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# The genetic history of whaling in the Cantabrian Sea during the 13th–18th centuries: Were North Atlantic right whales (*Eubalaena glacialis*) the main target species?



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# ABSTRACT

For millennia, whales have been used as a food source, initially probably opportunistically, with the use of stranded animals on beaches, and later by active hunting. The Basques pioneered commercial whaling first in the neighbouring Cantabrian Sea (11th century) and then in Newfoundland and Labrador (16th century). The North Atlantic right whale (*Eubalaena glacialis*) is believed to have been the main target species of the Cantabrian fleets off the coast of Spain although other large whale species could have occasionally been targeted. At present, no molecular identification study has been performed to corroborate which species constituted the main catch for local whalers. Here we use historical bone remains to identify the main target species of medieval whaling in the Cantabrian Sea (13–18th centuries). Our results confirm the North Atlantic right whale as the main target species in Iberia suggesting that direct hunting could have played a role in the depletion of the species.

## 1. Introduction

Marine mammals have been part of the diet of coastal human populations for millennia (Stringer et al., 2008), including several coastal societies such as the Vikings, Inuits, Japanese and Basques that have been using whales as a resource for centuries (e.g. Ellis, 1991; Mccartney, 1980; Mccartney and Savelle, 1993; Szabo, 2008; Kalland and Moeran, 2010). Initially, these resources were probably restricted to the opportunistic use of stranded animals on beaches (Szabo, 2008). During the Roman period, marine mammals were occasionally, but not systematically, targeted for food (López, 2014). Today, whales belong to one of the most threatened group of mammals, almost exclusively due to the industrial hunting practices of the last few centuries (Denny, 2008). Archaeological investigations into the history of whaling and marine mammal hunting in general are vital for understanding the long-term exploitation of these important resources, and also to provide essential ecological baseline data on whale populations prior to industrial overhunting. Even though these materials are abundantly present in the archaeological collections their exploration for scientific purposes has been minimal, probably due to its fragmentary nature which hinders species or even genus identification; making tracking of species distributions and investigating changes in exploitation through time almost impossible.

The first records of dedicated whaling were in medieval times when it became an important economic activity. The blubber, the most valuable good, was melted into oil and used for lighting the streets of Europe and America up to the advent of better fuel. The meat was salted and the baleens and bones were used to make tools, utensils and load bearing columns in houses (López, 2014). Industrial whaling was probably pioneered by the Basques in the 11th century, even though Norse and other populations hunted whales for subsistence years before that (Szabo, 2008; Seersholm et al., 2016). The earliest whaling dates by the Basques correspond to references from Bayonne (Gulf of Biscay) in 1059 CE and Navarre (Northern Spain) in 1150 CE (Aguilar, 1986). In the Basque Country, the first whaling reference dates to 1190 CE (Ciriquiain-Gaiztarro, 1961). In 1199 CE and 1232 CE, there are references to whale hunting in Cantabria and Asturias (Northern Spain) and in 1286 CE in Galicia (North-western Spain) (Ciriquiain-Gaiztarro, 1961), while in Portugal the first reference to whaling is from 1229 CE (Teixeira et al., 2014). This temporal pattern suggests this activity

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spread from east to west due to the transfer of whaling experience and techniques, rather than a fast depletion of stocks in the Cantabrian Sea (i.e. northern coast of Spain and the southwest side of the Atlantic coast of France) or the search of better hunting grounds (Azpiazu, 2000).

In the Cantabrian Sea, Basque whaling peaked during the 16th and 17th centuries (Aguilar, 1986). From the 13th-18th centuries Basque whalers had settlements in up to 47 ports along the coasts of Northern Spain and Southern France (French Basque country, Spanish Basque Country, Santander, Asturias and Galicia) (Aguilar, 1986). Even though catch numbers may not have been high, additional factors would have had a negative effect on the whale population (i.e. whalers showed a preference for mother and calf pairs) (Aguilar, 1986). In the 16th century. Basque whalers started annual journeys to the NW Atlantic in search of new hunting grounds due to a reduction of whale stock in the Cantabrian Sea (Aguilar, 1986). The local coastal whaling activities had paved the way for the Newfoundland enterprise (Azpiazu, 2000). From approximately 1530 CE to 1630 CE, Basques whalers travelled from the Cantabrian Sea to the Strait of Belle Isle, a narrow strait located between Newfoundland and Labrador, to hunt whales (McLeod et al., 2008). This represented the first directed commercial whale hunting in the western North Atlantic (McLeod et al., 2008). It has been suggested that between 25,000 and 40,000 whales were killed during this time (Aguilar, 1986). Basque whaling in Newfoundland not only had an economical impact, but also a great effect on the whale populations. Gaskin (1991) suggested that Basque whaling in the 16th-17th centuries in the western North Atlantic might have been one of the largest right whale human-induced reductions.

Five species have been identified as the main targets of the local coastal whaling period, 13th–18th century, in the Cantabrian Sea: the North Atlantic right whale (*Eubalaena glacialis*), the bowhead whale (*Balaena mysticetus*), the gray whale (*Eschrichtius robustus*), and to a lesser extent the humpback whale (*Megaptera novaeangliae*) and the sperm whale (*Physeter macrocephalus*) (López, 2014). While most evidence (e.g. historical records, drawings) suggests the North Atlantic right whale dominated the catch (López, 2014), this has not yet been confirmed by biological or archaeological evidence. McLeod et al. (2008) used ancient DNA to identify the main target species along the coasts of Newfoundland and Labrador (Canada). The study found that bowhead whales were the main catch species, as opposed to the general belief that the most caught species in that area were North Atlantic right whales.

Here, we attempt to uncover the main target species of the early whaling period (13th–18th century) along the Western Cantabrian Sea. To do this we collected historical specimens from museums and private collections or from the seabed off historical whaling harbours (Table S1, Fig. 1). We used two fragments of mitochondrial DNA to genetically identify the species of the different specimens. Bone has been extensively used in ancient DNA studies to uncover past population dynamics (e.g. Campos et al., 2010), phylogenetic relationships among extinct and extant species (e.g. Willerslev et al., 2009) and for species identification (e.g. McLeod et al., 2008; Schlumbaum et al., 2010; Sremba et al., 2015). This work reveals, for the first time, which species dominated the catch during the early whaling period in the Western Cantabrian Sea and brings some insight into the past diversity of large marine mammals.

#### 2. Material and methods

#### 2.1. Sample collection

A total of 300 whale bones were collected by CEMMA (Coordinadora para o Estudo dos Mamíferos Marinos, Galicia) and collaborators during the spring and summer of 2014. Permission was obtained from all museums and institutions to access the collections and all samples were on loan for scientific purposes. A subset of 72 samples, representative of all the surveyed ports, was used in this study (Table S1). Samples were collected from local museums, private collections and in underwater sampling campaigns. Underwater sampling targeted areas described in several historical records (Valdés Hansen, 2010) as medieval whaling ports, and they were concentrated in Galicia (Bares and San Cibrao; Fig. 1). Several written records confirm the ports of Bares, Luanco and San Cibrao (Ciriquiain-Gaiztarro, 1961; Valdés Hansen, 2010; López, 2014) as old whaling ports active between the 13th and 18th century, which allow us to confidently place our samples in this time interval. All studied samples, even the ones from private collections, can be confidently assigned to these areas.

Underwater sampling was conducted by either snorkelling or using autonomous diving equipment. The latter underwater sampling was carried out by CEMMA as part of a dedicated project to study historic whaling in the Cantabrian Sea, while snorkelling sampling was usually opportunistic (e.g. carried out while spearfishing). Detailed information



Fig. 1. Sampling locations. Geographical range of NA right whale (red polygon), with an insert of the geographical locations of sampling sites, historical whaling harbours in Galicia and Asturias, Western Cantabrian Sea. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

regarding the sampling method used for each sample can be found in Table S1.

Bones or bone fragments were sampled using a Dremel drill and either powdered at the collection site or subsampled (for the latter a minimum of  $1 \text{ cm}^3$  of bone was sampled). When drilling the bones, the uppermost layer (a few millimetres) of a small patch (approx.  $3 \times 3$ cm) was scraped off using a drill. The powder used in DNA extractions was obtained by drilling bone remains after the superficial layer was eliminated. Samples from underwater campaigns were immersed in freshwater for 15 days, changing the water every second day. Afterwards, bones were left to dry at room temperature in a dark environment, for a minimum of 30 days, prior to sampling.

To avoid cross contamination when handling different samples, we used either new drill bits or cutting disks, or if drill bits were re-used, they were carefully cleaned with diluted sodium hypochlorite and 70% ethanol between samples. All samples were then stored at CEMMA headquarters in Nigrán, Galicia, Spain, at -20 °C for better DNA preservation.

#### 2.2. DNA extraction, amplification and sequencing

DNA extraction and pre-PCR manipulation were carried out at the University of Copenhagen, in a dedicated ancient DNA facility designed for dealing with potentially degraded samples such as these, which are particularly susceptible to contamination from exogenous sources of DNA. Contamination was monitored during the extraction and PCR processes by blank controls. Total cellular DNA was extracted from 72 specimens according to the following protocol: between 0.01 and 0.09 g of bone powder, obtained by drilling the bone with a Dremel drill, was incubated overnight at 37  $^\circ C$  in 1.0 mL of 0.5 M EDTA and 25 mg/ml proteinase K. To pellet the non-digested powder, the solution was centrifuged at 12,000 rpm for 5 min. The liquid fraction was then transferred into a Centricon micro-concentrator (30-kDa cut-off), and spun at 4000 rpm for 10 min. When the liquid was concentrated down to 200 to 250 µl, the DNA was purified using the MinElute PCR purification kit (Qiagen), with the following modifications: a)  $10 \times PB$ buffer (Qiagen) was used for the DNA binding step; b) spins were done at 8000 rpm with the exception of the final one at 13,000 rpm; c) in the elution step, spin columns were incubated in 40 µl buffer EB at 37 °C for 10 min, spun down, and repeated once more. The eluates from both rounds of elution were pooled.

All specimens were first screened for 200 base pairs (bp) of the mitochondrial DNA (mtDNA) control region (CR) using the primers (297F: 5-CCGCTCCATTAGATCACGAG-3; dip5R: 5-CCATCGWGATG-TCTTATTTAAGRGGAA-3', (Borge et al., 2007)) originally designed for bowhead whales. For some of the samples, either because the first primer pair did not produce any amplification or to confirm the previous results, we also targeted a 116 bp fragment of the 16S ribosomal RNA (rRNA) using general mammalian primers (16S3 5'-TGGGGTGACCTCGGAGAAY-3'; 16S4 5'- TAGGGTAACTTGKTCCGTT-GA-3', (Haile et al., 2009)). PCR amplification was performed in 25 µl volumes, using 1× PCR buffer (600 mM Tris-SO<sub>4</sub> (pH 8.9), 180 mM (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>), 2 mM of MgSO<sub>4</sub>, 1.6 mg/ml bovine serum albumin, 0.4 µM of each primer, 1 µM of dNTPs, 0.5 U of High Fidelity Platinum Taq (Invitrogen, Carlsbad, CA) and 1 µl of DNA. Cycling conditions were: 94 °C for 2 min; 50 cycles of 94 °C for 30 s, 50 °C (CR)/54 °C (16S) for 30 s and 68 °C for 45 s followed by 72 °C for 7 min.

Following visualization on agarose gels, amplified PCR products were purified using MinElute PCR purification kits (Qiagen). Purified products were sequenced in both directions using the PCR primers and ABI sequencing chemistry by the commercial facility offered by Macrogen (Seoul, South Korea). To guard against incorporation of erroneous data derived from DNA damage, some PCR products were diluted 1:10 and subsequently cloned using TOPO TA cloning kit for sequencing (Invitrogen, Carlsbad, CA). Ten percent of the samples were randomly selected for cloning. A minimum of 7 clones were Sanger sequenced for each sample for primer pair CR. A second amplification followed by direct sequencing was also done for 16 individuals (Table S1) for both primer pairs to demonstrate reproducibility of results. DNA sequences were edited and aligned using Geneious v 6.0 (Kearse et al., 2012) and inspected by eye. Unique sequences have been deposited in GenBank under accession no KU302595–KU302605.

# 2.3. Species identification

All sequences were aligned against the southern right whale complete mtDNA sequence (GenBank accession number NC\_006930). For species identification, nucleotide BLAST (Basic Local Alignment Search Tool) (Johnson et al., 2008) searches were performed against the NCBI nucleotide database for the 16S and CR sequences. To perform our species identification, we used a cut-off of 98% identity match in our BLAST searches. We also used phylogenetic trees to confirm the species identification (see below).

# 2.4. Minimum number of individuals (MNI)

The MNI within the sample set was calculated as in McLeod et al. (2008). Samples were identified as unique individuals when either presenting a unique location (samples from different whaling ports or underwater sampling areas) or a unique haplotype based on the CR. Those samples sharing site and haplotype, but consisting of skeletal pieces known to represent unique specimens (e.g. skulls) were also considered as different individuals.

# 2.5. Population genetic and phylogenetic analyses

The number of segregating sites (S), haplotypes (h), haplotype (Hd) and nucleotide  $(\pi)$  diversities (Tajima, 1983) were calculated using DNASP version 5 (Librado and Rozas, 2009) for the CR haplotypes by species. Phylogenetic relationships for the haplotypes were estimated using Bayesian inference methods. A Bayesian tree was calculated in MrBayes v.3.6.2. (Ronquist and Huelsenbeck, 2003) using the KHY + I nucleotide model for our sequences as estimated in jModeltest 2 (Darriba et al., 2003). Markov chain Monte Carlo (McMC) sampling was performed in two separate analyses with four chains of 8 million generations, sampling every 1000 generations, and discarding the first 25% as burn-in. A control region sequence representative of each of the five whale species putatively targeted by the whalers (North Atlantic right whale, bowhead whale, sperm whale, humpback whale and gray whale), as well as representatives of the other large whales present in the Cantabrian sea: blue whale (Balaenoptera musculus), sei whale (Balaenoptera borealis), fin whale (Balaenoptera physalus), minke whale (Balaenoptera acutorostrata), killer whale (Orcinus orca); and the two other species of right whale: the southern right whale (Eubalaena australis) and the North Pacific right whale (Eubalaena japonica) were combined with the haplotypes described in our study to construct the tree (Table S2).

# 3. Results

For the 72 samples tested, we were able to successfully amplify and sequence the 200 bp CR fragment for 70 bones, 10% of the samples were cloned and no alternative sequence was found among the seven colonies picked per sample. There was complete agreement between the forward and reverse sequence and the cloned sequences for each of the analysed samples. In addition, 16S rRNA fragments were sequenced for 37 of the samples to double check species identification. We are confident that the control region sequences are of mitochondrial origin and are not nuclear-encoded copies of mitochondrial sequences (numts), as no putative heterozygous sites were found and no alternative sequence was observed among the clones.

No DNA was amplified from the negative controls, indicating that

there was no contamination during DNA extraction or PCR set up. We did not see any difference in amplification results between samples that were stored in museums and collected in underwater campaigns.

#### 3.1. Species identification

We were able to identify three different species among the screened specimens: North Atlantic right whale (n = 68), gray whale (n = 1), and humpback whale (n = 1). Within the North Atlantic right whale specimens, we identified nine different control region haplotypes (Table S3). Based on haplotypes and location, the MNI in our sample set is 29: North Atlantic right whale (n = 27), gray whale (n = 1), and humpback whale (n = 1). When corrected for the type of bone, the MNI increased to 50 individuals: North Atlantic right whale (n = 48), gray whale (n = 1), and humpback whale (n = 1).

#### 3.2. Phylogeny and population genetic analyses

The final dataset of 48 unique North Atlantic right whale individuals consists of 154 bp CR sequences, which define nine different haplotypes with a total of 7 polymorphic sites. Haplotype diversity for this fragment is 0.7660 and nucleotide diversity is 0.01047. To further confirm species identification and to infer the relationship between the different haplotypes a phylogenetic tree was reconstructed. The Bayesian phylogeny clearly show a clade with all the North Atlantic right whales, both the ones derived from the present study as well as sequences from the NCBI database. The gray whale sequence is placed in the tree clustering with other sequences from the same species, as it does the humpback whale with other sequences from its species. The low bootstrap values for some of the branches are due to the short length of the sequenced fragment. Nevertheless, the tree clustering combined with the BLAST results clearly support the robustness of our species identification (Fig. 2). The gray whale sequence obtained in this study constitutes a new haplotype when compared with other published gray whale sequences.

# 4. Discussion and conclusions

In this study, we have sequenced the CR of 72 historical whale samples derived from the Basque whaling activity in the Cantabrian Sea during the 13th–18th centuries. Our results confirm the North Atlantic right whale as the main target of whalers during this period. This differs from what has been previously described in the Western Atlantic off the coast of Newfoundland and Labrador, where DNA analyses on historical remains from the 16–17th century found that bowhead whales were the main targets of whalers in the area (Rastogi et al., 2004; McLeod et al., 2008). Teixeira et al. (2014), based on morphological and comparative analyses, also confirmed the exploitation of North Atlantic right whales at Peniche, off the coast of Portugal, during the 16th–17th century (samples dated by context, i.e. deduced by association with materials/ artefacts found in the same archaeological context).

North Atlantic right whales behavioural and physiological characteristics make them an easy target for whalers. This species lives close to shore, especially during the calving season (November–April) and they are slow swimmers (Greene and Pershing, 2004). This would have allowed Cantabrian whalers to use shore-based lookout towers to spot the animals and to approach them in small rowing boats. The whales' buoyancy after death made them an ideal prey, as whalers would pull the carcasses to shore where they started processing the remains (Greene and Pershing, 2004). Some authors (Aguilar, 1986) speculated that by the end of the 16th century the North Atlantic right whale stock off the coast of the Spanish Basque country was already depleted and that the opening of new hunting grounds would temporarily increase the catch. The genetic confirmation of the right whale as the main



**Fig. 2.** Bayesian phylogeny. MrBayes phylogenetic tree for the 154 bp sequences of the CR. Colours in the tips refer to the different species included in the tree. Labels in the nodes indicate posterior probabilities higher than 0.5. H1–H9 represents the NA right whale haplotypes from this study. H10 defines the gray whale haplotype and H11 the humpback whale haplotype from this study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

target species suggests the negative effect that whaling may have had in the North Atlantic right whale stock, indicating that this might have had an impact in the functional extinction of the eastern NA population. Up to the 18th century, prior to commercial exploitation, the NA right whale was common on both sides of the NA, with a range that spread from the Western Sahara to the North Cape (Norway), on the eastern side, and from Florida to Nova Scotia on the western (Aguilar, 1986; Monsarrat et al., 2015). In the last 60 years, less than ten confirmed sightings of the species have been recorded in the eastern NA including sightings in Madeira (1959 CE, Freitas et al., 2012), Galicia (1993 CE, Arcos and Mosquera, 1993), and Canary Islands (2008 CE, Halpin et al., 2009). It is not clear whether these observations are part of a remnant population or strays from the western NA stock (Reilly et al., 2012). The western NA stock itself only numbers between 272 and 686 individuals, with the NA right whale species as a whole listed as endangered by the IUCN (Pettis, 2014).

Besides North Atlantic right whales, remains of a humpback and a gray whale were also identified in the present study. Gray whale became extinct in the Atlantic Ocean probably during the 17th century (Reilly et al., 2008) being the only whale species that went extinct throughout an entire ocean basin in historical times. Several authors (Fraser, 1970; De Smet, 1981; Aguilar, 1986) considered the gray whale as a target species of the Basque whalers during the Middle Ages. Pacific gray whales live in near-shore waters and, assuming that the extirpated Atlantic gray whale population had a similar habitat preference as their Pacific counterparts, they would have been easy targets during the early whaling period. However, the present study identified only one gray whale specimen, which suggests that gray whales probably represented opportunistic catches. This is not a new observation since an archaeological dig in Campa de Torres, Gijón in 1996 CE, recovered a potential scapula of a gray whale, dated to the 3rd-4th century BCE (Quesada, 2001), suggesting humans have exploited these animals since ancient times in the studied area. The scarcity of gray whales in our sampling could also be explained by over-exploitation of this species already by the 13th century, however we do not have any evidence to support this hypothesis. We have compared the gray whale sequence obtained from our specimen with all the other control region sequences covering the same fragment available for gray whale in GenBank (Arnason et al., 1993; LeDuc et al., 2000; Lang et al., 2014; Alter et al., 2015; Meschersky et al., 2015). The sequence reported in this study constitutes a new haplotype not previously described, suggesting that not all past genetic diversity of the species has been uncovered.

This local study in the Cantabrian Sea confirms the potential of combining material from new archaeological sampling campaigns and archival material to genetically characterize whale hunting targets during the past whaling periods. It also remarks the potential of this material for inferring pre-whaling genetic diversity in these populations, as the effect of commercial whale exploitation on genetic diversity and population structure remains largely unknown. Estimates of pre-whaling population sizes, essential for determining sustainable population levels, are controversial because they are based either on notoriously inaccurate historical records (e.g. whaling vessel logbooks and written documents of early settlers or explorers), or on molecular models using widely uncertain rates of DNA substitution and gene flow. As a result, census-based estimates and molecular models often conflict by orders of magnitude (Baker et al., 2004; Ho et al., 2008). Thus, the accurate species identification of geographically and temporally distributed archaeological whale remains are essential for estimating the population sizes and geographic ranges of cetacean species prior to population collapse. Our study aims to contribute in the genetic characterization of archaeological whaling remains that could be used in future studies for a better assessment of past genetic diversity, past population sizes, and present population estimates.

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