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ABSTRACT

The grey whale, *Eschrichtius robustus*, occurred in the Atlantic Ocean until c.300 years ago, having been extirpated probably owing to hunting by humans. Three records of fossil grey whale bones were known previously from Cornwall and Devon in the 18th and 19th centuries. Morphological identification to species of cetacean remains from palaeontological and archaeological sites is problematic, because the bones are often fragmentary or have been modified by humans. The application of ancient DNA analysis and collagen fingerprinting (ZooMS) allows the identification of fragmentary and modified cetacean bone to species and/or generic level, thus offering new opportunities to understand the exploitation of cetaceans by human coastal communities. Analyses of cetacean bone from Orkney and Shetland have identified for the first time the presence of grey whale at archaeological sites in Scotland, extending the geographical range of records in Britain. These findings confirm for the first time that the seas around Scotland were part of the range of the grey whale in the eastern North Atlantic, thereby linking records of this species (from southern Scandinavia, the Northern Isles of and southwest Britain, the southern North Sea and Netherlands, to the Iberian Peninsula and Morocco) over a similar latitudinal range that the species still occupies in the Pacific Ocean.

INTRODUCTION

The grey whale, *Eschrichtius robustus*, once inhabited both the Pacific and Atlantic Oceans. Originally described from fossil remains from Gräso, Sweden by Lilljeborg (1861), the species has since been extirpated from the North Atlantic and is today found only in the Pacific Ocean (Jefferson *et al.* 2015), although two vagrants have been recorded recently in the Atlantic (Scheinin *et al.* 2011; Elwen & Gridley 2013) and a further live animal was recorded off Rabat, Morocco in March 2021. Radiocarbon dating and historical accounts suggest that the species was extirpated from the North Atlantic within the last 300 years, probably because of human hunting (Mead & Mitchell 1984; Bryant 1995, Kitchener *et al.* 2008). In the past decade, there has been a considerable increase in the numbers of grey whale fossils discovered on both sides of the Atlantic Ocean, with a particular hot spot in the southern North Sea off the coast of the Netherlands, and it has now been confirmed at several archaeological sites in the Mediterranean and elsewhere in Western Europe (Alter et al. 2015; Rodrigues *et al.*

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2018; van den Hurk 2020). The presence of a breeding population in the North Atlantic has not been demonstrated unequivocally. Evidence for a persistent population with annual migrations between feeding and breeding grounds, rather than the presence of occasional vagrants from the Pacific Ocean, is supported by genetic differences between Atlantic and Pacific grey whales, and the increasing number of fossil and archaeological Atlantic records that span around 60,000 years over a wide latitudinal range (Alter et al. 2015; Rodrigues et al. 2018). Although grey whale fossil or archaeological remains have been reported from a few sites in southwest England (Bryant 1995, Kitchener *et al.* 2008), no grey whale fossil or archaeological remains have yet been reported from Scotland or elsewhere in the British Isles. Whale skeletal remains occur frequently at archaeological sites, but they can be difficult to identify owing to fragmentation or modification. This often results in a lack of identification or mis-identification (Buckley *et al*. 2014; Hufthammer *et al.* 2018). Analysis of ancient DNA (aDNA) is increasingly being used to identify archaeological bone fragments to species and can offer additional information, such as sex and aspects of population genetics. These data inform the interpretation of skeletal remains within an archaeological context, but also provide information on aspects of species demographics over time. However, aDNA may be poorly or not preserved and can be relatively expensive to extract and analyse, requiring uncontaminated laboratory conditions for successful extraction. In recent years collagen fingerprinting (ZooMS) has been developed to identify a wide array of cetacean species, including the larger mysticete whales, which are the most difficult to identify morphologically in archaeological contexts (Buckley *et al.* 2014; Hufthammer *et al.* 2018; van den Hurk *et al*. 2021). Collagen preservation is often much better than aDNA and occurs in conditions in which aDNA is rapidly degraded. Collagen fingerprinting is also relatively inexpensive compared with aDNA analysis and does not require such stringent laboratory conditions. However, collagen fingerprinting may limit the level of taxonomic identification to family or genus, especially for closely related species. However, this is not the case for mysticete whales, except for the family Balaenidae, which includes the right whales, *Eubalaena* spp. and bowhead whale, *Balaena mysticetus* (Buckley *et al.* 2014, Hufthammer *et al.* 2018).

As part of the interdisciplinary NSF-funded project, *Assessing the Distribution and Variability of Marine Mammals through Archaeology, Ancient DNA, and History in the North Atlantic (*henceforth *Norse North Atlantic Marine Mammals)*, archaeological cetacean bones from several sites in Orkney and Shetland were sampled for aDNA analyses and collagen fingerprinting, in order to identify them to species level and provide a more complete and accurate assessment of the utilisation of cetaceans in the Norse period. Here we report on five bones of grey whale from three sites in Orkney and one site in Shetland that were identified using a combination of aDNA analysis and collagen fingerprinting. These are the first records from Scotland and the first confirmed records from archaeological sites in Britain.

MATERIALS AND METHODS

As part of the continuing *Norse North Atlantic Marine Mammals* project, 109 cetacean bones from archaeological sites were selected for aDNA analysis and collagen fingerprinting from the collections of National Museums Scotland and Orkney Museums, and material from continuing excavations of the UHI Archaeology Institute in Orkney. This sample set is comprised primarily of bone fragments that are not identifiable to species using traditional morphological methods. To date, these bones comprise specimens that have been sampled and analysed from 11 sites in Orkney and Shetland, Scotland. An additional bone (Specimen 5) was later added to the current study. Although all 110 specimens were submitted for aDNA (except for Specimen 5) and collagen fingerprinting, only results pertaining to identified grey whale identifications are discussed further.

Ancient DNA analysis

All 109 specimens (excluding Specimen 5) underwent bone tissue collection/subsampling, aDNA handling and DNA extraction as per Rastogi *et al.* (2004) and McLeod *et al.* (2008). Briefly, all ancient DNA analysis was conducted in a designated workspace fully isolated from any contemporary marine mammal DNA or PCR products. All surfaces, tools and appliances were regularly decontaminated with a 30% bleach solution. Daily workflow occurred in a manner whereby tasks were carried out working from areas of non-DNA to non-amplified DNA and then amplified DNA areas, with no 'back-flow' within a single day. For all DNA extractions, we used 150mg of bone shavings and a modified version of the QIAamp® protocol for isolation for genomic DNA from compact bone (Qiagen, Mississauga, ON). In all steps of DNA analysis (e.g., DNA extraction, amplification, sequencing), negative (or 'null') controls were included as a means to detect potential DNA contamination.

We examined for the presence of analysable DNA by amplifying and sequencing a ~445 basepair (bp) fragment of the cytochrome *b* gene (using primers CBCet4F (5' ACA TGG ACT TCA ACC ATG AC 3') and CBCet5R (5' CTC AGA ATG ATA TTT GTC CTC AGG 3'). PCR product was evaluated for quantity and quality using agarose electrophoresis, then prepared for sequencing, cycle sequenced, and size separated and visualised on an ABI 3500xl Genetic Analyzer (Applied Biosystems) after McLeod *et al.* (2014). All samples were amplified in duplicate and then each duplicate was sequenced in both directions (e.g., with both primers of the primer pair used for amplification). Sequences were then examined visually using 4Peaks v1.8 (Nucleobytes.com) and edited and aligned in MEGAX v10.2.4 (Kumar et al. 2018). Species identity was confirmed through phylogenetic analysis using Bayesian inference of phylogeny in the program MrBayes v3.2.7a (Huelsenbeck and Ronquist 2001). In this analysis we included the sequences identified in this study as well as reference sequences for all known mysticete species known to have inhabited the North Atlantic (Table S1) and the sperm whale (*Physeter macrocephalus*) as an outgroup. We used the best-fit model of molecular evolution as determined in MEGAX v10.2.4; HKY (Hasagawa *et al*. (1985) with gamma distributed rate variation across sites (HKY+G). The run parameters consisted of four chains, 100,000,000

generations, samples taken every 100th generation and 25% of the initial burn-in steps discarded. The tree was visualized in FigTree v1.4.4 (https://github.com/rambaut/figtree/releases).

Collagen fingerprinting

Approximately 50 mg bone powder was collected from each of the 110 specimens and demineralised with 1 mL 0.6 M hydrochloric acid (HCl) overnight. The samples were then centrifuged and ultrafiltered at 12,400 rpm into 100 µL 50 mM ammonium bicarbonate (ABC) and incubated overnight (~18 h) with 0.4 µg sequencing grade trypsin (Promega, UK) at 37 °C. The diluted collagen digest (1 µL) was spotted onto a Bruker Ultraflex 384 stainless steel target plate with an equal volume of 10 mg/mL alpha-cyano hydroxycinnamic acid matrix following Buckley et al. (2017) and analysed at the University of Manchester using a Bruker Ultraflex II Matrix Assisted Laser Desorption Ionisation Time of Flight (MALDI-ToF) mass spectrometer with up to 2000 laser acquisitions. Our aim was to screen specifically for grey whale remains as done elsewhere (Hufthammer et al. 2018), by making reference to grey whale reference markers in comparison with those of other marine mammals (Buckley et al. 2014).

RESULTS

Amongst the 110 samples examined from Scotland as part of this current study, five bones (4.54%) were identified as being from the grey whale using DNA and/or collagen analysis (Table 1). While collagen analyses successfully identified five samples from the 110 specimens as grey whale (MMB0177, MMB0311, MMB0334, MMB0358, WH665) through the presence of peptide markers at approximately m/z 1079.6, 1453.7, 1566.8, 1652.8, 2135.1, 2899.3 and 3023.4, ancient DNA phylogenetic analyses successfully identified two samples as grey whale (MMB0177 and MMB0311) (N.B. Specimen 5 was not analysed for DNA) (Figure 1). Table 1 shows all previously known grey whale specimens identified in Britain to date (n=4) along with those presented here.

During the aDNA analyses, all negative aDNA controls were blank, indicating that there was no detectable DNA contamination in the ancient DNA analysis. For the two samples that were successful in DNA analysis we identified a single haplotype (EROCB001; NCBI # MW767461). Further, replicate sequences obtained from each sample were identical and there were no obvious indications of any deamination resulting from DNA damage over time.

Specimen 1: Caudal vertebra (Finds no. 4688; Lab. no. MMB0311)

This sample was identified as grey whale using both collagen and cytochrome *b* DNA (NCBI # MW767461). This bone originates from a multi-phase settlement dating from the Middle to Late Iron Age period and includes a monumental roundhouse, or broch, and village buildings, at The Cairns, South Ronaldsay, Orkney (Carruthers 2018). The substantial vertebra is highly worked and extremely well-preserved (Figure 2), possessing an apparently complex, extended series of uses. Both surfaces of the centrum are incised with multiple deep linear marks, V-shaped in profile indicating a considerable period, or intense use, as a chopping board. A circular hole was also present on the bone, cut deeply into one of the surfaces, and, together with its findspot, within the entrance area of one the village buildings, suggests it could have been used as a structural element, as a pivot for a door post, after its earlier use as a chopping board. The bone came from a building with an overall chronological span of the later 2nd to mid-4th centuries common era (CE).

Specimen 2: Fragment (Finds no. 5549; Lab. no. MMB0177)

This sample was identified as grey whale using both collagen and cytochrome *b* DNA analysis (NCBI # MW767461). This bone fragment originates from the Middle Iron Age broch at Howe, Mainland, Orkney (Figure 3). This sample was one of a series of large bone fragments probably originating from a cetacean rib found in the Phase 7 abandonment layers in one of the southern ancillary buildings (context 1223; c.1st – 4th centuries CE).

Specimen 3: Rib (Register no. NMS.Z.1940.11.34; Lab. no. MMB0358)

This sample was identified as grey whale using collagen, but failed aDNA analysis. This bone originates from Aikerness (Gurness) Broch, Orkney, which is dated to the Iron Age (Richardson 1948). This fragment of a proximal rib is in the collections of National Museums Scotland (Figure 4). This specimen probably dates to the Middle and Late Iron Age, i.e. 200 BCE (before common era) to 500 CE (Hedges 1987). There is no further information about its context, and it has not been radiocarbon dated.

Specimen 4: Rib (Register no. NMS.Z.1935.50.34C; Lab. no. MMB0334)

This sample was identified as grey whale using collagen, but failed aDNA analysis. This bone originates from Jarlshof, Shetland, which is a multi-period site, covering the Late Neolithic to 16th Century CE. (Curle 1933, 1934a, 1934b, 1935a, 1935b). This fragment of rib has been cut at each end and across its width, revealing cancellous bone along one side (Figure 5). It is in the collections of National Museums Scotland. This specimen was excavated from a Viking dwelling and probably dates from 800 - 1200 CE (Curle 1934a, 1935). There is no further information about its context, and it has not been radiocarbon dated.

Specimen 5: Vertebra (Register no. NMS.X.HAS 3210; Lab. no. WH665)

This specimen was identified as grey whale using collagen fingerprinting and was not subjected to DNA analysis (van den Hurk & McGrath 2021). This bone is a hollowed-out vertebral cup dating to the Iron Age from Jarlshof. Cut and chop marks are present all over the bone, as well as fresh breaks (Figure 6). The specimen has been identified as a thoracic vertebra, from which the transverse processes have been removed. Orange glue, used to reattach a small piece of bone, is visible. Both the cranial and caudal sides are fused, indicating that the specimen was probably an adult individual. It is in the collections of National Museums Scotland.

Table 1: All known fossil and archaeological finds of grey whale, Eschrichtius robustus, found in Britain to date.

Location	Date of finding	Skeletal element	Archaeological date	Radiocarbon date bp	Collagen ID?	DNA ID?	Laboratory no.	Museum register no. /Finds no./ Laboratory no.	References
Pentuan (=Pentewan), Cornwall	1780-1829	Partial skeleton; only humerus remains		1,329 ±195	NA	NA	-	RCM; loan from RGSC TRURI : LOAN.350.8	Colenso 1832; Flower 1872; Bryant 1995; Alter et al. 2015
Babbacombe, Devon	<1864; ?1861	Cervical vertebra			NA	NA	-	TM Z10167.1; cast in NHMUK.ZD.1997.154	Gray 1865
Petitor Beach, Babbacombe, Devon	May 1865	Cervical vertebra		340 ± 260	NA	NA	-	TM Z10167	Gray 1865; Pengelly, 1865, 1878; Bryant 1995; Alter et al. 2015
Petitor Beach, Babbacombe, Devon	1867	Cervical vertebra			NA	NA	-	TM Z10185	Gray 1865; Pengelly, 1865, 1878; Bryant 1995; Alter et al. 2015
Jarlshof, Shetland	1935	Rib	800-1200 CE		Y	N	MMB0334	NMS.Z.1935.50.34C	Curle 1935a, 1935b
Jarlshof, Shetland	<1956	Thoracic vertebra	Iron Age		Y	NA	WH665	NMS.X.HAS 3210	van den Hurk and McGrath 2021
Aikerness Broch, Gurness, Orkney	1940	Rib	200 BCE-500 CE		Y	N	MMB0358	NMS.Z.1940.11.34	Richardson 1948
Howe, Orkney	1978-1982	Fragment	1st-4th centuries CE		Y	Y	MMB0177	5549 (context 1223)	Ballin-Smith 1994
The Cairns, Orkney	2018	Caudal vertebra	later 2nd-mid-4th centuries CE		Y	Y	MMB0311	4688	Carruthers 2018

Figure 1: Bayesian inference phylogenetic tree (50% majority rule consensus) of grey whale mitochondrial cytochrome b sequences obtained in this study (EROCB001), along with other North Atlantic mysticetes and the sperm whale as an outgroup species. Reference species sequence accession numbers can be found in Table S1. BPHYS – *Balaenoptera physalus*; BMUS – *B. musculus*; BBOR – *B. borealis*; BACU – *B. acutorostrata*; MNOV – *Megaptera novaeangliae*; EROB – *Eschrichtius robustus*; EGLA – *Eubalaena glacialis*; BMYS – *Balaena mysticetus*; PMAC – *Physeter macrocephalus*.

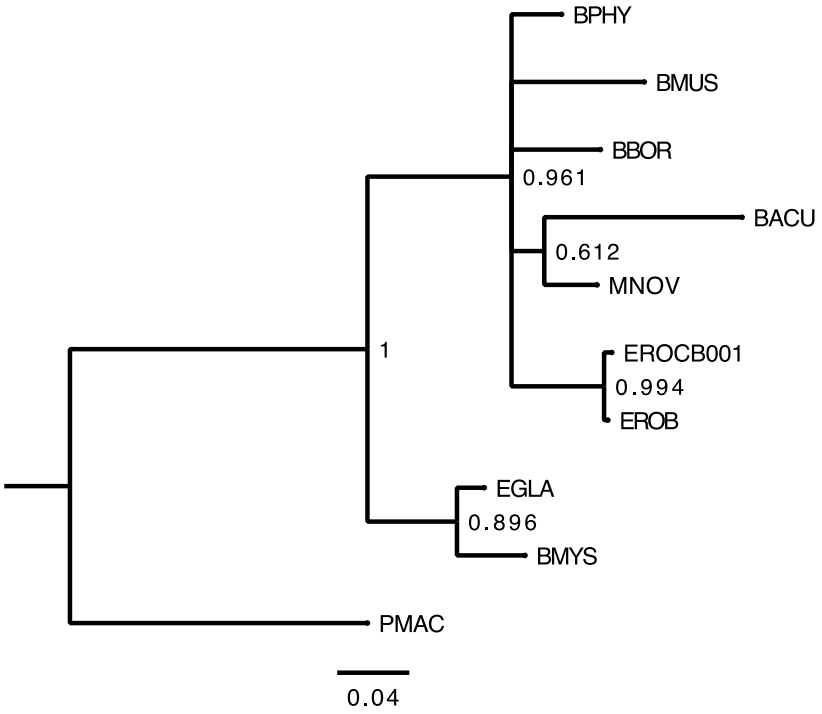

Figure 2: Specimen 1, caudal vertebra of a grey whale from the multi-age Iron Age site of The Cairns, Windwick Bay, Orkney.

Figure 3: Specimen 2, unidentified bone fragment from a grey whale from Howe, Mainland, Orkney, a site dated to the 2nd-4th CE. a. All the fragments and b. Close-up of sampled fragment.

Figure 4: Specimen 3, rib fragment from a grey whale from Aikerness (Gurness) Broch, Orkney (NMS.Z.1940.11.34).

Figure 5: Specimen 4, two views of a rib fragment from a grey whale from the Iron Age site of Jarlshof, Shetland (NMS.Z.1935.50.34A).

Figure 6: Specimen 5, three views of the vertebra from a grey whale from the Iron Age site of Jarlshof, Shetland (NMS.X.HAS 3210). Upper left: dorsal side. Bottom left: ventral side. Right: caudal side.

DISCUSSION

Five bones or fragments of bone out of a total of 110 were identified as being from the grey whale. All five were identified using collagen fingerprinting, while two were also identified using aDNA analysis. Therefore, collagen fingerprinting was more successful than aDNA in identifying the species of origin in those specimens subjected to both analyses, confirming the better preservation of collagen in these fragmentary samples. None of the specimens could be identified to species from their morphology because of their fragmentary nature. Therefore, these analytical techniques were essential for their correct identification.

The five Scottish archaeological grey whale samples date from 200 BCE-500 CE contexts, c.300 BCE – 1200 CE, including the sites of Jarlshof, Gurness, Howe and The Cairns (Curle 1933, 1934a, 1934b, 1935a, 1935b, Richardson 1948, Ballin-Smith 1994). The Cairns and Howe allow more subtle chronological resolution than the other sites, and molecular consideration of complete cetacean bone assemblages would likely allow archaeologists to comment more fully on changing reliance upon cetacean use over time. Each of these multi-period sites is located near to the shoreline, allowing ready access to stranded cetaceans. We are not aware of the hunting of larger mysticete whales in Orkney and Shetland at this time and hence it is likely that these bones were recovered from stranded individuals, although we cannot exclude the possibility that some or all were the result of in-shore hunting. All five samples come from whale bones that were highly worked and generally well preserved but offered few morphological clues for analysis apart from the anatomical identification of the skeletal elements in four cases (Jarlshof, Gurness, and The Cairns). While the samples from Jarlshof and Gurness were not excavated with firm controls for environmental contexts, the bones from Howe and The Cairns were excavated under more rigorous controls for analysis of organic and environmental data.

These new records of grey whale more than double the current number of records for this species from Britain. Previous British records are from Pentewan, Cornwall and Babbacombe, Devon (Table 1) and have been radiocarbon dated as late Iron Age/early medieval (1,329 ±195 ya bp; Pentewan) or much more recently (340 ± 260 ya bp; Babbacombe) than the Scottish specimens (Bryant 1995; Alter et al. 2015). They also confirm that the species' distribution during these time periods in the English Channel and North Sea comprised mainly shallow waters, which are the characteristic feeding grounds of this mostly intermittent benthic feeder at similar latitudes of the Pacific population (Dunham & Duffus 2002; Moore et al. 2003; Swartz 2018). It is likely that as collagen fingerprinting and aDNA analysis are increasingly applied to both previously and newly excavated cetacean archaeological remains in the future, the temporal and geographical records of grey whale in Britain will increase significantly. In the case of the grey whale, these additional records will help improve our knowledge of its behaviour and ecology in the eastern Atlantic through the use of additional analyses, such as stable isotopes and radiocarbon dating. Accurate identification of archaeological cetacean remains will also allow us to develop a clearer picture of the importance of different species to coastal communities through time and provide insights into whether they were sourced primarily from strandings or hunting on both sides of the Atlantic, which may indicate whether human over-exploitation of large whales, and especially the grey whale, began much earlier than the historical period, thereby requiring a re-evaluation of current conservation actions.

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Table S1: Reference sequences included in phylogenetic analysis

Abbreviation	Species	Common Name	Reference Citation	Reference Accession Number
BACU	*Balaenoptera acutorostrata*	Minke whale	Sasaki *et al.* (2005)	AP006468
BBOR	*Balaenoptera borealis*	Sei whale	Sasaki *et al.* (2005)	AP006470
BMUS	*Balaenoptera musculus*	Blue whale	Arnason *et al.* (1993)	X72204
BMYS	*Balaena mysticetus*	Bowhead whale	Arnason *et al.* (2004)	AJ554051
BPHY	*Balaenoptera physalus*	Fin whale	Arnason *et al*. (1991)	X61145
EROB	*Eschrichtius robustus*	Grey whale	Sasaki *et al*. 2005	AP006471
MNOV	*Megaptera novaeangliae*	Humpback whale	Sasaki *et al*. 2005	AP006467
PMAC*	*Physeter macrocephalus*	Sperm whale	Arnason *et al.* (2000)	AJ277029
EGLCB1	*Eubalaena glacialis*	North Atlantic right whale	McLeod *et al*. 2008	EU303335
EROCB001	*Eschrichtius robustus*	Grey whale	This study	MW767461