <3000 years (12 samples) and sequences >3000 years (13 samples). Briefly, sequences were bootstrapped to create a sampling distribution for the difference in Hd, and a two-tailed confidence interval was constructed around this difference such that one limit touches zero.

Predictive habitat modelling

We used the AquaMaps approach (www.aquamaps.org) to species distribution modelling for mapping current, potential Pleistocene and future gray whale distributions in the Pacific and Atlantic Oceans. AquaMaps is a bioclimatic envelope or environmental niche model that combines existing point occurrence data with available expert knowledge on species occurrence in environmental and geographic space to generate large-scale predictions of the relative occurrence of marine species (Ready *et al.* 2010). In this context, habitat usage of species is described through environmental envelopes for a predefined set of parameters including depth, temperature, salinity, primary production and sea ice concentration. Default envelopes are computed as percentiles based on the range of environmental conditions in so-called presence cells (i.e. cells containing at least one species' occurrence record) in a global grid of 0.5 degree latitude by 0.5 degree longitude cells. AquaMaps was developed specifically to deal with overall data paucity in marine environments but also with the nonrepresentative sampling of marine species ranges and therefore allows for the incorporation of expert knowledge about habitat usage in both environmental and geographic space, through an expert review process.

For gray whales, there are several thousand occurrence records available through online data portals such as GBIF (www.gbif.org) or OBIS (www.iobis.org). However, distribution of these records does not fully reflect current knowledge about the habitat usage of gray whales, which, for example, have been reported recently from the Laptev Sea (Shpak *et al.* 2013) or have been shown during recent tag studies (e.g. OSU Marine Mammal Institute 2012) to migrate across much deeper waters than thought previously. For the purpose of this study, we therefore reviewed and modified default envelope settings (calculated based on 162 presence cells containing occurrence records downloaded from GBIF). The review was carried out in consultation with a species expert and member of the IUCN Western Gray Whale Advisory Panel (R.R. Reeves, pers. comm.). We subsequently computed the relative suitability of habitats for gray whales in geographic space using AquaMaps. Predictions were generated for three different time periods (Pleistocene, current and 2100) using environmental data for different time periods and assuming no changes in species-specific habitat usage over time but excluding the primary production parameter from the model, as there are no corresponding data for the Pleistocene. As the climate has been relatively stable throughout the Holocene, with variability being small compared with differences between glacial cycles (Folland *et al.* 2001), current environmental conditions were assumed to be representative of conditions throughout the Holocene. Current distribution was based on the compiled standard AquaMaps environmental data as described by the metadata available at http://www.aquamaps.org/download/main.php and includes only the current native range of the species (e.g. North Pacific). Overall current suitable habitat including the southern hemisphere and Atlantic is available at http://www.aquamaps.org and in the supporting information. Pleistocene environmental conditions reconstructed for the LGM (26.5–19 ka ago) as part of the GLAMAP project were used in the hind-casting scenario (Schäfer-Neth & Paul 2003). We computed mean annual environmental conditions during the Pleistocene based on the available interpolated winter and summer predictions for sea surface temperature and salinity deduced from sediment core data. As an approximation for mean annual sea ice concentration required as input by the AquaMaps model, we used the mean proportion of time a given cell had been defined to be covered by ice in the GLAMAP data set. Future annual average environmental conditions for the 2091–2100 decade were based on the Special Report on Emissions A2 climate change scenario (IPCC 2000). Scenario A2 represents an intermediate scenario assuming continuous global population growth, but more regionally orientated economic growth. Projected maximum increases in mean

temperature by the year 2100 are slightly lower than in scenario A1, but higher than B1 or B2 (IPCC 2000).

As indicated by validation analyses comparing predictions with observations of relative species occurrence, highly suitable habitat was defined to include all cells with predicted suitabilities >0.6 (Kaschner *et al.* 2011).

Results and discussion

We sequenced mitochondrial DNA from 33 Atlantic gray whale subfossils and performed predictive habitat modelling based on modern and fossil occurrence data, revealing new insights about the frequency and timing of gene flow between Pacific and Atlantic populations as well as habitat usage across different climate regimes. From each subfossil, we generated a 510-base pair (bp) sequence fragment of the mitochondrial control region (mtCR). Thirty-two subfossils were dated using both radiometric and AMS measurement techniques. The dates range from modern to >50 000 calibrated years Before Present (calBP; calendar years relative to AD 1950; Table 1 and supporting information). Of these 32 dated samples, seven were of late Pleistocene age, ranging from ~40 000 to >50 000 calBP, while the remaining samples dated to the Holocene, ranging from <250 to ~10 000 calBP. None of the samples produced dates between ~11 000 and ~40 000 calBP, likely reflecting displacement from habitats in the North Sea, believed to be an uninhabitable subaerial floodplain or dry land during this time. The predicted distribution for the LGM corroborates this extreme constriction of habitat, suggesting that only 61% of suitable habitat available today in the North Atlantic was available during the height of the last glaciation, and with respect to predicted highly suitable habitat (probabilities > 0.6), the reduction was even more extreme (i.e. only 39% of what would be available today). Interestingly, the timing of inferred recolonization of the North Sea based on fossil age distribution suggests that gray whales reappeared in this region after bowhead whales, which are present from the late Pleistocene, but earlier than North Atlantic right whales (Foote *et al.* 2013). This successional sequence is consistent with the habitat preferences and ecology of the three species, which differ in tolerance to sea ice concentration, preferred temperature and other environmental parameters (Kaschner *et al.* 2011).

Phylogenetic relationships and timing of dispersal between Atlantic and Pacific gray whales

We aligned our data to published sequences from 181 modern and ancient Pacific gray whales to assess the phylogenetic relationship between Atlantic and Pacific

populations and infer the population history of the Atlantic gray whale. Bayesian analyses reveal that the Atlantic gray whales tend to cluster into several groups of sequences in the resulting genealogies, indicating multiple dispersal events (Fig. 1). We identified a set of highly divergent Atlantic sequences that fall outside all Pacific sequences, comprising all Pleistocene-age and some Holocene-age (~4340 calBP or older) Atlantic gray whales (Fig. 1, box A). While the topology of the genealogy suggests an Atlantic origin of modern gray
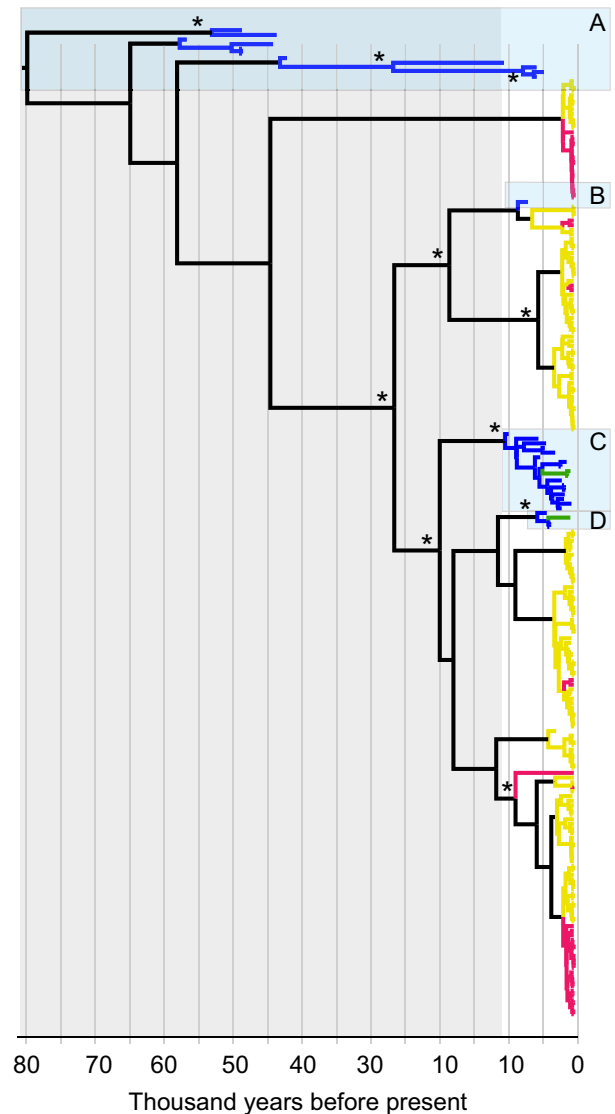

Fig. 1 Phylogenetic tree constructed using a Bayesian MCMC framework, indicating the relationship between North Pacific and North Atlantic gray whale haplotypes. Tip colours indicate the sampling location: western Atlantic = green, eastern Atlantic = blue, eastern Pacific = yellow, western Pacific = pink. Nodes represented by >95% posterior support are indicated with a star. Groups of sequences marked as A, B and C, and D contain Atlantic sequences and are described in the text.

whales, this is likely to be an artefact, attributable to the lack of Pleistocene gray whales from the Pacific in our data set. Apart from a single sample dated to ~6600 cal-BP (Fig. 1B), all remaining Holocene sequences cluster together within two clades comprised of samples dated to <250–9000 calBP (Fig. 1C), and samples dated to ~500–3000 calBP (Fig. 1D).

To infer the timing of post-LGM dispersals from the Pacific into the Atlantic Oceans, we estimated the age of the most recent common ancestor (MRCA) shared by each clade containing Atlantic gray whales and its most closely related Pacific gray whale lineage. Because this common ancestor probably lived in the Pacific Ocean, this estimate does not represent the precise timing of dispersal, but instead places an upper boundary on the estimated timing, which must have occurred after the time point represented by that common ancestor. The oldest and most divergent Atlantic sequences share a common ancestor between 63 and 102 ka ago, with a median of 79 kya. The wider range reflects the 95% highest posterior density (HPD) estimate of the age of the most recent common ancestor of all sequences within that clade. Recent climate models indicate that the Bering Strait was open consistently from ~70 to 135 ka ago (Hu *et al.* 2010, 2012), and high numbers of subpolar planktonic foraminifers from Arctic ice cores suggest reduced ice conditions ~65–85 ka ago (MIS 5a) and during MIS 5e (~115–130 ka ago) (Polyak *et al.* 2010). It is likely that dispersal through the Bering Strait occurred most frequently during these peak warm periods. MIS 5e, in particular, is associated with reduced ice cover or even ice-free conditions over continental shelves and sea levels close to or higher than modern-day levels (Polyak *et al.* 2010), which may have allowed comparatively easy passage across the Arctic.

The three lineages comprising only Holocene-age Atlantic gray whales all share a MRCA with Pacific whales during the early to mid-Holocene (lineage B: 95% HPD 6600–13 500 years BP (median = 9000), clade C: 95% HPD 9400–13 200 (median = 10 400), clade D: 95% HPD 3900–9000 (median = 5800)). These dates fall into a fairly narrow time frame that overlaps with the early Holocene, when warming temperatures, lighter sea ice and sea level rise permitted passage through the Bering Strait for the first time in ~60 000 years (Polyak *et al.* 2010).

The estimated ages for each of these three lineages are very recent in the context of separation between Atlantic and Pacific populations in other whale species. With the exception of ice-adapted bowhead whales, in which gene flow between ocean basins has occurred both frequently and recently (late Holocene; Alter *et al.* 2012a), estimated divergence times between North Atlantic and North Pacific populations in other baleen whales are on the order of millions of years (fin whales, 1.05–2.70 Ma (Bérubé *et al.* 1998); common minke whales, ~1.5 Ma (Pastene *et al.* 2007); humpback whales ~2–3 Ma (Baker *et al.* 1993); and right whales, >3.5 Ma (Rosenbaum *et al.* 2000)), and some of these taxa are considered to represent different species. Our results suggest that gray whale dispersals between the Pacific and Atlantic Oceans took place as soon as climatic conditions (sea level and ice cover) permitted during the Pleistocene and Holocene. This large difference in divergence times probably reflects the distinct ecology of gray whales relative to other species, particularly with respect to their dependence on high-latitude shelf habitat, and underscores their importance as an Arctic 'sentinel species' (Moore 2008). The discovery that Atlantic gray whale lineages are polyphyletic and recently diverged, as well as the observation that three of the four groups of sequences are nested within the wider genetic diversity shown by Pacific gray whales, also counters the suggestion that the Atlantic gray whale may have represented a distinct, extinct species (Mead & Mitchell 1984). Rather, genetic data show that Atlantic gray whales represented a population connected to the Pacific through intermittent exchange. The only cetacean species likely to have been extirpated during historical times therefore remains the Yangtze River dolphin or baiji (Turvey *et al.* 2007).

Despite the profound climatic shifts observed during the most recent glacial cycle, at least one lineage of Atlantic gray whales appears to have persisted from the last glacial into the Holocene (Fig. 1A). While the possibility remains that inclusion of additional Pleistocene-age subfossils from the Pacific (if discovered) could change this pattern, the fact that this well-supported clade has an MRCA in the Pleistocene and no Pacific members strongly indicates persistence of this lineage in the Atlantic through the LGM. Habitat reconstructions suggest shallow shelf habitat required by gray whales would have existed during this interval, including the Celtic Sea and the Bay of Biscay, Rockall Bank and coastal shelves off of the coasts of Labrador, Newfoundland and Nova Scotia (Fig. 2). Our reconstructions show that the Mediterranean Sea, the Azores and Canary Islands, and the coasts of Spain and northwest Africa, all of which have been proposed as LGM refugia for benthic marine species (Macé 2003; Maggs *et al.* 2008), could have also been available but would likely have represented less suitable refugia.

Population history of gray whales in the Atlantic

Our relatively small sample size and the wide temporal range of sample ages preclude a robust analysis of gray
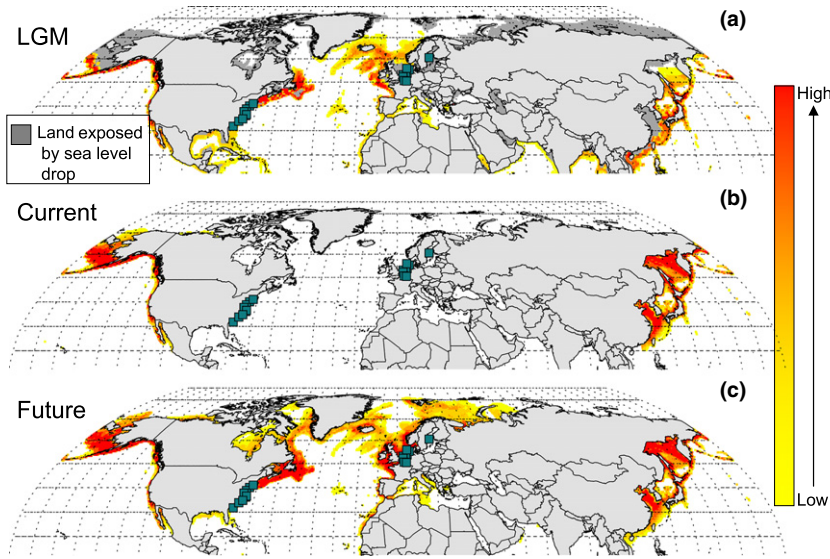
Fig. 2 Predicted suitable habitat for gray whales throughout the Northern hemisphere during different time periods generated using AquaMaps environmental niche modelling and input parameter settings described in Table 3. Maps shown represent (a) the predicted suitable habitat of gray whales (*Eschrichtius robustus*) during the last glacial maximum (LGM) (top), (b) current suitable habitat limited to the known native species range in the North Pacific and (c) forward projections of suitable habitat for the year 2100 (bottom). Blue squares represent sites where Atlantic fossil and subfossils used in this study were collected.

Table 2 Genetic diversity estimates for each sample set N = number of samples; S = number of segregating sites; H = number of haplotypes; Hd = haplotype diversity; π = nucleotide diversity

	N	S	H	Hd	π
Atlantic (Holocene)	25	14	7	0.748	0.0107
Atlantic (Pleistocene)	7	6	4	0.71429	0.0076
Atlantic (All)	33[*]	16	11	0.8333	0.0145
North Pacific (Eastern)	120	19	20	0.9164	0.0141
North Pacific (Western)	45	15	9	0.6989	0.0159
North Pacific (Eastern, ancient)	16	8	8	0.9238	0.0081
Pacific (All)	181	21	23	0.8994	0.0151
All samples	214	26	34	0.9219	0.0155

*The total number of sequences includes one sample that was not dated and thus is not included in either the Atlantic (Holocene) or Atlantic (Pleistocene) category.

Table 3 Environmental envelope settings used for AquaMaps species distribution modelling based on 162 presence cells and modified based on current expert knowledge

	Min	Pref Min (10th percentile)	Pref Max (90th percentile)	Max
Expert-modified envelopes for gray whales				
Depth (m)	1	30	500	2500
Temperature (°C)	−2	3	19	30
Salinity (psu)	20.00	31.21	33.70	35.34
Sea Ice Concentration	0.00	0.00	0.13	0.9

whale effective population size in the Atlantic Ocean. However, our data indicate that despite the deep genetic divergence represented by Pleistocene individuals in the Atlantic, the overall genetic diversity among Atlantic lineages is lower than for Pacific lineages during the Holocene (Table 2). Unless significant population substructure existed in the Atlantic, the low observed genetic diversity suggests that gray whale abundance was lower in the Atlantic than that in the Pacific during the Holocene, even before human-mediated declines. An analysis of effective female population size using a Markov chain Monte Carlo approach (Hey & Nielsen 2007) to compare Atlantic (Holocene only) and Pacific (all samples) data sets produced a maximum-likelihood estimate of $N_{e(f)}$ that was 2.2 times greater in the Pacific compared with the Atlantic. An important caveat

of this analysis is that our data set violates the assumption that the two populations were sampled at the same time point. However, if the samples analysed represent a random sample of genetic diversity in the Atlantic across time, integrating the Atlantic gray whale data across the Holocene should result in an overestimate, rather than underestimate, of the effective population size in this ocean basin, supporting the hypothesis that abundance never reached the same level as in the Pacific. The predicted distribution of highly suitable habitat corroborates this difference as well: despite the fact that the overall area of predicted range is larger in the Atlantic, models predict 23% more highly suitable habitat (suitability >0.6, Kaschner *et al.* 2011) in the Pacific as compared to the Atlantic during the LGM, and 29% more under today's climate.

Finally, our analyses indicate that the population decline of gray whales in the Atlantic began prior to historical-era whaling. The low genetic diversity in the late Holocene and the reduction in haplotype diversity over time suggest that population decline may have begun in the mid-Holocene when sea ice cover increased. The lineage that persisted through the LGM may have died out in the mid-Holocene, as no samples younger than 4290–4390 years (calBP) are represented in this group. Late Holocene samples (<3000 years), which represent approximately half of our Holocene samples, show only two closely related haplotypes and have an overall Hd = 0.167. This level of haplotype diversity is significantly lower than that in mid-/early Holocene Atlantic sequences (>3000 years) (Hd = 0.871; P < 1E-5) and also contrasts with higher diversity in Pleistocene Atlantic sequences (Hd = 0.714; P < 1E-3) and in eastern Pacific sequences (Hd = 0.948; P < 1E-6). Because the majority of our samples come from a single area (the North Sea), it is possible that the low diversity we observe reflects population substructure within the Atlantic. However, of the three samples sequenced from the western Atlantic, all three match common eastern North Atlantic haplotypes (two are late Holocene and one is undated).

It is difficult to explain how advancing ice cover in the mid-Holocene alone could be responsible for the decline of the Atlantic population, in particular since the population persisted through the LGM. It is possible that loss of habitat occurred much more rapidly during the Holocene than during the Pleistocene, or that habitat loss affected marine ecosystems in a fundamentally different way during these two intervals. The mid-Holocene saw a relatively rapid shift in temperature, sedimentation, sea level and sea-ice extent, possibly as a result of changes in North Atlantic circulation following the complete deglaciation of the Canadian Arctic (Williams *et al.* 1995; Darby *et al.* 2006), as well as profound changes in ocean productivity (Polyak *et al.* 2010;

Fahl & Stein 2012). The dearth of Atlantic bowhead and walrus subfossils from the period ~6–7 ka ago (relative to earlier and later in the Holocene) suggests that these transitions may have affected other marine mammals as well (Dyke *et al.* 1996, 1999). In addition, the mid-Holocene decline of the Atlantic gray whale population may have been accelerated (or exacerbated) by premodern exploitation of marine mammals by coastal human communities (Mulville 2002). While very few gray whale remains have been identified in archaeological materials from the Atlantic, genetic analysis of unidentified whale bone fragments may reveal more in the future. Finally, commercial whaling may have contributed to the decline and ultimate extirpation of this population during the last several hundred years, although little direct evidence is available for extensive commercial whaling of Atlantic gray whales (Clapham & Link 2006).

Conclusions

The recent sightings of gray whales in the Atlantic have been interpreted as a possible early sign of climate change-driven shifts in range (Scheinin *et al.* 2011), and coincide with increasing reports of climate-related changes in gray whale behaviour and distribution (Stafford *et al.* 2007; Moore 2008), as well as a sizeable (40%) predicted increase in available habitat based on environmental suitability models and an intermediate IPCC-A1B model by the year 2050 (Kaschner *et al.* 2011). Outcomes from this analysis, based on a longer time period and the IPCC A2 emission scenario, however, are much less optimistic, suggesting that gains in available habitat maybe smaller than previously predicted. Independent of the emission scenario used, it is nevertheless very likely that additional highly suitable habitat will be available farther north in the Beaufort and Chukchi Seas, increasing the likelihood of dispersal to the Atlantic. However, while predicted climate change may have a potentially positive effect on gray whale habitat range and population size, it is notable that much of the most suitable gray whale habitat that exists in the Atlantic overlaps with areas of high anthropogenic impact, including shipping channels, oil and gas drilling, and commercial fishing (Halpern *et al.* 2008). Thus, habitat protection, as well as conservation of genetic diversity in Pacific populations, will be important as we consider how to preserve evolutionary potential in this species.

The data presented here show that gray whales made the passage between the Atlantic and Pacific at least several times during the last ~100 ka, when sea level and climatic conditions permitted. These patterns demonstrate the profound impact of Pleistocene and Holocene climatic changes on their range, as has also been shown for bowhead whales (Foote *et al.* 2013). As sea ice

continues to decline in the Arctic, the results shown here indicate we might expect additional gray whale dispersal events from the Pacific into the Atlantic, with this species expanding its habitat beyond its current realized range. Such climate-related distributional shifts are likely to extend to other marine taxa, including many important in fisheries, and will also be accompanied by other alterations to fundamental biological processes such as changes in growth rates and trophic interactions (Grebmeier 2012). Thus, while ancient DNA can give a useful long-term perspective on species distributions, suggesting that the range of some species may expand as sea-ice declines, systemwide ecological changes brought on by changing climate make it difficult to predict outcomes for most taxa. As these shifts occur in gray whales and other species, an ecosystem-based approach will be needed to understand and manage the fate of marine species in oceans affected by climate change and other stressors.

Acknowledgements

References

Alter SE, Palumbi SR (2009) Comparing evolutionary patterns and variability in the mitochondrial control region and cytochrome b in three species of baleen whales. *Journal of Molecular Evolution*, **68**, 97–111.

Alter SE, Ramirez SF, Nigenda S, Ramirez JU, Bracho LR, Palumbi SR (2009) Mitochondrial and nuclear genetic variation across calving lagoons in eastern North Pacific gray whales (*Eschrichtius robustus*). *Journal of Heredity*, **100**, 34–46.

Alter SE, Rosenbaum HC, Postma LD *et al.* (2012a) Gene flow on ice: the role of sea ice and whaling in shaping Holarctic genetic diversity and population differentiation in bowhead whales (*Balaena mysticetus*). *Ecology and Evolution*, **2**, 2895–2911.

Alter SE, Newsome SD, Palumbi SR (2012b) Pre-whaling genetic diversity and population ecology in eastern Pacific gray whales: insights from ancient DNA and stable isotopes. *PLoS ONE*, **7**, e35039.

Baele G, Lemey P, Bedford T, Rambaut A, Suchard MA, Alekseyenko AV (2012) Improving the accuracy of demographic and molecular clock model comparison while accommodating phylogenetic uncertainty. *Molecular Biology and Evolution*, **29**, 2157–2167.

Baker CS, Perry A, Bannister JL *et al.* (1993) Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. *Proceedings of the National Academy of Sciences*, **90**, 8239–8243.

Bérubé M, Aguilar A, Dendanto D *et al.* (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. *Molecular Ecology*, **7**, 585–599.

Bisconti M (2008) Morphology and phylogenetic relationships of a new eschrichtiid genus (Cetacea: Mysticeti) from the Early Pliocene of northern Italy. *Linnean Society of London*, **153**, 161–186.

Bisconti M, Varola A (2006) The oldest *Eschrichtius* mysticete: and a new morphological diagnosis of Eschrichtiidae (gray whales). *Rivista Italiana di Paleontologia e Stratigrafia*, **112**, 447–457.

Bryant PJ (1995) Dating remains of gray whales form the eastern North Atlantic. *Journal of Mammalogy*, **76**, 857–861.

Burrows MT, Schoeman DS, Buckley LB *et al.* (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science*, **334**, 652–655.

Clapham PJ, Link J (2006) Whales, whaling and ecosystems in the North Atlantic. In: *Whales, Whaling and Ecosystems* (ed Estes J.), pp. 241–250. University of California Press, Berkeley, CA.

Clark PU, Dyke AS, Shakun JD *et al.* (2009) The last glacial maximum. *Science*, **325**, 710–714.

Darby DA, Polyak L, Bauch HA (2006) Past glacial and interglacial conditions in the Arctic Ocean and marginal seas – a review. *Progress in Oceanography*, **71**, 129–144.

De Bruyn M, Hall BL, Chauke LF, Baroni C, Koch PL, Hoelzel AR (2009) Rapid response of a marine mammal species to Holocene climate and habitat change. *PLoS Genetics*, **5**, e1000554.

Deméré TA, Berta A, McGowen MR (2005) The taxonomic and evolutionary history of fossil and modern balaenopteroid mysticetes. *Journal of Mammalian Evolution*, **12**, 99–143.

Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7**, 214.

Drummond AJ, Rambaut A, Shapiro B, Pybus OG (2005) Bayesian coalescent inference of past population dynamics from molecular sequences. *Molecular Biology and Evolution*, **22**, 1185–1192.

Dyke AS, Hooper J, Savelle JM (1996) A history of sea ice in the Canadian Arctic Archipelago based on postglacial remains of the bowhead whale (*Balaena mysticetus*). *Arctic*, **49**, 235–255.

Dyke AS, Hooper J, Harington CR, Savelle JM (1999) The Late Wisconsinan and Holocene record of walrus (*Odobenus rosmarus*) from North America: a review with new data from Arctic and Atlantic Canada. *Arctic*, **52**, 160–181.

Edwards CJ, Suchard MA, Lemey P *et al.* (2011) Ancient hybridization and an Irish origin for the modern polar bear matriline. *Current Biology*, **21**, 1251–1258.

Excoffier L, Laval G, Schneider S (2005) ARLEQUIN (version 3.0): an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, **1**, 47.

Fahl K, Stein R (2012) Modern seasonal variability and deglacial/Holocene change of central Arctic Ocean sea-ice cover:

new insights from biomarker proxy records. *Earth and Planetary Science Letters*, **351**, 123–133.

Folland CK, Karl TR, Christy JR *et al.* (2001) *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (eds Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA). Cambridge University Press, Cambridge, UK.

Foote AD, Hofreiter M, Morin PA (2012) Ancient DNA from marine mammals: studying long-lived species over ecological and evolutionary timescales. *Annals of Anatomy-Anatomischer Anzeiger*, **194**, 112–120.

Foote AD, Kaschner K, Schultze SE *et al.* (2013) Ancient DNA reveals that bowhead whale lineages survived Late Pleistocene climate change and habitat shifts. *Nature Communications*, **4**, 1677. doi:10.10.1038/ncomms2714.

Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. *Annual Review of Marine Science*, **4**, 63–78.

Halpern BS, Walbridge S, Selkoe KA *et al.* (2008) A global map of human impact on marine ecosystems. *Science*, **319**, 948–952.

Hazen EL, Jorgensen S, Rykaczewski RR *et al.* (2013) Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change*, **3**, 234–238.

Heide-Jorgensen MP, Laidre KL, Quakenbush LT, Citta JJ (2012) The Northwest Passage opens for bowhead whales. *Biology Letters*, **8**, 270–273.

Hey J, Nielsen R (2007) Integration within the Felsenstein equation for improved Markov chain Monte Carlo methods in population genetics. *Proceedings of the National Academy of Sciences*, **104**, 2785–2790.

Hijma MP, Cohen KM (2011) Holocene transgression of the Rhine river mouth area, The Netherlands Southern North Sea: palaeogeography and sequence stratigraphy. *Sedimentology*, **58**, 1453–1485.

Ho SY, Saarma U, Barnett R, Haile J, Shapiro B (2008) The effect of inappropriate calibration: three case studies in molecular ecology. *PLoS ONE*, **3**, e1615.

Ho SY, Lanfear R, Phillips MJ *et al.* (2011) Bayesian estimation of substitution rates from ancient DNA sequences with low information content. *Systematic Biology*, **60**, 366–375.

Hofreiter M, Jaenicke V, Serre D, von Haeseler A, Pääbo S (2001) DNA sequences from multiple amplifications reveal artifacts induced by cytosine deamination in ancient DNA. *Nucleic Acids Research*, **29**, 4793–4799.

Hu A, Meehl GA, Otto-Bliesner BL *et al.* (2010) Influence of Bering Strait flow and North Atlantic circulation on glacial sea-level changes. *Nature Geoscience*, **3**, 118–121.

Hu A, Meehl GA, Han W *et al.* (2012) Role of the Bering Strait on the hysteresis of the ocean conveyor belt circulation and glacial climate stability. *Proceedings of the National Academy of Sciences*, **109**, 6417–6422.

Ichishima H, Sato E, Sagayama T, Kimura M (2006) The oldest record of Eschrichtiidae (Cetacean: Mysticeti) from the Late Pliocene, Hokkaido, Japan. *Journal of Paleontology*, **80**, 367–379.

Intergovernmental Panel on Climate Change (IPCC) (2000) *Special Report on Emissions Scenarios: A Special Report of Working Group III of the Intergovernmental Panel on Climate Change* (eds Nakicenovic N, Swart R, eds). Cambridge University Press, Cambridge, UK.

Kaschner K, Tittensor DP, Ready J, Gerrodette T, Worm B (2011) Current and future patterns of global marine mammal biodiversity. *PLoS ONE*, **6**, e19653.

Lang AR, Calambokidis J, Scordino J *et al.* (2014) Assessment of genetic structure among eastern North Pacific gray whales on their feeding grounds. *Marine Mammal Science*, **30**, 1473–1493.

Larkin MA, Blackshields G, Brown NP *et al.* (2007) CLUSTAL W and CLUSTAL X version 2.0. *Bioinformatics*, **23**, 2947–2948.

LeDuc R, Weller DW, Hyde J *et al.* (2002) Genetic differences between western and eastern gray whales *Eschrichtius robustus*. *Journal of Cetacean Research and Management*, **4**, 1–5.

Longin R (1971) New method of collagen extraction for radiocarbon dating. *Nature*, **230**, 241–242.

Lorenzen ED, Nogués-Bravo D, Orlando O *et al.* (2011) Species-specific responses of Late Pleistocene megafauna to climate and humans. *Nature*, **479**, 359–364.

Macé M (2003) Did the gray whale, *Eschrichtius robustus*, calve in the Mediterranean? *Lattara*, **16**, 153–164.

Maggs CA, Castilho R, Foltz D *et al.* (2008) Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. *Ecology*, **89**, S108–S122.

Mead JG, Mitchell ED (1984) Atlantic gray whales. In: *The Gray Whale: Eschrichtius robustus* (eds Jones M. L., Swartz S. L. & Leatherwood S.), pp. 33–53. Academic Press, Orlando.

Mecklenburg CW, Stein DL, Sheiko BA, Chernova NV, Mecklenburg TA, Holladay B (2007) Russian-American long-term census on the Arctic: benthic fishes trawled in the Chukchi Sea and Bering Strait, August 2004. *Northwestern Naturalist*, **88**, 168–187.

Meyer M, Stenzel U, Hofreiter M (2008) Parallel tagged sequencing on the 454 platform. *Nature Protocols*, **3**, 267–278.

Mook WG, Streurman HJ (1983) Physical and chemical aspects of radiocarbon dating. First Symposium on ^{14}C and Archaeology, Groningen. *PACT Publications*, **8**, 31–55.

Moore SE (2008) Marine mammals as ecosystem sentinels. *Journal of Mammalogy*, **89**, 534–540.

Moore SE, Grebmeier JM, Davies JR (2003) Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. *Canadian Journal of Zoology*, **81**, 734–742.

Mueter FJ, Litzow MA (2008) Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecological Applications*, **18**, 309–320.

Mulville J (2002) The role of Cetacea in prehistoric and historic Atlantic Scotland. *International Journal of Osteoarchaeology*, **12**, 34–48.

Noakes SE, Pyenson ND, McFall G (2013) Late Pleistocene gray whales (*Eschrichtius robustus*) offshore Georgia, USA, and the antiquity of gray whale migration in the North Atlantic Ocean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **392**, 502–509.

OSU Marine Mammal Institute. http://mmi.oregonstate.edu/Sakhalin2011. Accessed February 20, 2014.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Pastene LA, Goto M, Kanda N *et al.* (2007) Radiation and speciation of pelagic organisms during periods of global warming: the case of the common minke whale, *Balaenoptera acutorostrata*. *Molecular Ecology*, **16**, 1481–1495.

Paterson J (2013) A rare and mysterious visitor in Walvis Bay. http://namibiadolphinproject.blogspot.com. Accessed February 10, 2014.

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science*, **308**, 1912–1915.

Polyak L, Alley RB, Andrews JT *et al.* (2010) History of sea ice in the Arctic. *Quaternary Science Reviews*, **29**, 1757–1778.

Pompa S, Ehrlich PR, Ceballos G (2011) Global distribution and conservation of marine mammals. *Proceeding of the National Academy of Sciences*, **108**, 13600–13605.

Ready J, Kaschner K, South AB *et al.* (2010) Predicting the distributions of marine organisms at the global scale. *Ecological Modelling*, **221**, 467–478.

Reimer PJ, Bard E, Bayliss A *et al.* (2013) IntCal13 and Marine13 Radiocarbon age calibration curves 0–50,000 years cal-BP. *Radiocarbon*, **55**, 1869–1887.

Rohland N, Hofreiter M (2007) Ancient DNA extraction from bones and teeth. *Nature Protocols*, **2**, 1756–1762.

Rohland N, Malaspinas AS, Pollack JL, Slatkin M, Matheus P, Hofreiter M (2007) Proboscidean mitogenomics: chronology and mode of elephant evolution using mastodon as outgroup. *PLoS Biology*, **5**, e207.

Römpler H, Dear PH, Krause J *et al.* (2006) Multiplex amplification of ancient DNA. *Nature Protocols*, **1**, 720–728.

Rosenbaum HC, Brownell RL Jr, Brown MW *et al.* (2000) Worldwide genetic differentiation of *Eubalaena*: questioning the number of right whale species. *Molecular Ecology*, **9**, 1793–1802.

Rozas J, Sánchez-DelBarrio JC, Messeguer X, Rozas R (2003) DNASP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics*, **19**, 2496–2497.

Schäfer-Neth C, Paul A (2003) The Atlantic Ocean at the last glacial maximum: Objective mapping of the GLAMAP sea-surface conditions. In: *The South Atlantic in the Late Quaternary: Reconstruction of Material Budgets and Current Systems* (eds Wefer G., Mulitza S. & Ratmeyer V.), pp. 531–548. Springer-Verlag, Berlin.

Scheinin AP, Kerem D, MacLeod CD, Gazo M, Chicote CA, Castellote M (2011) Gray whale (*Eschrichtius robustus*) in the Mediterranean Sea: anomalous event or early sign of climate-driven distribution change? *Marine Biodiversity Records*, **4**, e28.

Shapiro B, Drummond AJ, Rambaut A *et al.* (2004) Rise and fall of the Beringian steppe bison. *Science*, **306**, 1561–1565.

Shapiro B, Ho SY, Drummond AJ, Suchard MA, Pybus OG, Rambaut A (2011) A Bayesian phylogenetic method to estimate unknown sequence ages. *Molecular Biology and Evolution*, **28**, 879–887.

Shpak OV, Kuznetzova DM, Rozhnov VV (2013) Observation of the gray whale (*Eschrichtius robustus*) in the Laptev Sea. *Biology Bulletin*, **40**, 797–800.

Stafford KM, Moore SE, Spillane M, Wiggins S (2007) Gray whale calls recorded near Barrow, Alaska, throughout the winter of 2003–04. *Arctic*, **60**, 167–172.

Thomas MG, Weale ME, Jones AL *et al.* (2002) Founding mothers of Jewish communities: geographically separated Jewish groups were independently founded by very few female ancestors. *The American Journal of Human Genetics*, **70**, 1411–1420.

Turvey ST, Pitman RL, Taylor BL *et al.* (2007) First human-caused extinction of a cetacean species? *Biology Letters*, **3**, 537–540.

Van der Plicht J, Hogg A (2006) A note on reporting radiocarbon. *Quaternary Geochronology*, **1**, 237–240.

Vermeij GJ, Roopnarine PD (2008) The coming Arctic invasion. *Science*, **321**, 780–781.

Williams KM, Short SK, Andrews JT, Jennings AE, Mode WN, Syvitski JP (1995) The Eastern Canadian Arctic at ca6 ka BP: a time of transition. *Geographie Physique et Quaternaire*, **49**, 13–27.

Data accessibility

DNA sequences: GenBank Accession nos KP714216–KP714248 and uploaded as online supporting information (Table S1).

Full sample collection data uploaded as online Supporting Information (Table S1).

Final DNA sequence assembly: Dryad doi:10.5061/dryad.4fj54.

Tree files: Dryad doi:10.5061/dryad.4fj54.

Habitat modelling parameters: Table 3, online Supporting Information (Fig. S1), and Dryad doi:10.5061/dryad.4fj54.

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Supporting information describing detailed sample information for all ancient Atlantic specimens, including sampling location and date and collection numbers, NCBI accession numbers, and additional sample data for other sequences used in the analysis.

Fig. S1 Predicted suitable habitat with and without including primary productivity as an environmental parameter. Current suitable habitat is overlaid with the known native species range in the North Pacific as delineated by the IUCN.

Fig. S2 Current predicted suitable habitat for gray whales without limiting habitat to current native range.