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Forgotten Mediterranean calving grounds of gray and North Atlantic right whales: evidence from Roman archaeological records

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Abstract

Right whales (*Eubalaena glacialis*) were extirpated from the eastern North Atlantic by commercial whaling. Gray whales (*Eschrichtius robustus*) disappeared from the entire North Atlantic in still-mysterious circumstances. Here we test the hypotheses that both species previously occurred in the Mediterranean Sea, an area not currently considered part of their historical range. We used ancient DNA barcoding and collagen fingerprinting methods to taxonomically identify a rare set of 10 presumed whale bones from Roman and pre-Roman archaeological sites in the Strait of Gibraltar region, plus an additional bone from the Asturian coast. We identified three right whales, and three gray whales, demonstrating that the ranges of both of these species historically encompassed the Gibraltar region, likely including the Mediterranean Sea as calving grounds. Our results significantly extend the known range of the Atlantic gray whale, and suggest that 2,000 years ago right and gray whales were common when compared to other whale species. The disappearance of right and gray whales from the Mediterranean region is likely to have been accompanied by broader ecosystem impacts, including the disappearance of their predators (killer whales) and a reduction in marine primary productivity. The evidence that these two coastal and highly accessible species were present along the shores of the Roman Empire raises the hypothesis that they may have formed the basis of a forgotten whaling industry.

Keywords: Atlantic gray whale, North Atlantic right whale, Antiquity, shifting baseline, ancient DNA barcoding, collagen fingerprinting (ZooMS)

1. Introduction

The human influence on Earth's ecosystems has become so pervasive, that many have started referring to the Epoch we now live in as the Anthropocene [1]. Yet, understanding the full extent to which humans have modified natural ecosystems is not straightforward, because we have been doing so for millennia [2], and then forgetting about it. Our collective amnesia stems from what Pauly called the 'shifting baseline syndrome': a progressive adjustment, with each new human generation, in the collective perception of what 'natural' ecosystems look like [3], particularly pervasive whenever ecosystem changes take place over long and poorly documented periods [4]. The shifting baseline makes us underestimate our cumulative impacts on the Planet, misjudge the ecology of species and the functioning of ecosystems, and lowers our ambitions for their future conservation [5].

The global-scale industrial exploitation of large whales nearly emptied the world's oceans of their largest animals [6,7], affecting marine ecosystem function and structure [8,9]. The final chapters of this industry (up to the 1986 moratorium by the International Whaling Commission) are reasonably well documented by statistics of catches and trade [6]. But industrial whaling started long before such systematic records began, and its earlier impacts remain poorly understood.

Medieval Basque whalers are credited with being the first large-scale commercial whalers [10]. Whaling itself goes back millennia [11], but there is currently no evidence that pre-Basque whaling translated into catches substantial enough to impact whale populations. In contrast, Basque whaling undeniably developed into a major industry, combining efficient methods for capturing these large animals and for processing the huge quantities of meat and oil produced with trade networks for distributing these products across Europe. Records of Basque whaling go back to the 11th century, in the coasts of the Gulf of Biscay [12]. By the 16th century, it had expanded across the North Atlantic into Iceland, Norway, Spitzbergen and Newfoundland [13]. Eventually, as other whaling nations joined in, whaling became a global-scale industry [11]. The eastern North Atlantic is nonetheless the region for which records of commercial whaling span the longest period of time: nearly one millennium.

Early Basque whaling focused on the North Atlantic right whale (*Eubalaena glacialis*) [12]. This species migrates between high-latitude summer feeding areas and temperate calving grounds, being highly coastal during the calving and migration seasons [14]. It was historically found across the North Atlantic [15], possibly as two sub-populations – eastern and western – with separate calving areas (figure 1*a*). Early Basque whaling was a strictly coastal activity, targeting eastern right whales calving in and/or migrating through the Bay of Biscay, particularly cows and their calves [12]. Basques and other whaling nations subsequently targeted right whales offshore, in their northern feeding grounds, whereas coastal American whaling exploited the western migration and calving areas [16]. One of the most valuable and most easily captured species, right whales were a main target of all whaling operations across the North Atlantic until becoming commercially extinct in the mid-18th Century. Even afterwards, the few remaining individuals continued to be opportunistically taken whenever found [16]. The species came very close to biological extinction, with just a few dozen individuals probably remaining by the time it was given full legal protection in 1935 [16]. Today, it is functionally extinct in the eastern North Atlantic, subsisting in the western North Atlantic as a small and endangered population of about 500 individuals [14], less than 6% of the estimated original population [17].

There is another species missing from the eastern North Atlantic, and indeed from the entire North Atlantic, but the circumstances of its disappearance remain poorly understood. The gray whale

(*Eschrichtius robustus*) is currently found only in the North Pacific, where it too was heavily whaled and highly depleted [6]. Like the right whale, it feeds in high-latitude summer grounds, and migrates along the coastline to lower-latitude coastal calving grounds [18]. Early-20th century whalers and scientists alike considered gray whales restricted to the North Pacific, but subsequent archaeological studies revealed over 40 bone specimens on the European and North American Atlantic coasts [19]. These, supported by a few rare sources of documentary evidence [20,21], demonstrate that gray whales survived in the North Atlantic into the 18th century (figure 1*b*; electronic supplementary material, Appendix 1). Although the historical records show that gray whales were economically valuable and pursued by whalers, the extreme paucity of these records (when contrasted with those for the right whale) raises doubts that whaling could have been solely responsible for its extinction in the North Atlantic [10,22]. It may have also been naturally rare, a hypothesis supported by recent genetic analyses indicating a decline in genetic diversity, and thus in population size, previous to historical-era whaling [19].

The Mediterranean region falls in similar latitudes to those where right and gray whales calve today or are known to have calved historically (figure 1), but it is not considered part of the natural range of either species [14,18]. Indeed, the very few known records in this region (electronic supplementary material, Appendix 1) are seemingly more compatible with occasional vagrancy than with a regular past presence. Given the depth of the historical record in the Mediterranean region, one might assume that if large, conspicuously coastal whales were present, it would be well-known. However, given that by the 18th century both right and gray whales were already extremely rare in the eastern North Atlantic, searching for evidence of a putative previous presence in the Mediterranean requires going further back in time. As one does so, historical records become not only progressively scarcer but also substantially more ambiguous. Indeed, whale taxonomy – describing the different species as we recognise them today – is a very modern discipline, and as a result designations used in historical texts do not necessarily match current species. Sometimes, such designations are too broad to allow the identification of a particular species (e.g. *ketos/cetus*, a “sea monster” that included whales, seals, turtles and sharks); sometimes, they appear precise, but their exact meaning has been lost (e.g. , “ram-fishes”) (electronic supplementary material, Appendix 3, [23]). Furthermore, prior to the 18th century very few of the authors writing about whales had ever seen one, much less so alive, and so descriptions generally blend factual information with guesswork and mythology [24].

Archaeology, however, can provide definite evidence of a species’ past occurrence in a given area. Given that the Mediterranean region is one of the world’s hotspots of archaeological work, one would expect that if right or gray whales were previously part of this region’s fauna, there should be substantial archaeological evidence. In fact, and counter-intuitively given their large size, whales are notoriously difficult to investigate through archaeological studies [25]. Indeed, most archaeological work focuses on understanding human history, but whale bones seldom make it to human settlements. Most whales die and sink in the sea; and those that make it to the shore typically have their skeletons broken down and dispersed by the action of the waves. Even when actively exploited by humans, their huge size results in them being butchered on the beach, and the meat and blubber that are transported inland are invisible in the archaeological record [26]. Bones themselves can be valuable raw materials (e.g., [27,28]) and thus transported inland, but when that happens they are often fragmented or highly transformed, rendering identification through classical comparative anatomy methods very challenging, even more as most museums lack proper reference collections for whales (given the space required to curate their huge skeletons). Consequently, whale bones are not only rare in the archaeological record, but also frequently neglected, labelled only in general terms (e.g., “cetacean”), and sometimes attributed to the wrong species [25].

It is thus possible that right and/or gray whales were once present in the Mediterranean region and subsequently forgotten. Fortunately, new technological developments in DNA and collagen fingerprinting are now making it possible to identify with certainty ancient cetacean remains even from small fragments [25,29,30], opening a new window into the pre-whaling distribution of these species. Here, we take advantage of these technologies to test the hypotheses that right whales and gray whales previously occurred in the Mediterranean, by analysing a rare set of presumed whale bones in the Strait of Gibraltar region, at the entrance of the Mediterranean Sea. We complement these results with the analysis of a bone from Gijón, northern Spain, previously identified as a gray whale based on anatomical methods [31]. We discuss the implications of our findings to our understanding of the historical distribution and ecology of right and gray whales in the eastern North Atlantic, as well as of historical human impacts on marine ecosystems.

2. Data and methods

(a) Archaeological records in the Gibraltar region

We analysed a set of 10 presumed whale bones (table 1) from four archaeological sites in the Gibraltar region: the ancient cities of *Baelo Claudia* (modern Tarifa, Spain [32]), *Iulia Traducta* (modern Algeciras [33]) and *Septem Fratres* (modern Ceuta [34]); and the Hellenistic city and Roman military camp of *Tamuda* in northern Morocco [27] (figure 2; electronic supplementary material, Appendix 2). The bones were found during excavations by the University of Cádiz, as part of a programme of work on ancient marine resource exploitation, with a focus on Roman fish-salting plants, which is exploring the hypothesis of a forgotten industry of cetacean exploitation in Antiquity [35].

(b) Archaeological record in the Gijón region

We analysed a whale scapula found near Gijón (Asturias, northern Spain), in the pre-Roman/Roman archaeological site of *La Campa Torres*. It was previously identified as a gray whale through anatomical comparisons with other scapulae of gray whale and North Atlantic right whale [31].

(c) Species identification

Some of the 11 bones we analysed had been previously identified through anatomical methods, but most were too fragmented to even attempt this (table 1). We have analysed these specimens through two laboratory methods that have proven effective for the identification of ancient cetacean bones: collagen peptide mass fingerprinting (PMF) and DNA barcoding [25].

Species identification through collagen PMF (also known as ZooMS) and DNA barcoding followed the protocol described in reference [25] (details in electronic supplementary material, Appendix 2). Briefly, for ZooMS, between 10-30mg of bone was demineralised in 0.6 M hydrochloric acid, gelatinised, digested with trypsin, and purified using a C18 resin ZipTip® pipette tip (EMD Millipore). Each sample was run in triplicate on a Bruker ultraflex III MALDI TOF/TOF mass spectrometer, and mass spectra were assigned to species based on the list of *m/z* markers presented in references [30,36,37]. Raw MALDTI-TOF data files are available in the Dryad Digital Repository [38]. For DNA barcoding, DNA was extracted from the ancient bones using a modified silica-spin method [39,40], and PCR amplifications initially targeted a 182bp fragment of the mitochondrial cytochrome b gene which has been demonstrated to successfully distinguish cetacean species [41,42]. Samples that failed initial amplifications were amplified with alternative primer sets targeting cytochrome b fragments <100 bp. Cetacean species identifications were assigned through comparison with published references through GenBank BLAST and through 'DNA surveillance' [43]; eight sequences were uploaded to Genbank under accessions MH193488-95.

(d) Dating

Specimens were dated through two complementary methods: through their stratigraphic position in the archaeological context; and directly via radiocarbon (^{14}C) dating (table 1; details in electronic supplementary material, Appendix 2). The first method gives an estimate of when the specimen was last used or abandoned, whereas the second estimates when the individual was alive and growing. It is thus expected that the latter is older than the former, with the date at which the individual died somewhere in-between.

3. Results

The combined results of DNA and collagen analyses shed light on the identity of all 11 specimens analysed (table 1), reinforcing the value of fingerprinting methods for the analysis of species assemblages in archaeological records [25]. Of these specimens, one (WH819) is not a cetacean, most likely an African elephant; another (WH816) corresponds to a dolphin (*Delphinus sp.*). Nine specimens where identified as whale species: three as gray whale (including the record from Gijón), three as right whale, one as fin whale (*Balaenoptera physalus*), one as long-finned pilot whale (*Globicephala melas*), and one as sperm whale (*Physeter catodon*).

Results from both analytical methods proved consistent and highly complementary (table 1). Indeed, collagen PMF (ZooMS) provided information on three specimens for which the DNA analyses failed: one to the species level (WH810, gray whale), and two to the family level (WH818, Balaenidae; WH819, Elephantidae). Record WH818 is very likely North Atlantic right whale, given that the other species in the family occur in different oceans [14], and given that DNA analyses of two other specimens confirm that this species was previously presence in the region. Record WH819 is very likely African elephant (*Loxodonta africana*), which is currently absent but was present in Northern Africa during the Roman period [44].

Conversely, DNA barcoding allowed a more precise identification than the collagen analysis for five specimens, four to the species level (WH812, WH813, WH814, WH822) and one to the genus level (WH816). As collagen PMF is less susceptible to environmental contamination, and more amenable to a high-throughput approach, it is an ideal screening technique ahead of more resource-intensive DNA analyses, which may not be needed in all cases. For example, collagen-based identification is particularly cost-effective for identifying species that are sole members of their family (e.g. gray whales).

One specimen coming from an old museum collection (WH812) could not be dated though its stratigraphic position, while two (WH810, WH822) could only be dated approximately; all other specimens come from recent archaeological excavations by well-trained teams for which stratigraphic data could be obtained. For three specimens (WH810, WH813, WH819) dating via radiocarbon was not possible. There were seven specimens for which both dating methods could be applied. Of these, five provided consistent results across methods, with radiocarbon pointing to an earlier date than stratigraphy, as expected. In two cases (WH814 and WH816) the results from the radiocarbon dating are not congruent with the stratigraphic information (too recent), likely indicating an over-correction of the marine reservoir effect in these two particular cases (discussion in electronic supplementary material, Appendix 2).

Overall, these results demonstrate that both right and gray whales occurred in the Strait of Gibraltar region during the Roman period, and that gray whales occurred in the Asturian coast during pre-Roman times.

4. Discussion

(a) Forgotten whale distributions

Seven out of 11 specimens analysed correspond to species currently absent from the regions where the bones were collected: three gray whales, three right whales (two certain, one very likely), and one very likely African elephant. Whereas our focus is on the whale specimens, the elephant is interesting too, as it likely corresponds to the extinct Northern African elephant subspecies, *Loxodonta africana pharaoensis*. These elephants were used by Carthaginians against Rome in the Punic wars (264 BC to 146 BC), and the subspecies is believed to have become extinct by the end of the 2nd Century AD through overexploitation for ivory and as war animals [44].

Our results demonstrate that the ranges of both right and gray whales historically encompassed the Gibraltar region at the entry of the Mediterranean Sea. They also suggest that both species were previously common in this region. Indeed, both gray whales (with two records) and right whales (with three records) appear in the Gibraltar set of 10 bones more frequently than any of the other three whale species identified: fin whale, sperm whale, and long-finned pilot whale, with a single record each. The latter are all regularly found in the Gibraltar region today [45], and were probably even more abundant in the past, particularly fin and sperm whales, which were heavily depleted in Gibraltar by 19th and 20th century whalers [46]. Even if the number of bones found is very small, they are remarkable given how rare whale bones are in the archaeological record (for all the reasons detailed in the Introduction). Indeed, the Gibraltar specimens analysed here are 10 out of only 70 bones inventoried in a recent review of archaeozoological whale records (from the Upper Palaeolithic to Late Antiquity) across the whole of the Mediterranean Sea [47]. The odds that a rare species would end up being represented among these few bones are very low.

Our results should also be placed in the context of a previous fingerprinting analysis of 17 bones from the Late Bronze Age to the Early Middle Age, from the north-western Mediterranean (13 from southern France; 3 from Sardinia, 1 from Tuscany). Among the 14 bones that could be identified to the species level, eleven were of fin whale, one of sperm whale, one of Cuvier's beaked whale (*Ziphius cavirostris*), and one of right whale (in Southern France) [25]. This study thus did not find evidence for the presence of gray whale, but it demonstrated right whales were present. In this sample, right whales appeared as frequently as sperm whale and Cuvier's beaked whale (both currently present in the Mediterranean), but much less frequently than fin whales (which are the most common species in the Mediterranean today [45]).

In the case of the right whale, it was already known that its historical range extended as far south as Cintra Bay on the Western Sahara coast (figure 1*a*), but our results (together with the previous record from southern France [25]) demonstrate that in the Roman period its range extended into the western Mediterranean, and suggest that it was common in the Gibraltar area.

For the gray whale, our new records in the Strait of Gibraltar substantially expand the knowledge of the historical range of this species in the eastern North Atlantic. Prior to our study, archaeological records attested the past presence of gray whales in the North Sea and English Chanel, with the southernmost bone recorded in the Asturian coast of Northern Spain [22] (figure 1*b*; also confirmed by our specimen from Gijón). There was also the extraordinary observation of a single individual in the Mediterranean Sea in May 2010, but this corresponded almost certainly to a vagrant from the North Pacific population [48] and as such it says little about the historical presence of this species in the region. In contrast, our two bone specimens are reliable evidence of regular past presence, because occasional vagrant individuals are very unlikely to end up in the archaeological record. Our records thus demonstrate that the historical range of gray whales previously extended into the entrance of the Mediterranean Sea. They are in agreement with archaeological records in the western North Atlantic that extend as far south as Florida (figure 1*b*), and indicate that like today's eastern North Pacific population, the extinct North Atlantic gray whale also migrated to sub-tropical waters.

(b) Forgotten whale calving grounds

Given the ecology of gray and North Atlantic right whales, the individuals we found in Gibraltar were most likely either in their winter calving grounds, or migrating between feeding grounds and a calving ground elsewhere. A description by Pliny the Elder from the Roman period (1st century AD) provides independent support to the former possibility: it describes whales that come to the Cadiz region "*before the winter solstice, and that at periodical seasons they retire and conceal themselves in some calm capacious bay, in which they take a delight in bringing forth"* (electronic supplementary material, Appendix 3). This does not fit with any other species currently present in the region [23] but it matches perfectly with the ecology of either gray or right whales, and strongly supports the hypothesis that at least one of these species regularly calved near Cadiz.

If our specimens came from migratory individuals, their respective calving grounds would have been either further south of Gibraltar (in the Atlantic coast of Africa), or further east (in the Mediterranean Sea). Right whales historically calved off the Western Sahara (figure 1*a*), and individuals migrating to/from this area may well have hugged the coast near Gibraltar during migration. However, it seems unlikely these individuals would regularly enter the Mediterranean Sea, as right whales do not make feeding stopovers during migration [14]. As two of our right whale records (WH818 in Tetouan, WH822 in Ceuta) are east of Gibraltar, and given the previous record from Southern France [25], it seems very likely that this species previously entered the Mediterranean Sea to calve. In further support of this hypothesis, there are two very reliable late-19th century records of right whales in the Mediterranean Sea during the calving season: in the Gulf of Taranto, in February 1877, and off Alger, in January 1888 (electronic supplementary material, Appendix 1). These could have corresponded to some of the last individuals using this calving area, at a time when the eastern North Atlantic population still persisted. Finally, a 3rd Century description by Aelian of mysterious "ram-fishes" raises the possibility of a past right whale calving ground between Corsica and Sardinia (electronic supplementary material, Appendix 3) [23].

For gray whales, both records we found in the Gibraltar region are east of the Strait, again suggesting that the species entered the Mediterranean Sea to calve. Given current knowledge, it is not possible to say whether they calved in the Gibraltar region itself, or further east. It is also not possible to say whether the record in the Asturian coast corresponds to the location of a past migratory route or to a calving area; but given the latitude of today's calving areas in the eastern North Pacific, the former option seems more likely.

(c) Forgotten ecosystem impacts

If gray and right whales visited the Gibraltar region and Mediterranean Sea in reasonably large numbers, their disappearance would have had broader ecosystem implications.

Killer whales (*Orcinus orca*) seldom attack adult gray and right whales, but they are important predators of their calves, particularly in the calving grounds and during migration [49]. A detailed description by Pliny the Elder of '*orcas'* attacking whales and their calves off Cadiz during winter (electronic supplementary material, Appendix 3) is strong evidence that such predation previously took place in Gibraltar. Killer whales are still present in this area today, but they specialise on bluefin tuna [45]. While currently considered a single species, killer whales are structured into distinctive ecotypes specialised on particular prey, with specific methods of coordinated hunting [50]. Pliny's record shows that an ecotype that preyed on large whales was previously present in the Gibraltar region.

Whales have broader impacts on marine ecosystem function and structure [8,9]. In particular, whale migrations are "conveyor belts" of nutrients: from their high-latitude, highly-productive feeding areas, to their lower latitude, often nutrient-poor, calving grounds [8]. Indeed, right and gray whales fast during the calving season, using their lipid reserves for maintenance metabolism and – in the case of lactating females – for producing milk to feed their calves. Hence, the nutrients they excrete during this period (particularly N in the form of urea) originate in the high-latitude feeding areas. If large whale populations were historically present in the Gibraltar region and/or in the Mediterranean Sea, they may have had a measurable effect on local primary productivity [8], with cascading effects across the broader ecosystem [9].

(d) A forgotten whaling industry?

During the Roman period, the Strait of Gibraltar region was a centre of massive fish processing industry, as testified by the ruins of more than two hundred processing plants in both the European and African coasts [51] (electronic supplementary material, figure S3). The name of these plants – *cetariae*, from the Greek *ketos,* big fish – and their large salting vaults (frequently above 2 m^3 and up to 18 m^3) reflect the fact that they were used to process large fish, in particular tuna. Previous authors [35,52] raised the hypothesis that these same infrastructures could have been used to salt whale meat and blubber. Our finding that right and gray whales were present in the Gibraltar region in Roman times renders this hypothesis ecologically plausible [23]. Indeed, pre-modern whaling focused almost exclusively on a narrow set of species whose ecology puts them predictably in coastal areas during a part of their life cycle: bowhead whales, *Balaena mysticetus*; right whales, *Eubalaena sp*.; grey whales, *Eschrichtius robustus*; and humpback whales, *Megaptera novaeangliae* [11]. Unlike the other whale species still present in the Mediterranean today (e.g. fin whales, sperm whales), calving and/or migrating right whales and gray whales would have been found reliably close to the shore at predictable seasons, and could thus have formed the basis of a coastal whaling industry [23]. Furthermore, the Gibraltar region – a narrow bottleneck to populations entering/leaving the Mediterranean – would have been a geographically strategic area to develop such an industry, in the same way that it was (and still is) a strategic area for fisheries of migratory tuna.

The technology for coastal whaling was certainly available at the time: a text from the 2nd-3rd Century AD (Oppian's *Haliaeutica*) describes the capture of a sea-monster (a *ketos*) through methods very similar to those used in coastal whaling operations elsewhere, including approaching the monster by rowing boats, and its capture using harpoons, long ropes and buoys (electronic supplementary material, Appendix 3). The same methods (salting) and the same infrastructure (*cetariae*) that were used for processing large quantities of fish products could have been applied to the products of whaling. And the same extensive trade networks used for distributing fish and other Mediterranean products (oil, wine) could have been used to transported whale products (meat, fat) into a wide network of consumers in faraway parts of the Roman Empire.

None of this demonstrates that a Roman whaling industry existed, but it indicates that Romans had the means, the motive and the opportunity to capture gray and right whales at an industrial scale. Nonetheless, if such industry did exist, it could have had an impact on the eastern North Atlantic populations of these two species, as it would have affected particularly adult females, with disproportionate demographic consequences in these long-lived, slowly reproducing species [14,18]. Thus in turn could explain the results of genetic analyses suggesting that the Atlantic gray whale population declined substantially before the onset of industrial Basque whaling [19].

Further investigating the hypothesis of a forgotten Roman whaling industry will require an interdisciplinary approach, including a continuation of archaeological work, a re-analysis of historical records in the light of this hypothesis, and new genetic analyses to shed light on the past size and population dynamics of right and gray whale populations on the western North Atlantic.

5. Conclusions

Our results emphasise the value of accurately identified archaeological records as windows into past ecosystems, and thus the value of applying new barcoding methods to previously unidentifiable specimens [25]. Thanks to these methods, we present new evidence that both North Atlantic right whales and gray whales were previously found, and were likely common, in the Gibraltar region, at least up until the Late Roman period (6th Century AD). Based on the migratory ecology of these species, these records furthermore suggest that they previously calved in the Mediterranean Sea.

These findings open new perspectives for our understanding of the past ecology of coastal marine ecosystems in the Gibraltar region and the Mediterranean Sea, and of the magnitude of human impacts on these ecosystems. By placing coastal whale populations at a time and place of a major historical fisheries industry, our results provide an ecological basis to the hypothesis of a forgotten Roman whaling industry, thus opening new insights into the nature and intensity of past marine resource exploitation around the Mediterranean.

Data accessibility

DNA sequences: Genbank accessions MH193488-95. Proteomic data: MALDI-TOF raw spectra available at Dryad doi:10.5061/dryad.v2432b2.

Authors' contributions

ASLR and AC conceived the study. DBC, AG, CN and JAPM obtained the archaeological specimens. KMcG and CFS carried out the molecular laboratory work. ASLR wrote the first draft. All authors commented on the manuscript and approved the final version.

Competing interests

We declare we have no competing interests.

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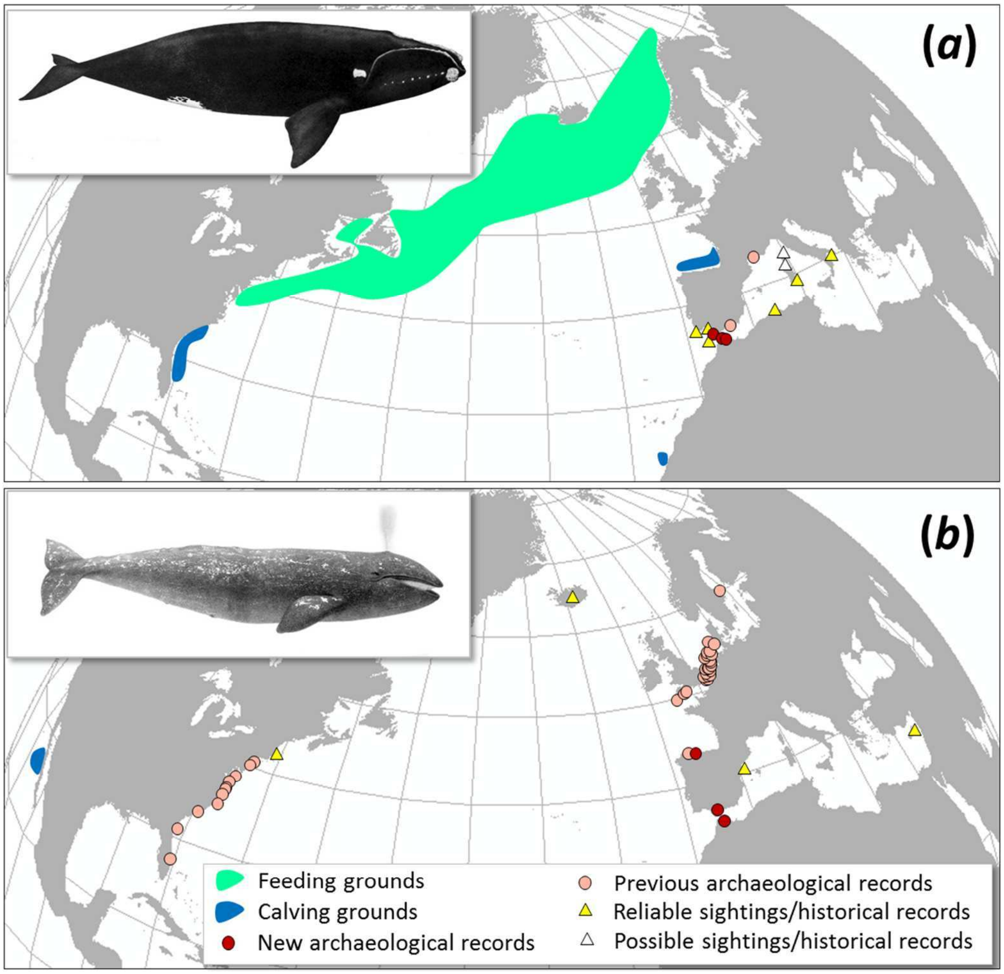
Table 1. Details of the specimens analysed in this study. TPQ (*terminus post quem*), limit after which; TAQ (*terminus ante quem*), limit before which. Species identification through DNA analyses and collagen from this study; cal^{14}C dating also from this study, except for samples WH812 and WH822. More details and references in electronic supplementary material, Appendices 1-2, tables S1-S5.

Lab Code	Location (excavation date)	Species ID through anatomy methods	Species ID through DNA analyses	Species ID through collagen	Chronology from stratigraphy (TPQ - TAQ)	cal^{14}C dating
WH810	*La Campa de Torres*, Gijon, Asturias, Spain (1996)	Gray whale, *Eschrichtius robustus*	Undetermined (amplification failure)	Gray whale, *Eschrichtius robustus*	Pre-roman (estimated 400 BC – 200 BC)	-
WH812	*Baelo Claudia*, Tarifa, Cadiz, Spain (1980s)	Fin whale, *Balaenoptera physalus*?	North Atlantic right whale, *Eubalaena glacialis*	Balaenidae, likely North Atlantic right whale, *Eubalaena glacialis*	-	232 BC – 23 BC
WH813	*Baelo Claudia*, Tarifa, Cadiz province, Spain (2009)	undetermined whale	Fin whale, *Balaenoptera physalus*	Fin/ humpback/ gray/right whale	Mid Roman (200 AD -250 AD)	-
WH814	*Baelo Claudia*, Tarifa, Cadiz province, Spain (2013)	undetermined whale	Long-finned pilot whale, *Globicephala melas*	Risso's dolphin/ pilot whale/false killer whale	Late Roman (450 AD - 550 AD)	642 AD - 773 AD
WH815	*Iulia Traducta*, Algeciras, Cadiz province, Spain (2001)	*Balaenoptera physalus*/ *Physeter catodon*?	Gray whale, *Eschrichtius robustus*	Gray whale, *Eschrichtius robustus*	Late Roman (475 AD - 525 AD)	251 AD - 422 AD
WH816	*Septem*, Ceuta (N. Africa), Spain (2008)	Delphinus spp.?	Common dolphin, (*Delphinus* sp.)	Dolphin/ Porpoise/ Orca	Roman (475 AD -500 AD)	720 AD - 896 AD
WH817	*Septem*, Ceuta (N. Africa), Spain (2006)	undetermined whale	Sperm whale, *Physeter catodon*	Sperm whale, *Physeter catodon*	Mid Roman (225 AD - 250 AD)	88 AD - 296 AD
WH818	*Septem*, Ceuta (N. Africa), Spain (2006)	undetermined whale	Undetermined (poor sequence quality)	Balaenidae, likely North Atlantic right whale, *Eubalaena glacialis*	Late Roman (475 AD - 500 AD)	226 AD - 410 AD
WH819	*Tamuda*, Tetouan, Morocco (2010)	undetermined whale	Undetermined (amplification failure)	Elephantidae, likely African elephant, *Loxodonta africana*	Republican-Roman (200 BC - 100 BC)	-
WH820 / WH821	*Tamuda*, Tetouan, Morocco (2012)	undetermined whale	Gray whale, *Eschrichtius robustus*	Gray whale, *Eschrichtius robustus*	Late Roman (400 AD - 450 AD)	71 AD - 245 AD
WH822	*Tamuda*, Tetouan, Morocco (1955)	undetermined whale	North Atlantic right whale, *Eubalaena glacialis*	Balaenidae, likely North Atlantic right whale, *Eubalaena glacialis*	Late Roman (estimated 320 AD –425 AD)	180 AD – 396 AD

Figure 1. Summary of knowledge on the historical distribution of: (*a*) the North Atlantic right whale (*Eubalaena glacialis*), with a focus on records in the Mediterranean Sea and nearby Gibraltar area; (*b*) the Atlantic population of the gray whale (*Eschrichtius robustus*), with current Pacific calving grounds illustrated for reference. Dark red circles correspond the new archaeological records added by the present study. Details in electronic supplementary material, Appendix 1. North Atlantic right whale illustration from NOAA United States, National Marine Fisheries Service (public domain); gray whale illustration from [53] (public domain).

Figure 2. Location of the archaeological sites referred to in this study. Panel (*a*) shows the location of *La Campa de Torres*, Asturias (1), and the general location of panel (*b*) (box). Panel (*b*) shows the location of the four archaeological sites in the Strait of Gibraltar: (2) *Baelo Claudia*, Tarifa; (3) *Iulia Traducta*, Algeciras; (4) *Septem*, Ceuta; and (5) *Tamuda*, Tetouan. Satellite images from NASA World Wind (open source).



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