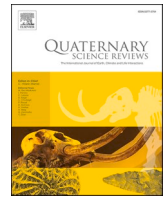




Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Dating the first historic extirpation of a whale species: The demise of the grey whale (*Eschrichtius robustus*) in the eastern North Atlantic

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ARTICLE INFO

Handling editor by: Rivka Rabinovich

Keywords:

Historical ecology
 Whaling
 Radiocarbon dating
 Radiogenic isotopes
 Extinction
 Europe
 North Atlantic
 Zooarchaeology
 Holocene

ABSTRACT

The grey whale (*Eschrichtius robustus*), once present in both the eastern and western North Atlantic, is the only whale species to have been extirpated from an ocean in historical times. For several centuries the species has been confined to the North Pacific, with the exception of isolated vagrants in recent decades that may be harbingers of its return to the Atlantic. Yet the chronology and causation of the past Atlantic extirpation have been unclear. A new radiocarbon dating programme applied as part of this study, including archaeological and palaeontological grey whale specimens from mainly European contexts, reveals the past spatiotemporal range of the species in the eastern North Atlantic as inferred from subfossil evidence. The new radiocarbon evidence dates the extirpation to between the mid twelfth and mid fourteenth centuries CE, earlier than previously assumed and a period of pre-industrial, yet extensive, European whaling activity undertaken by several medieval societies along the likely migration route of this coastal species. Pre-modern whaling may thus have contributed to this first anthropogenically driven extirpation of a whale species from an ocean and, by extension, eliminated the

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<https://doi.org/10.1016/j.quascirev.2025.109583>

Received 11 February 2025; Received in revised form 4 August 2025; Accepted 19 August 2025

Available online 9 September 2025

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grey whale's distinctive and important ecosystem services, such as sediment reworking and near-coastal translocation of nutrients, from the eastern North Atlantic.

1. Introduction

Whales have been hunted globally for centuries, with the populations of many species currently being only a fraction of their original pre-whaling size. Yet, only one species has been extirpated from an entire ocean in historical times: the grey whale (*Eschrichtius robustus*) from the North Atlantic Ocean (Speller et al., 2016; van den Hurk et al., 2023b). Grey whales are currently confined to the North Pacific where they display a near-coastal migratory pattern from warm coastal low-latitude waters for breeding and calving to cold high latitude waters along shallow continental shelves where they employ a modified mode of suction-feeding to prey on benthic invertebrates (Jones et al., 2009). This unique ecological niche contributes important Marine Functional Connectivity (MFC) services by reworking of sediments and translocating nutrients (Alter et al., 2007).

Palaeontological, archaeological, and historical evidence indicates that the grey whale was once a denizen of the North Atlantic Ocean (Alter et al., 2015). Early grey whale osteological specimens could only be identified based on morphological criteria, which limited identification to (partially) complete bones with diagnostic features, such as the holotype partial skeleton in Gräsö, Sweden (Lilljeborg, 1861), and other early findings from southern England, the southern North Sea, and the Netherlands (Van Deinse and Junge, 1937; Bryant, 1995; Alter et al., 2015). However, the recent development and advancement of biomolecular methods, such as Zooarchaeology by Mass-Spectrometry (ZooMS) and ancient DNA (aDNA), have enabled the identification of numerous fragmented and highly worked bones, including from Scotland (Evans, 2021; van den Hurk and McGrath, 2021; Kitchener et al., 2021), Norway (Hufthammer et al., 2018), France (Pétillon et al., 2019; McGrath et al., 2025), Spain (Rey-Iglesia et al., 2018; Rodrigues et al., 2018; McGrath et al., 2025), Morocco (Rodrigues et al., 2018), Germany (McGrath et al., 2025), and the Netherlands (van den Hurk et al., 2020). A systematic study of subfossil cetacean bones from the Atlantic coast of Europe revealed another 108 grey whale specimens from Norway, Germany, the Netherlands, Belgium, France, Spain, and England, indicating that the species was both present and common in the eastern North Atlantic (van den Hurk et al., 2023b). At the time of writing, 190 subfossil grey whale specimens have been identified from archaeological and palaeontological contexts in the eastern North Atlantic, plus 18 from the western North Atlantic (all USA).

Besides osteological remains, limited historical evidence attests to the past presence of the grey whale in the North Atlantic. A geographically unspecific reference from the English Muscovy Company (an early modern trading company), which operated in the Barents Sea region, dating to 1611, may describe isolated early seventeenth-century Arctic sightings of the species, referred to as “*Otta Sotta*”. However, the description of the *Otta Sotta* was provided by Basque whalers to the Muscovy Company and therefore is more likely to reflect the transmission of earlier knowledge. It remains unclear whether the Muscovy actually encountered any grey whales themselves (Mead and Mitchell, 1984; Supplementary file 1). Jón Guðmundsson lærði, a mid-seventeenth-century Icelandic authority also provides a detailed description as well as a good illustration of grey whale (Lindquist, 2000; Supplementary file 1). Subsequent Icelandic sources copy this earlier work (referring to the grey whale as “*sandlægia*”, “*sandætta*”, or “*hrann-lægia*”), potentially suggesting the grey whale was present up until the early eighteenth century in Icelandic waters (Lindquist, 2000). Lastly, descriptions of the “*scrag whale*” in New England waters in the seventeenth and early eighteenth century also match the grey whale (Dudley, 1725; Mead and Mitchell, 1984; Lindquist, 2000). Thus, isolated written records describe the grey whale in the North Atlantic as

late as the seventeenth and eighteenth centuries, but only in the west and far north. The grey whale's presence in the western North Atlantic up to the seventeenth or eighteenth century is furthermore attested by radiocarbon dates of several grey whale specimens (Mead and Mitchell, 1984). However, the eastern North Atlantic population is essentially invisible to history (Supplementary file 1).

The timing and causes of the grey whale's extirpation from the eastern North Atlantic remain to be understood. We address these issues by considering 91 new and legacy radiocarbon dates from 84 specimens (with several specimens being dated multiple times). Given major Pleistocene and post-Pleistocene changes in sea level (Hoebe et al., 2024), relevant archaeological and palaeontological coverage pre-dating the Holocene is very limited and chronologically biased (the worked grey whale bone specimens dating to the Upper Palaeolithic from Spain, France, and Germany identified by McGrath et al. (2025) being notable exceptions). The present study therefore focuses on the 76 Holocene dates from 69 specimens.

In analysing the resulting data it is necessary to optimize radiocarbon dating of grey whale bone specimens by approximating a species-specific marine reservoir correction useable with the Marine20 calibration curve (ΔR_{20}) (Heaton et al., 2020, 2023) for the extirpated eastern North Atlantic population. This is achieved by using the archaeological dates of twelve well-stratified European and North-western African grey whale specimens. When combined using chronometric modelling (Bronk Ramsey, 2017; Herrando-Pérez and Saltré, 2024), the new corpus of radiocarbon dates and ΔR_{20} values provide a strong empirical basis for assessing the spatiotemporal range and ultimate loss of the grey whale from the eastern North Atlantic, the first major stage in its extirpation from the entire Atlantic basin.

The resulting wealth of new evidence gives us the opportunity to elucidate when the grey whale disappeared from European waters. We then put these findings in a broader historical context to show that the eastern North Atlantic population of this species was very likely extirpated in association with early but widespread medieval whaling along its European coastal range, before whaling off North American shores extirpated the western population. The grey whale's extirpation from the eastern North Atlantic, and simultaneously the disappearance of its unique MFC services, likely had extensive implications for entire ecosystems (Alter et al., 2007). Understanding the timing of this extirpation event is thus an important step towards both understanding past whaling and quantifying historical ecosystem effects of whale population depletions.

2. Methods

2.1. Sample selection and radiocarbon dating by accelerator mass spectrometry (AMS)

Thirty-nine AMS radiocarbon dates on 37 (two in duplicate) previously undated archaeological and palaeontological subfossil grey whale specimens from the eastern North Atlantic were conducted at the National Laboratory for Age Determination (NLD), Norwegian University of Science and Technology (NTNU), Norway (Supplementary Table 1). The dated specimens were selected to cover a large temporal range, based on pre-existing archaeological information, and to include the most recent suspected grey whale finds (see Supplementary Table 2 for list of all known Atlantic grey whale specimens and relevant radiocarbon dates). Two other previously unpublished dates (provided by co-authors) were dated at the Poznań Radiocarbon Laboratory, Poland (Poz-77177), and the Radiocarbon Dating Laboratory of Lund University, Sweden (LuS-9587) respectively. All these newly published dates

are on Holocene specimens confirmed as grey whale based on ZooMS (Hurk et al., 2023b; van den Hurk et al., 2020), except the specimen dated in Lund which was confirmed to be a grey whale using aDNA (Supplementary File 3). Three previously dated eastern North Atlantic grey whale specimens were redated by AMS at the NLD to confirm their age, resulting in the discard of one inaccurate legacy date (see below). An additional 32 legacy Holocene radiocarbon dates, on 29 specimens including the two valid redated cases, were drawn from publications, with missing details (e.g. uncalibrated dates, lab codes) acquired by corresponding with the relevant authors and/or laboratories. For completeness, known Pleistocene/Palaeolithic radiocarbon dates on grey whale subfossils are also provided in Supplementary Table 2, but they are excluded from the above-mentioned totals. Species identifications for legacy data using aDNA, ZooMS or (in the case of partially intact specimens) morphology have been accepted as published. To avoid spurious precision rounded dates were used in analyses.

Of the three redated specimens, one from Babbacombe Bay, England (Bryant, 1995) was reanalysed because it was reported as the most recent known grey whale despite an uncalibrated error range of 200 radiocarbon years, and two from the Netherlands (NMR999100001790/SP1453 and NMR999100001780/SP1347) (Alter et al., 2015) were reconsidered because they were discovered to have been conserved with glue. After glue removal using the Soxhlet method (Bruhn et al., 2001), the latter two dates remained essentially unchanged (Supplementary Table 1) and have been retained with caution. They are not among the most recent results and will thus not meaningfully bias the extirpation date. Conversely, the original Babbacombe Bay date proved to be inaccurate as well as imprecise and has been excluded.

Samples for the newly published dates were taken using a ©Dremel rotary tool removing a small piece of bone typically weighing c.500 mg. Collagen was extracted using a modified Longin (1971) method as detailed in Seiler et al. (2019), with the addition of a lipid extraction step and the use of a higher acid concentration, at the NLD. See van den Hurk et al. (2023b) for full details.

Between 2.0 and 3.0 mg of collagen per specimen were weighed, placed into a tin capsule and AMS dated following the protocol detailed in Seiler et al. (2019). The samples were reduced to produce homogeneous graphite material in the automated reduction system TOR (Trondheim Oxidation and Reduction system). The system performed the iron-catalyzed hydrogen reduction of CO₂ (Vogel et al., 1984), freezing out the residual water with Peltier coolers (Wacker et al., 2010). The ¹⁴C measurements were undertaken at the NLD 1 MV AMS system made by High Voltage Engineering Europa B.V. The specimens, and those previously dated, were subsequently calibrated using the Marine20 curve (Heaton et al., 2020) with a ΔR_{20} correction we calculated based on methods described below.

2.2. Marine reservoir correction

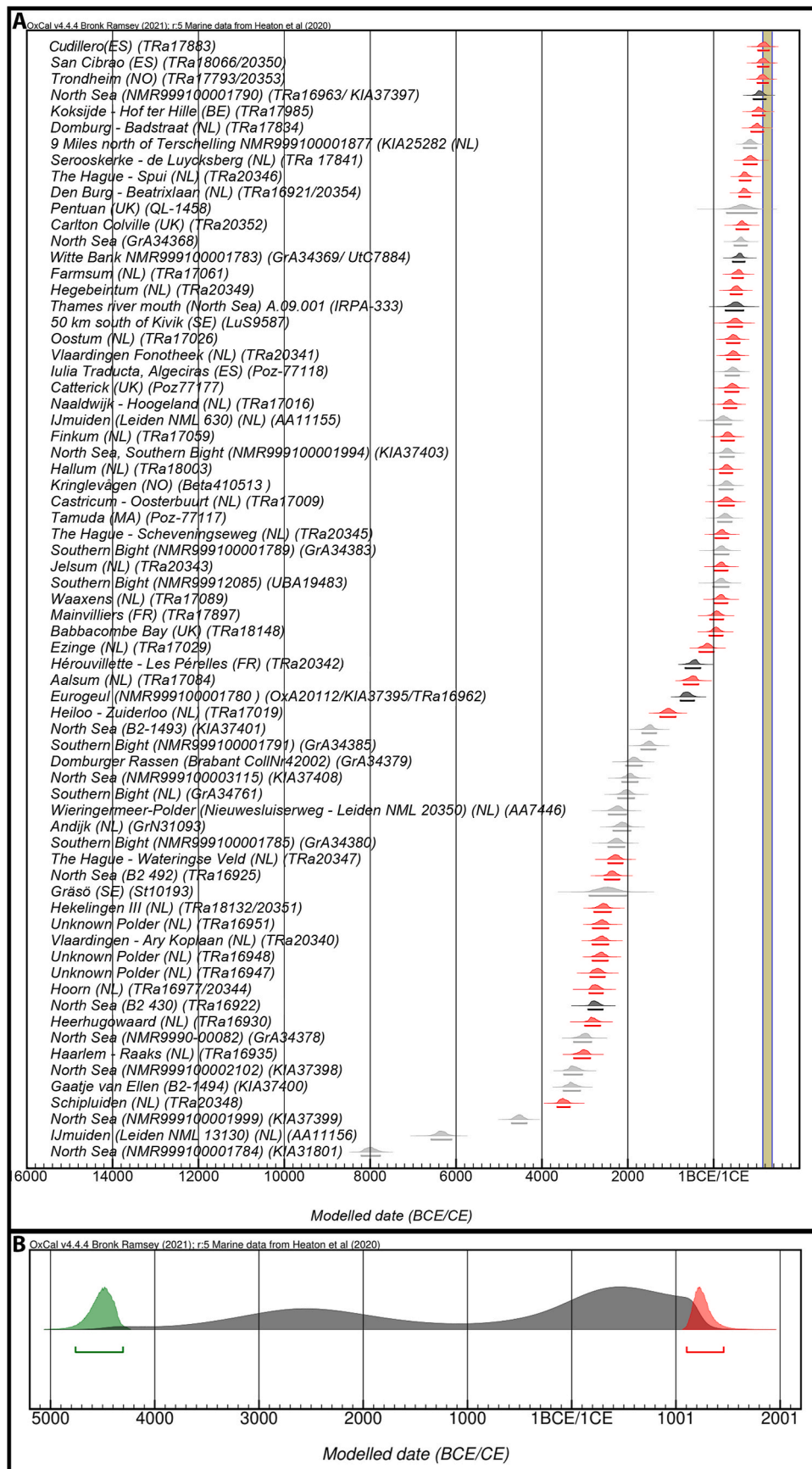
Unless otherwise specified, all dates were calibrated using the Marine20 curve of Heaton et al. (2020) and a ΔR_{20} estimated for grey whales of the eastern North Atlantic. Regionally specific ΔR_{20} values, as typically extracted from the database <http://calib.org/marine/> (Reimer and Reimer, 2001), are not appropriate for grey whales because the species is strongly migratory. The foraging strategy of the Atlantic grey whale is poorly understood given its pre-modern extirpation and the previous paucity of known subfossil specimens. However, grey whales in the North Pacific undertake long migrations, feeding in both high-latitude waters and along migration routes (Sund, 1975). It is appropriately cautious to assume that Atlantic grey whales behaved similarly. A species-specific ΔR_{20} for Atlantic grey whales was thus estimated by AMS radiocarbon dating ten well-stratified archaeological grey whale specimens from European contexts. These specimens were previously dated based on their archaeological stratigraphy and association with other archaeological finds (e.g., coins, ceramics

archaeologically datable to a particular period, dendrochronologically dated wooden remains, and/or terrestrial AMS dated specimens). We also incorporated two radiocarbon dates on archaeological grey whale specimens reported by Rodrigues et al. (2018) which came from archaeologically well-dated contexts (Supplementary Table 3). The ΔR_{20} calculation is based on Late Holocene specimens given that the present study aims to ascertain the timing of the recent extirpation of the grey whale.

ΔR_{20} calculation is typically achieved using either the Deltar package (Reimer and Reimer, 2017; Divola et al., 2024) or through Bayesian modelling in OxCal (Bronk Ramsey, 2009; Bronk Ramsey et al., 2012; Macario et al., 2023). We adopted the latter approach given its flexibility; some of the relevant archaeological contexts include more than a single marine-terrestrial date pair. We adopted a normally distributed prior with mean of 0 and standard deviation of 500 years to accommodate diversity within potential eastern North Atlantic ΔR_{20} values as tabulated in <http://calib.org/marine/> (Reimer and Reimer, 2001). Sensitivity analysis using an alternative uniform prior of -800 to 1000 years (cf. Macario et al., 2023) yields an identical ΔR_{20} rounded to the year. Details of the specimens used for ΔR_{20} calculation can be found in Supplementary Table 4. The OxCal code is provided in Supplementary File 2 and the resulting output in Supplementary Fig. 1 and Supplementary Table 5. Note that many of the unmodelled dates are reported as potentially extending out of range in Supplementary Table 5; this is because the prior has been assigned a broad chronology to allow the model to extract an estimate of ΔR_{20} from the data (see Bronk Ramsey and Lee, 2013).

2.3. Assessing the timing of the extirpation event

In order to infer the spatiotemporal distribution of the grey whale and its extirpation from the eastern North Atlantic, the estimated taxon-specific ΔR_{20} for the eastern North Atlantic (-56 ± 21) was applied with the Marine20 curve (Heaton et al., 2020) in OxCal v.4.4.4 to calibrate the dates of individual specimens. The results are provided in Fig. 1 and Supplementary Table 4. For the mid to late Holocene, when the distribution of known dates is continuous, the radiocarbon data were combined in OxCal using a Kernel Density Estimation probability distribution (KDE_Plot), together with a Bayesian phase model that estimates the 95.4 % probability range of the start and end boundaries of this group of dates (Fig. 1 and Supplementary Table 6) (Bronk Ramsey, 2017). All OxCal code can be found in Supplementary File 4. The resulting Bayesian end boundary provides one estimate of the extirpation date, but may be inaccurate because it assumes a uniform underlying distribution (see Bronk Ramsey, 2008) and does not fully account for the “Signor-Lipps” effect; the last surviving individual is unlikely to be included among the dated samples (Signor and Lipps, 1982; Herrando-Pérez and Saltré, 2024). Thus the Gaussian-Resampled Inverse-Weighted McInerny Method (GRIWM) was also employed. Using the unbiased estimator of Herrando-Pérez and Saltré (2024), this method models the minimum theoretical date of extinction, correcting for the assumption that subfossil frequencies are uniformly distributed, preferentially weighting observations closer to the present to minimise bias from chronological gaps, and resampling dating errors (creating 10,000 time series from which a median and 95 % inter-quantile range is determined) (Herrando-Pérez and Saltré, 2024). The accuracy and precision of GRIWM can be limited by the fact that it treats calibrated radiocarbon dates as normally distributed. However, this issue is not acute in the present context because marine calibration curves are smooth compared with atmospheric curves, and thus produce Probability Density Functions (PDFs) that are typically unimodal (see Fig. 1). Existing alternative methods that resample PDFs of calibrated dates (Herrando-Pérez and Saltré, 2024) do not incorporate a ΔR and are thus unsuitable for whales. GRIWM was executed using the R package Rextinct (Herrando-Pérez and Saltré, 2024), entering calibrated BP dates (multiple dates combined) from OxCal output for the 69 Holocene



(caption on next page)

Fig. 1. A. All Holocene radiocarbon dated specimens - including previously dated specimens (light grey = single radiocarbon dates; dark grey = combined dates of multiple radiocarbon dates), specimens dated as part of this study (red), and GRIWM calculated extirpation period (beige box; 1142–1368 CE (interquartile range; median 1241 CE)). The data are calibrated in OxCal v4.4.4 (Bronk Ramsey, 2009) using the Marine20 curve (Heaton et al., 2020) and a ΔR_{20} of -56 ± 21 ^{14}C yrs; B. Kernel Density plot (Bronk Ramsey, 2017) of 74 radiocarbon dates on 67 European and North African grey whale specimens from the mid to late Holocene. The data are calibrated in OxCal v4.4.4 (Bronk Ramsey, 2009) using the Marine20 curve (Heaton et al., 2020), a ΔR_{20} of -56 ± 21 ^{14}C yrs and a single phase grouping with start and end boundaries. Red = modelled phase-end boundary of 1105–1459 cal. CE; Green = modelled phase-start boundary of 4760–4305 cal. BCE.

specimens, also using the Marine20 curve and a ΔR_{20} of -56 ± 21 . The R code for applying Rextinct is provided in Supplementary file 2 and the GRIWM input data (of calibrated dates BP, as mu and sigma in two columns) in Supplementary file 5.

3. Results

By radiocarbon dating twelve well-stratified Late Holocene

archaeological specimens and modelling the resulting dates using Bayesian approaches in OxCal (Bronk Ramsey, 2009; Bronk Ramsey et al., 2012; Macario et al., 2023), a ΔR_{20} of -56 ± 21 ^{14}C years is estimated for the eastern Atlantic grey whale population to mitigate uncertainties in the Marine Reservoir Effect (Supplementary Fig. 1, Supplementary Table 5). The OxCal model agreement index (A_{model}) and overall individual agreement index (A_{overall}) are 195.1 and 194.8 respectively, above the recommended threshold values of 60 (Bronk

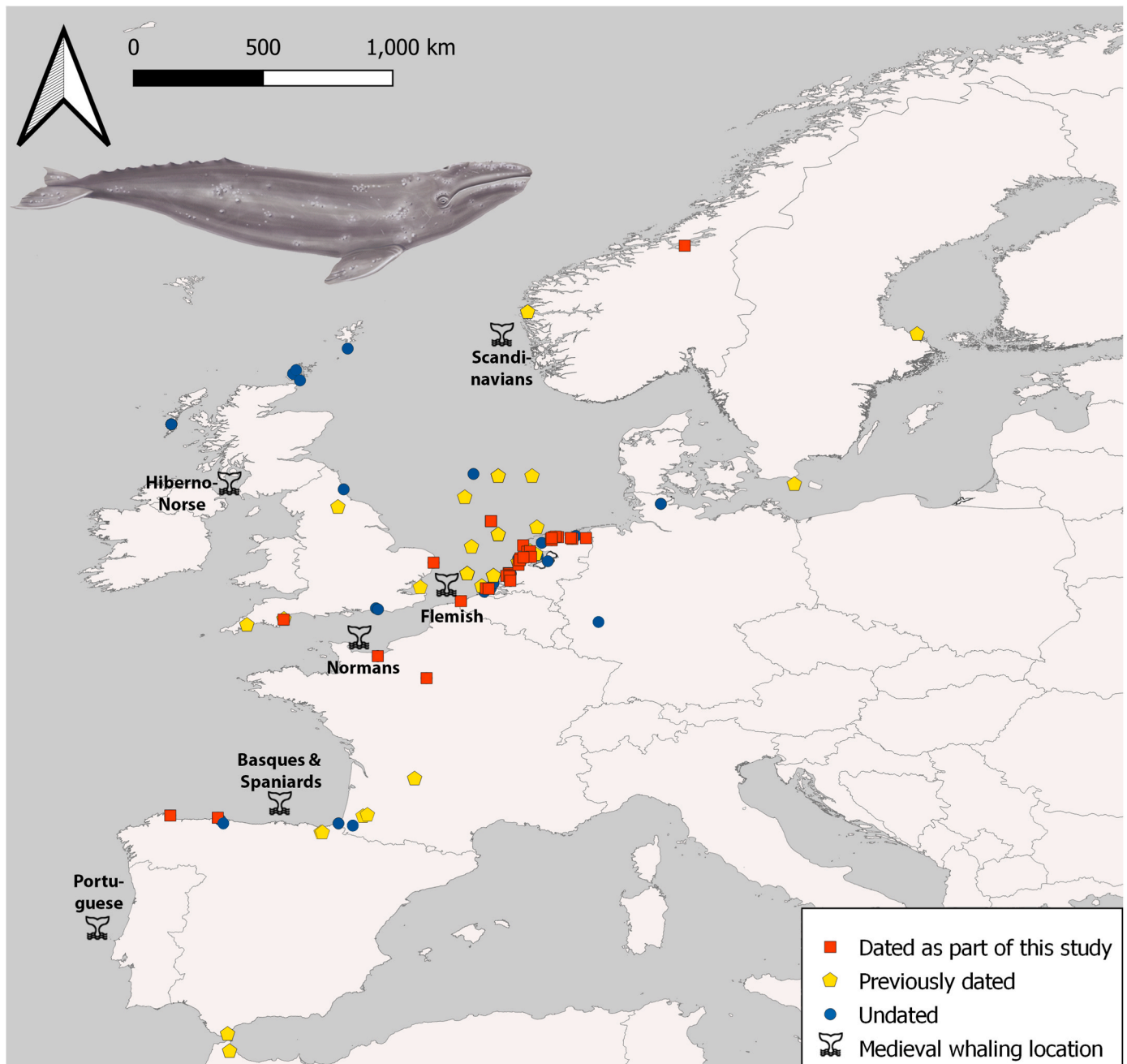


Fig. 2. Locations of grey whale specimens from the eastern North Atlantic. Specimens from the North Sea are shown with approximate find locations.

Ramsey, 2009). Pending additional known-age specimens providing more thorough spatiotemporal coverage, -56 ± 21 thus provides an empirically-based best estimate of ΔR_{20} used to calibrate the radiocarbon dates of the Holocene eastern North Atlantic specimens considered in the present study.

The majority of the 69 Holocene grey whale specimens considered here originate from the southern North Sea area, with smaller numbers of specimens northward, as far as Trondheim, Norway, and southward to Tamuda, Morocco (Figs. 2 and 3). Two comparatively old Holocene specimens, having calibrated dates of 8204-7770 and 6577-6108 cal. BCE (95.4 % prob.) using the Marine20 curve (Heaton et al., 2020) and a ΔR_{20} of -56 ± 21 ^{14}C yrs, are outliers. The former has been recovered from an area of the North Sea that was flooded early in the Holocene, while the latter was originally found in IJmuiden, the Netherlands, in 1879 but its context information is unclear (Alter et al., 2015; Hoebe et al., 2024). Otherwise, the relevant dates begin in the fifth millennium BCE, after the final flooding of Doggerland in the seventh or sixth millennium BCE (Hoebe et al., 2024). When the remaining 74 radiocarbon dates from 67 Holocene specimens are calibrated using the Marine20 curve, a ΔR_{20} of -56 ± 21 ^{14}C yrs, a Bayesian single-phase grouping with start and end boundaries and kernel density plotting in OxCal

(Bronk Ramsey, 2017), they show a modelled range from 4760 to 4305 cal. BCE to 1105–1459 cal. CE at 95.4 % probability (Fig. 1, Supplementary Table 4). The three most recent single specimens are: TRa-17883 from Cudillero, Spain dating to 1036–1291 cal. CE; TRa-18066/20350 from San Cibrao, Spain dating to 1029–1280 cal. CE; and TRa-17793/20353 from Trondheim, Norway dating to 1020–1271 cal. CE (all 95.4 % prob.).

Bryant (1995) previously reported a ^{14}C date of 1610 ± 260 cal. CE for a grey whale specimen from Babbacombe Bay, United Kingdom, using the 1986 marine model curve (Stuiver et al., 1986). We undertook new AMS dating of this specimen in order to clarify this low-precision finding. Our dating yields 101 cal. BCE to 210 cal. CE (95.4 % prob.) using the Marine20 curve and a ΔR_{20} of -56 ± 21 ^{14}C yrs. Thus, this specimen is significantly older than previously assumed and the original low-precision date has been excluded from consideration. Re-dating of the Babbacombe Bay whale is pertinent because this find from Devon, UK, has long been considered the most recent Atlantic grey whale, used to argue that the species was extirpated from European waters in the seventeenth century CE (Bryant, 1995).

A further two specimens potentially dating to a more recent time period than our results (based on their archaeological contexts) turned



Fig. 3. Selection of whale bone specimens dated as part of this study (all TRa numbers except when noted differently) – see Supplementary Table 1 for specimen descriptions.

out to be considerably older using AMS dating. These two are Vlaardingen Fonotheek (TRa-20341) dating to 312–605 cal. CE and The Hague – Spui (TRa-20346) dating to 605–860 cal. CE (both 95.4 % prob.). The only known grey whale specimen that is potentially more recent than the latest individual dates reported here is specimen ‘1485’ from Bornais, Scotland, identified by Evans (2021), which is dated based on its archaeological context to 1200–1450 CE. This specimen has not been AMS dated and the range of its broad archaeological chronology is consistent with our results.

While TRa-17883 from Cudillero, Spain, dating to 1036–1291 cal. CE, is the most recent single specimen, the “Signor-Lipps” effect suggests that it is unlikely to represent the last surviving individual (Signor and Lipps, 1982; Herrando-Pérez and Saltré, 2024). Moreover, the modelled Bayesian phase-end boundary of 1105–1459 cal. CE using OxCal assumes a uniform underlying distribution (see Bronk Ramsey, 2008) between the mid-fifth-millennium BCE and extirpation (Fig. 1). This assumption may be incorrect, given the likelihood of declining numbers of whales through time. Therefore GRIWM, using the unbiased estimator of Herrando-Pérez and Saltré (2024), provides a potentially more accurate approach to estimating an extirpation date.

GRIWM results (based on the 69 dated specimens pertaining to the Holocene, all pre-calibrated (cal BP) in OxCal using the Marine20 curve and a ΔR_{20} of -56 ± 21 ^{14}C yrs), suggest that the grey whale was extirpated from the eastern North Atlantic between 1142 and 1368 CE (95 % inter-quantile range; median 1241 CE). Excluding the above-mentioned isolated historical records regarding Iceland and Arctic waters, which can be inferred to represent a different (western?) population, extirpation from the eastern North Atlantic thus probably occurred three to five centuries earlier than previously assumed, between the mid-twelfth and mid-fourteenth century (e.g. Bryant, 1995).

4. Discussion and conclusion

Understanding how grey whale populations have been affected by past anthropogenic and natural phenomena is vital to modern conservation planning given the recent movement of a few North Pacific grey whales into the Atlantic, presumably via the Northwest Passage in the context of increasingly ice-free conditions (Rodrigues et al., 2018; Supplementary file 2). For example, it is important to ascertain whether Atlantic grey whales were previously hunted out, potentially indicating that they could establish a viable population in the absence of whaling. By extension, this also has implications for entire ecosystems and the grey whale’s MFC services (Agiadi et al., 2024). Grey whales, as benthic feeders undertaking sediment reworking, fill a distinctive ecological niche. Their extirpation from the eastern North Atlantic would have resulted in a loss of ecosystem services, including nutrient cycling, and created shifts in benthic species dominance (Alter et al., 2007). The present chronological evidence is central to these questions, in addition to enhancing fundamental knowledge regarding the historical ecology of both Atlantic grey whales and past whaling.

The long presence of grey whales in the eastern Atlantic Ocean is attested by pre-Holocene specimens, including seven from the area that today corresponds to the North Sea dating to $>40,000$ cal. BP (Alter et al., 2015) and ten associated with the Bay of Biscay dating to ca. 18,000–16,000 cal. BP (McGrath et al., 2025). The latter correspond to worked bones tools, providing evidence of a long history of utilization and trade of bones of grey whales (as well as of other species) as valuable materials (McGrath et al., 2025). Corresponding to a period when the sea level was much lower than today (Hoebe et al., 2024), and thus its coastline inaccessible to today’s archaeologists, the transport of these specimens inland (in one case >200 km) enables a window into the marine ecosystems at the time, and suggests that the Bay of Biscay served as a Pleistocene refugium for grey whales (McGrath et al., 2025).

The subsequent Holocene cluster of grey whale dates, the focus of this study, starts c. 8000 BCE during the gradual formation of the North Sea (Hoebe et al., 2024), from which many of the specimens derive.

Excluding two older finds the specimens form a continuous time-series from the fifth millennium BCE, post-dating the flooding of Doggerland (Hoebe et al., 2024). The start of the Holocene cluster is thus related to the formation of the North Sea.

It is notable that specimens dating c.3300–2000 BCE mostly derive from the southern North Sea or the provinces of North- and South-Holland (the Netherlands) – the sole exception being the holotype from Gräsö, Sweden. This spatial and temporal clustering does not necessarily reflect higher abundance, but is likely influenced by variable preservation and archaeological accessibility. North- and South-Holland were dominated by intertidal systems at this time (Fig. 4). In North-Holland the specimens are palaeontological (not associated with human activities) and found in ancient riverbeds, ideal for preservation of osteological remains, whereas in South-Holland the finds are from archaeological sites of the Middle-Late Neolithic Vlaardingen Culture. It can thus be inferred that grey whales ventured into intertidal rivers (e.g. Vecht, Oer-IJ, and Rhine/Lek), which might have been important foraging grounds as grey whales feed on benthic fauna in low depth sediments, and occasionally stranded. In South-Holland, people of the Vlaardingen culture scavenged these strandings and/or hunted the whales in the intertidal systems (van den Hurk et al., 2023b).

Whale bones are rare finds during archaeological excavations in Europe, but comparatively few northwestern European archaeological whale remains derive from the Bronze and Iron Age periods (c.2000–800 BCE and c.800 BCE–1 CE respectively, although varying by region) (van den Hurk et al. (2023b), when there was instead a strong reliance on domesticated animals (Çakırlar et al., 2019). This trough in archaeological cetacean specimens is evident from the radiocarbon results (Fig. 1). Subsequently, it has been suggested that grey whales were hunted in the Roman period (between the end of the Iron Age and c.500CE, with chronology varying by region) (Rodrigues et al., 2018), although the number of known archaeological specimens of this date-range is also small.

Archaeological grey whale specimens are more abundant during the Middle Ages (c.500–1500 CE; Fig. 1), when they occur in archaeological sites along the Atlantic façade of Europe from Spain to Norway (Supplementary Fig. 2). The new radiocarbon evidence presented here, combined with a lack of historical evidence for grey whales in post-medieval European waters, suggests that the taxon was extirpated from the eastern North Atlantic between the mid-twelfth and mid-fourteenth centuries CE, during the period of widespread exploitation, including active hunting (see below).

The timing of this extirpation from European waters is corroborated by the absence of the species in early taxonomy texts where it would be expected, including Norwegian sources (Lindquist, 2000) and other early treatises on whales including Belon (1555), Rondelet (1558), and Coenen (1579). Early 18th century historical descriptions of grey whales in Iceland thus probably refer to individuals linked to the western North Atlantic population, that was still being hunted at this time (Dudley, 1725) (see supplementary file 1).

A multiplicity of factors may have contributed to the disappearance of grey whales from the eastern North Atlantic. Alter et al. (2015), based on ancient mitochondrial DNA analysis, have argued that low genetic diversity, a reduction in haplotype diversity, and loss of suitable habitat could have underlain the extirpation of the grey whale from the North Atlantic. Moreover, grey whales are sensitive to dynamic environmental conditions. In the modern North Pacific, grey whale mortality events have occurred; low prey biomass and high ice coverage led to a reduction in grey whale population by 15–25 % in 1999–2000 and 2019–2022 (Stewart et al., 2023). It may thus be relevant that the identified extirpation window of the twelfth to fourteenth centuries CE corresponds with the end of both the Medieval Climate Anomaly (c.950–1250 CE) and a period of low North Sea productivity (c.871–1290 CE) (Scherer et al., 2024). These environmental factors are associated with the timing of grey whale extirpation and could be causally related through food-web cascade effects.

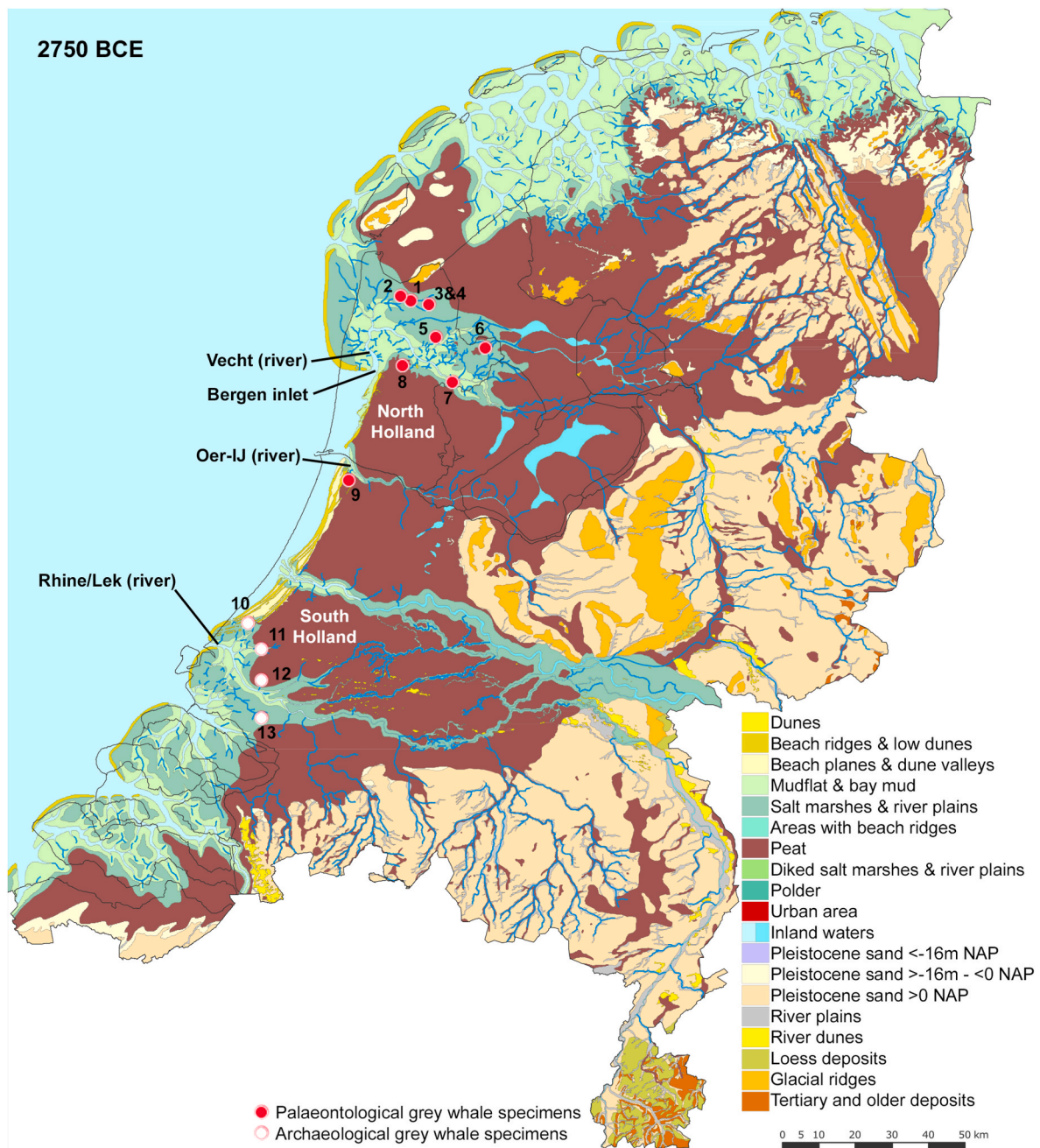


Fig. 4. Radiocarbon dated grey whale specimens dating to c.3300-2000 cal. BCE, plotted on palaeogeographic map of the Netherlands dating to c.2750 BCE - 1. Wieringermeer-Polder (Nieuwesluiserweg), 2. Wieringermeer 'Lot B22'; 3 + 4. Wieringermeer (unknown lot); 5. Oudelandertocht (Lambertschaag), 6. Andijk, 7. Hoorn, 8. Heerhugowaard, 9. Haarlem (De Raaks), 10. The Hague - Wateringse Veld, 11. Schipluiden, 12. Vlaardingse - Ary Koplaan, 13. Hekelingen III (see [Supplementary Table 1](#) for specimen details) (Basemap [Vos et al., 2020](#)).

However, since grey whales have been present in the North Atlantic for millennia, they survived numerous events linked to climatic variability. Anthropogenic factors must therefore also be considered. [Alter et al. \(2015\)](#) recognized that early modern whaling might have contributed to the extirpation of Atlantic grey whales, but only as a minor factor. At the time, few grey whale specimens derived from archaeological contexts indicative of human exploitation. However, since [Alter et al.'s \(2015\)](#) study, more than 100 grey whale specimens have been identified from archaeological contexts, with 23 radiocarbon dated specimens and another 38 archaeologically dated specimens deriving from medieval contexts (c.500-1500 CE). Moreover, our estimated extirpation window of the twelfth to fourteenth centuries CE corresponds with the apogee of many medieval European whaling

activities. Based on historical evidence, cultures along the Atlantic European façade conducted whaling during the medieval period, including the Scandinavians ([Lindquist, 1997](#); [Szabo, 2008](#)), Hiberno-Norse ([Laist, 2017](#)), Normans ([Musset, 1964](#)), Basques and northern Spaniards ([Aguilar, 1986](#)), Flemish ([De Smet, 1981](#)), and Portuguese ([Brito, 2011](#)) ([Fig. 2](#)).

After peaking in the Middle Ages, historically documented whaling activities declined in Atlantic Europe. Most Flemish whaling sources date to the eleventh and twelfth centuries CE, with fewer from the thirteenth and fourteenth centuries CE ([De Smet, 1981](#); [van den Hurk, 2020](#)). For the Normans and Portuguese, European active whaling is documented until the thirteenth century and fourteenth century respectively ([Musset, 1964](#); [Brito, 2011](#)). Much Scandinavian whaling

activity also appears to have declined at the end of the Middle Ages, although in some areas, such as Iceland, it continued until the sixteenth century and beyond (Lindquist, 1997; Szabo, 2008). A differing chronology is evident for Basque and northern Spanish whalers. While whaling initially focused on the Bay of Biscay, the Basques ventured to increasingly distant grounds: from 1353 off Ireland, in 1412 off western Iceland, and in 1530 (for bowhead whales, *Balaena mysticetus*) the Strait of Belle Isle, Canada (McLeod et al., 2008; Loewen, 2009; Ciriquiain Gaiztarro, 2010; Valdés Hansen, 2010).

The primary target for these whaling cultures is presumed to have been the North Atlantic right whale (*Eubalaena glacialis*) (Reeves et al., 2007; Aguilar, 1986). This slow-moving species approaches the coast in its winter calving grounds (which included the Bay of Biscay; Aguilar, 1986) as well as during its spring and autumn migrations, which would have made it a predictable and accessible whaling target during these seasons. Furthermore, it was highly valuable for its meat, blubber and baleen. Initially exploited near the coast, and subsequently in the high seas, this species was massively exploited across its entire range, to the point of being considered commercially extinct by 1750 (van den Hurk et al., 2023b; Nabais et al., 2024; Reeves et al., 2007). No longer present in European waters, the North Atlantic right whale persists today as a small and Critically Endangered population in the western North Atlantic (Cooke, 2020). However, an increasing number of European archaeological specimens are consistent with the grey whale having been an important whaling target too, alongside the right whale. Indeed, it is the second most commonly identified taxon on European archaeological sites dating up to the medieval period (van den Hurk et al., 2023b).

An early focus of medieval whalers on grey whales is plausible because they would have been both valuable and accessible. Their value is attested by historical records. For example, Jean Chappé D'Auteroche described in the eighteenth century how the Indigenous peoples in Kamchatka (in the north-western Pacific) hunted grey whales for their meat (dried and eaten), blubber (smoked and eaten, rendered into oil for illumination and for heat), skin (dried and beaten, then transformed into shoe soles and belts), baleen (used to sew canoes and to make nets for fishing and hunting), intestines (used as containers), bladders (used as floaters, and to make waterproof clothing), and nerves and veins (converted into ropes) (Charpentier et al., 2022). In the Atlantic, all three reliable historical records of grey whales are in the context of whaling, and point to economically valuable products (Supplementary file 1): food ("well edible") and baleen according to Jón Guðmundsson lærði (Lindquist, 2000); and oil according to the Muscovy Company ("the best oil"; Mead and Mitchell, 1984) and Dudley (1725; "nearest the right whale [...] for quantity of oil").

Besides the Palaeolithic grey whale tools described by McGrath et al. (2025), a number of medieval specimens displayed chopmarks or signs of working for use as artefacts (Supplementary Table 2), indicating that besides meat, the bones of large whales were of value. However, these signs in themselves are not proof of active whaling since stranded whales could be exploited for their bones as well. In addition, van den Hurk et al. (2023a, 2023b) and McGrath et al. (2025) revealed that bones of a variety of different large whales species were used for the production of artefacts or tools, including species unlikely to have been hunted, including blue whale (*Balaenoptera musculus*) and sperm whale (*Physeter macrocephalus*).

As for accessibility, the ecology of grey whales (as it is known from the living North Pacific population; Swartz, 2014) is such that they could have been hunted throughout their entire life cycle: in their southern wintering calving grounds (likely in sheltered low-depth lagoons or bays); in their northern summer feeding areas (in low-depth waters); and during the autumn and spring migrations between the two (closely hugging the coast, particularly as cows migrate northwards with young). As such, grey whales would have been even more accessible to early whalers than right whales, and furthermore through their entire life cycle, which may explain why their complete extirpation from European

waters took place earlier than for right whales.

In sum, the historical pattern of European whaling is indicative of a serial exploitation/depletion, where over-use of favoured resources leads to shifts in the locations, populations and/or species targeted (c.f. Huitric, 2005; Barrett et al., 2020; Atmore et al., 2022), and that the extirpation of grey whales from Atlantic Europe contributed to many coastal cultures scaling back or ceasing their whaling activities in the thirteenth and fourteenth centuries CE, while the Basques instead ventured to increasingly distant whaling grounds focused on a broader set of species.

In clarifying the timing and correlates of the extirpation of the grey whale from the eastern North Atlantic, this study has indicated that the extirpation coincided with an apogee of whaling by many medieval European societies. The Atlantic grey whale population can probably be added to the list of anthropogenically driven marine mammal extinctions which includes, for example, Steller's sea cow (*Hydrodamalis gigas*) in 1768, Caribbean monk seal (*Neomonachus tropicalis*) shortly after 1952, Japanese sea lion (*Zalophus japonicus*) in the 1970s, and Baiji (*Lipotes vexillifer*) in 2006 (Perrin et al., 2009).

Ethics statement

All samples were taken with relevant permissions and were transported between the EU, UK, and Norway using the registered CITES institutional exemptions of the Globe Institute of the University of Copenhagen (DK014), GELIFES of the University of Groningen (NL014), the University Museum of the Norwegian University of Science and Technology (NO007), and the Department of Zoology of the University of Cambridge (GB014). One sample from the UK was sent to Norway using CITES export permit 627244/01 and CITES import permit 23NO-0100-IM.

Author contributions

Youri van den Hurk: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Validation; Visualization; Roles/Writing - original draft; and Writing - review & editing. Fanny Sikström: Formal analysis. Luc Amkreutz: Resources; and Writing - review & editing. Hidde Bakker: Resources; and Writing - review & editing. Danielle L. Buss: Resources; and Writing - review & editing. Erik Ersmark: Data curation; Formal analysis; Investigation; Methodology; Resources; and Writing - review & editing. Carlos Fernández-Rodríguez: Resources; and Writing - review & editing. Alexander Lehouck: Resources; and Writing - review & editing. Alfredo López: Resources; and Writing - review & editing. Jose Martínez Cedeira: Resources; and Writing - review & editing. Carlos Nores: Resources; and Writing - review & editing. José Antonio Pis-Millán: Resources; and Writing - review & editing. Ana S.L. Rodrigues: Resources; and Writing - review & editing. Martin Seiler: Data curation; Formal analysis; Investigation; Methodology; Resources; and Writing - review & editing. Camilla Speller: Resources; and Writing - review & editing. Bente Philippsen: Data curation; Formal analysis; Investigation; Methodology Resources; Validation; and Writing - review & editing. James H. Barrett: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Roles/Writing - original draft; and Writing - review & editing.

Funding

This paper is funded by the MSCA-IF project Demise of the Atlantic Grey whale (DAG) under the European Union's Horizon 2020 research and innovation programme (grant agreement no. 101025598) and under the European Research Council (ERC) Synergy Project 4-OCEANS under the European Union's Horizon 2020 research and innovation programme (grant agreement no. 951649). One sample was analysed

using funding received from the Poldermuseum, Heerhugowaard, the Netherlands. One sample of the Museo Marítimo de Asturias (Cudillero), was provided by CEMMA, as part of the 'Galicia no Lombo da Balea II' project, financed by the Grupo de Acción Costera GAC-7 Ria de Vigo-A Guarda. The work of A. López is supported by the CESAM by FCT/MCTES (UIDP/50017/2020+UIDB/50017/2020+LA/P/0094/2020), through Spanish national funds and by national funds (OE), through FCT-I.P., in the scope of the framework contract foreseen in the numbers 4, 5 and 6 of the article 23, of the Decree-Law 57/2016, of August 29, changed by Law 57/2017, of July 19.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Thea Christophersen, Mohsen Falahati-Anbaran, John Øystein Haarsaker, Torkel Johansen, Marie-Josée Nadeau, Helene Løvstrand Svarva, Eirik Sollid, Sølvi Stene, and Damaris Zurbach of NTNU, as well as the NTNU University Museum, are thanked for help during the sampling and the sample preparation process. The following people are thanked for providing samples, contextual information, and general input: Henk Aandewiel of the Poldermuseum Heerhugowaard; Joost van den Berg and Aagje Feldbrugge of the Zeeuws Archeologisch Depot and Mark Bosselaers of the Koninklijk Zeeuwsch Genootschap der Wetenschappen; Barry Chandler of Torquay Museum; Joanneke van den Engelhees of the Provinciaal Archeologisch Depot Noord-Holland; Kinie Esser, Leida van Hees, and Tijmen Moesker of Archeoplan Eco; Martijn van Haasteren of the Cultural Heritage Agency of The Netherlands; Robert van de Mijle-Meijer of DSB Department Archaeology of the Municipality of The Hague; Museo Marítimo de Asturias, Luanco; Julie Kennard of Bury St Edmunds Suffolk County Sites and Monuments Record; Carolien van Loon of the Archeologisch & Bouwhistorisch Depot of Vlaardingen; Arthur Oosterbaan, Adrie Vonk and Ineke Vonk of Ecomare; Mark Philippeau and Annemieke van Toor of the Provinciaal Archeologisch Depot Zuid-Holland; Klaas Post of Natural History Museum Rotterdam, Julie Riviere of the Direction of the Archaeology of Chartres métropole and Franck Verneau of INRAP for providing the grey whale bone sample of the site "L'enclos et la-Couture" (Commune of Mainvilliers, Département of Eure-et-Loir, OA number: 067636); Francis Robbesom of the Archeologisch & Bouwhistorisch Depot Haarlem; Carla Soonius of Archeologie West-Friesland; Dion Stoop of the Noordelijke Archeologisch Depot Nuis, and Chris-Cecile Vauterin of Inrap Normandie Occidentale. Anthony John T Jull, Mathieu Boudin, and Deborah Shapiro are thanked for chasing down raw data on previously radiocarbon dated grey whale specimens and Salvador Herrando-Pérez and Frederik Saltré for providing advice regarding the GRIWM analysis. We would like to thank two anonymous reviewers for their valuable suggestions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2025.109583>.

Data availability

All data and/or code is contained within the submission.

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