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Recent dating of extinct Atlantic gray whale fossils, *(Eschrichtius robustus)*, Georgia Bight and Florida, western Atlantic Ocean

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The Atlantic gray whale (*Eschrichtius robustus)* presents an interesting case study of climate related dispersal and local extinction. While (limited) fossil records confirm its presence in the Atlantic until the 18th century, its abundance and distribution with the Eastern and Western basins are still not well understood. The discovery of presumed gray whale fossil remains from the Georgia Bight and Atlantic coast of Florida from the mid-1980s to late-2000s, provide a new opportunity to recover additional data regarding their chronology within the Western basin. Here, we apply AMS (accelerator mass spectroscopy) radiocarbon dating technique to eight fossil whale finds, identifying dates within Marine Isotope Stage (MIS) 3 (59-24 ka) and the late Holocene, ~ 2000 cal yr BP. We additionally confirm the taxonomic identification of two fossil bone samples as *E. robustus* using collagen peptide mass fingerprinting (Zoo MS). The obtained dates, when combined with a larger corpus of previously published Atlantic gray whale fossil dates, support the hypothesis for a decline of the Atlantic gray whale in the late Pleistocene and the late Holocene. These new data augment other recent findings from the Eastern Atlantic basin and better incorporate the Western Atlantic basin into a pan-ocean understanding for the species.

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Recent dating of extinct Atlantic gray whale fossils (*Eschrichtius robustus*), Georgia Bight and Florida, western Atlantic Ocean

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ABSTRACT

The Atlantic gray whale (*Eschrichtius robustus*) presents an interesting case study of climate related dispersal and extinction. While (limited) fossil records confirm its presence in the Atlantic up until the 18th Century, its abundance and distribution within the Eastern and Western basins are still not well understood. The discovery of presumed gray whale fossil remains from the Georgia Bight and the Atlantic coast of Florida, from the mid-1980s to late-2000s, provide a new opportunity to recover additional data regarding their chronology within the Western basin. Here we apply AMS (accelerator mass spectrometry) radiocarbon technique to eight fossil whale finds, identifying dates within Marine Isotope Stage (MIS) 3 (59-24 ka) and the late Holocene, ~2,000 cal yr BP. We additionally confirm the taxonomic identification of two fossil bone samples as *E. robustus* using collagen peptide mass fingerprinting (ZooMS). The obtained dates, when combined with a larger corpus of previously published Atlantic gray whale fossil dates, support the hypothesis for the decline of the Atlantic gray whale in the late Pleistocene and the late Holocene. These new data augment the findings of the Eastern Atlantic Basin and better incorporate the Western Atlantic Basin into a pan-ocean understanding for the species.

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Key words: gray whale, western Atlantic basin, paleontology, stable isotopes, radiocarbon dating, protein studies.

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1. Introduction

Recent studies have suggested that changes in species distribution during the Late Pleistocene–Early Holocene transition were caused both by habitat tracking as well as by extirpation of populations outside of isolated habitat refugia (Dalén *et al*. 2007, de Bruyn *et al*. 2011, Hofreiter *et al*. 2004, Hofreiter 2008, Hofreiter and Stewart 2009; Stewart, 2009). The gray whale (*Eschrichtius robustus*) presents an interesting case study by which to study this type of climate-related dispersal and extinction. Based on fossil evidence, the gray whale was present in both the North Pacific and North Atlantic during the Late Pleistocene and early Holocene, and migration from the Pacific to the Atlantic is thought to have been strongly shaped by Pleistocene climate shifts affecting potential dispersal routes and benthic feeding habitats. Both fossil and historical accounts suggest that the Atlantic gray whale was extinct in the North Atlantic by the mid-1700's (Mead and Mitchell 1984; Lindquist 2000), with both climate and anthropogenic factors implicated in its demise. Nevertheless, due to a paucity of fossil data in both the Eastern and Western basins, the diachronic distribution and abundance of gray whales prior to their disappearance is not well understood.

The monotypic gray whale family (Eschrichtiidae) is one of four families within the Cetacea suborder Mysticeti. Taxonomically, the phylogenetic placement of Eschrichtiidae has been controversial, with several suggested topologies (*i.e.,* McLeod *et al*. 1993; Arnason *et al*. 1992, 1993; Arnason and Gullberg 1994, 1996; Sasaki *et al*. 2005). Ironically, the extant gray whale *Eschrichtius robustus* was originally described (as *Balaenoptera robusta*) based on a Holocene fossil skeleton from Gräsö, Sweden (Lilljeborg, 1861; English translation in Lilljeborg, 1867). *E. robustus* was discovered as a living animal in the Pacific shortly thereafter. As the North Atlantic gray whale population went extinct prior to formal analysis of its taxonomy (Barnes and McLeod 1984; Lindquist 2001), it was not clear if the Atlantic and Pacific populations represented distinct species. Recent genetic comparisons of North Atlantic fossil material and extant North Pacific populations by Alter *et al.* (2015), however, confirmed that they represent the same species, connected through intermittent inter-ocean exchange or dispersals from the Pacific during openings of the Bering Strait (Alter *et al.* 2015). Moreover, combined radiocarbon dating and genetic results led Alter *et al.* to conclude that “dispersal between the Pacific and Atlantic was climate-dependent, and occurred – at least twice - both during the Pleistocene prior to the last glacial period, and the early Holocene immediately following the opening of the Bering Strait.”

In the Eastern Atlantic Basin, Pleistocene marine mammal taxa are known from the southern part of the North Sea and the Eurogeul – recovered during the recent channel deepening project of the Rotterdam Harbor. Based on morphology and radiocarbon dates, the fossils from the Eurogeul locality belong to a cold Late Pleistocene fauna (Mol *et al*. 2006), and confirm with certainty the Late Pleistocene as well as the Holocene occurrence of gray whales in the eastern Atlantic Ocean. In contrast, only a dozen fossils have been recovered from the Western Basin of the Atlantic, with the majority of dated remains corresponding to Holocene (Mead and Mitchell 1984; Bryant, 1995). Only one study to date has recorded a late Pleistocene presence in this region (Noakes et al. 2013), raising questions about the extent to which the Western Basin was frequented by gray whales prior to the Holocene, and the genetic relationship between Western and Eastern populations of Atlantic gray whale. To date, relatively few archaeological or paleontological gray whale specimens have been identified on the Eastern seaboard of North America, and ancient DNA (aDNA) surveys of historic whaling assemblages in this region have failed to detect any additional gray whale specimens (Rastogi *et al*. 2004; McLeod *et al*. 2008). This overall paucity of fossil and genetic data makes it difficult to draw meaningful conclusions about the abundance, distribution, and chronology of Atlantic gray whales in the Western Basin during both the Pleistocene and Holocene.

Here we apply AMS dating to new fossil gray whale finds from Florida and Georgia, and confirm taxonomic identifications using collagen peptide mass fingerprinting. Our results provide new evidence for the Late Pleistocene presence of gray whale in the Western basin, and combined with other fossil dates for the Atlantic, support the decline of Atlantic gray whales in the Pleistocene prior to post-glacial re-population.

2. Methods

In our study, we analyzed eight new fossil gray whale specimens from the western Atlantic Ocean. We applied AMS dating to the finds, as well as collagen peptide mass fingerprinting to confirm taxonomic identifications based on standard morphological comparisons. Two skulls were found on Florida beaches (Fig. 1), four dentary elements and two vertebrae were recovered from an underwater site, offshore Georgia (Noakes *et al*. 2009; Garrison, *et al*. 2012*b*; Noakes *et al*. 2013) (Figs. 1, 2, 3).

The gray whale fossils from the Gray's Reef and JY Reef localities, offshore Georgia, are cataloged in the paleontology collection of the Georgia Museum of Natural History (GMNH), University of Georgia, Athens. The fossils from the Hobe Sound and Jacksonville Beach localities in Florida are cataloged in the vertebrate paleontology collection of the Florida Museum of Natural History, University of Florida (specimen acronym UF), Gainesville.

Figure 1. The Georgia Bight and Florida Peninsula, showing the location of the gray whale specimens discussed in the text. These records include specimens from the JY Reef and Gray's Reef National Marine Sanctuary in the Georgia Bight and Jacksonville Beach and Hobe Sound on the Atlantic Coast of Florida.

Figure 2. The late Pleistocene and Holocene specimens of the gray whale (*Eschrichtius robustus*), Research Ledge site, JY Reef, Georgia Bight used in this study. A: Lateral views of three dentary fragments (GMNH accession numbers, 00-28-09, 00-28-10, 00-28-13), B: Lateral view of right dentary, (GMNH 4281) with comparison to North Sea specimen (top), Rotterdam Museum of Natural History collections, scale is 20 cm; D: anterior (top) and posterior (bottom) views of two thoracic vertebrae, C (number 4024), D. (GMNH 4215). Measurements of these specimens are in Table 1.

Figure 3. Two partial Holocene skulls of gray whales (*Eschrichtius robustus*) from Florida (USA). Top row (A-C), Jacksonville Beach (UF 99000), A. posterior view, B. right lateral view, C. ventral view; Middle row (D-F) Hobe Sound National Wildlife Refuge (NWR) (UF 69000), D. posterior, E. right lateral and F. ventral views); Bottom row, two views of the left periotic (internal ear bone) from the Hobe Sound skull. Both braincases are relatively intact from the condyles to the broken frontals. All Scale bars are 10 cm; overall dimensions in Table 1.

Fossil localities of the Georgia and Florida gray whales

The Georgia locality is J-Reef a low exposure of shell beds about 16 km north of the Gray's Reef (fig. 1).

At J-Reef the shell beds are in a conformable relationship with finer grained sediment that dates to no earlier than the late Pleistocene (Garrison, et al, 2012).

Both vertebrae and the three dentary (?) fragments shown in figure 2 were recovered from the fine sediment or adjacent to the outcrop on the sea floor and are largely incomplete and badly eroded with little cortical bone present. Both are lacking complete neural arch, spinous, and transverse processes except for the remnants of their bases. Provisionally, we assign the larger of the vertebrae (4215; GMNH-27370) to the thoracic portion of the vertebral column. In cross section, and ventrally, this vertebra preserves a low ridge not seen in the other specimen. During subsequent dives, in fall 2006, the large fossil dentary was discovered partially embedded in the coquina (fig. 2 b).

The following details on the discovery and exact location of the gray whale skull from Hobe Sound (Fig. 3, Specimen UF 69000) were provided by Burkett S. Neely, Jr. (in litt., 6 June 1983) of the U. S. Fish and Wildlife Service (USFWS). The skull was discovered by a Mr. and Mrs. Kornit on 19 January 1983 at the edge of the surf on the northern end of Jupiter Island about 10 km south of St. Lucie Inlet, on the Hobe Sound National Wildlife Refuge (NWR), Martin County, southeastern Atlantic Coast of Florida (fig. 1). Exact coordinates for the Hobe Sound skull are 27°07’40” North latitude and 80°08’45” West longitude. The skull was collected later that same day by USFWS personnel. The discovery of the Hobe Sound skull apparently coincided with extensive beach erosion that occurred during a strong winter storm. Through the generosity of Burkett S. Neely, Jr. and the USFWS, the Hobe Sound gray whale skull was placed on permanent loan in the vertebrate paleontology collection of the Florida Museum of Natural History (FLMNH), University of Florida (UF), Gainesville (catalogue number UF 69000). Mead and Mitchell (1984, p. 48) stated that “The specimen consists of most of the cranium of what looks like an adult…” However, upon closer examination, this skull consists only of a braincase, including both periotics (Fig. 3), and is from a very young individual or calf probably less than a year old. Robert K. Bonde (in litt, 19 July 1983), likewise, estimated that this specimen was from a very young calf, probably less than three months old. The Hobe Sound skull represents the southernmost record of *E. robustus* in the Atlantic Ocean, based on distributional maps in Mead and Mitchell (1984). Attached to the internal portion of the periotic (Fig. 3) of this juvenile skull is a small sample of sediment, consisting of medium to coarse quartz sand and fragments of mollusk shells, forming a semi-indurated “coquina.” This coquina sand, possibly deposited on a beach or in a nearshore marine environment, was probably the original sediment in which the skull was preserved before being dislodged during a storm and washed up on the beach.

The second gray whale skull from Florida (FLMNH Specimen UF99000) was collected during the 1970s by Jesse S. Robertson of Jacksonville University on the beach at Jacksonville Beach, Duval County, northeastern Florida (approximate coordinates, 30°17’N, 81°23’W) (figs.

1). Although the collector was unable to remember the specific details surrounding the discovery of this fossil, he did recollect it was found after a strong storm. The Jacksonville Beach gray whale skull consists of a braincase of a juvenile, compared to that of the younger calf from Hobe Sound.

Carbon isotope analysis and AMS dating

For the stable isotope analysis of samples we used both a Finnigan MAT 252 mass spectrometer, which is a dual-inlet mass spectrometer as well as a National Electrostatics Corporation Model 1.5SDH-1 Pelletron 500 kV compact Accelerator Mass Spectrometer AMS) unit for precise analyses of carbon isotopes ^{12}C, ^{13}C and ^{14}C. The Finnigan spectrometer is a double collector gas source mass spectrometer and allows for the measurement of two isotopes of oxygen and three isotopes of carbon with the double collector. It measures the ratio on the sample and the standard by alternating dual inlets. By contrast the Model 1.5SDH-1 Pelletron 500 kV only analyzed for the three isotopes of carbon using Faraday cup collectors at the end of the beam line array.

All samples were quite poorly preserved and did not retain sufficient collagen for AMS analysis, so we applied the bioapatite fraction dating technique (Cherkinsky 2009). Specimens were chemically pretreated to remove all secondary carbonate and organics, but leave bioapatite in the bone structure. The specimens were treated with a weak acetic acid

(CH_3COOH) bath under vacuum. Once washed and dried the samples were treated with phosphoric acid (H_3PO_4) in reaction tubes and heated to ensure removal of all carbonates. The bone samples generated CO_2 in the vacuum system and this gas was then analyzed in the mass spectrometer against a Vienna Pee Dee Belemnite standard (VPDB) with the per mil [‰] values of $\delta^{13}C$ reported against VPDB and $\delta^{18}O$ reported against VPDB *and* VSMOW.

We have used the internal standards which are:

	δ13C ‰	δ18O ‰
Fisher	-0.64	-14.90
A 1296	+2.56	-O.60

These standards were calibrated with National bureau of Standards (now NIST) NBS 19 δ13C ‰ = +1.95 and δ18O ‰ = +28.60.

For accelerator mass spectrometer isotopic analyses carbon dioxide was cryogenically purified from the other reaction products and catalytically converted to graphite using the method of Vogel et al. (1984). Graphite $^{14}C/^{13}C$ ratios were measured by the Model 1.5SDH-1 Pelletron 0.5 MeV accelerator mass spectrometer. The sample ratios were compared to the ratio measured from the Oxalic Acid I (NBS SRM 4990). The sample $^{13}C/^{12}C$ ratios were measured separately using a stable isotope ratio mass spectrometer and expressed as $\delta^{13}C$ with respect to VPDB, with an error of less than 0.1 ‰

Protein Fingerprinting

The two Florida specimens (UF 69000, UF 99000) were taxonomically identified through collagen peptide mass fingerprinting (PMF), a rapid and cost-effective technique, whereby taxonomic groups are discriminated based on difference in the collagen protein sequence. Robust species identification can be accomplished by comparing collagen peptide fingerprints with the fingerprints from known samples using mass spectrometry (Collins *et al*. 2010). The success of this method has already been demonstrated for ancient North Atlantic cetacean species, including Atlantic gray whale (Kirby *et al*. 2013; Buckley *et al.* 2014).

Sample preparation, mass spectrometry and data analysis followed that described in Buckley *et al* (2014) and Evans *et al*. (2015) at the BioArCh centre, University of York. Briefly, between 10-30 mg of bone powder was fully demineralized through immersion in 0.6 M hydrochloric acid, followed by gelatinization in 100 µl of 50 mMol ammonium bicarbonate at 65˚C for 1 hour. The resulting collagen was incubated with 0.4µg of trypsin overnight at 37˚C, acidified to 0.1 % trifluoroacetic acid and purified using a 100 µl C18 resin ZipTip® pipette tip (EMD Millipore). The collagen extract was spotted in triplicate on a 384 spot MALDI target plate, with calibration standards and run on a Bruker ultraflex III MALDI TOF/TOF mass spectrometer. mMass software (Strohalm et al., 2008) was used to average spectra replicates from each specimen, and compare to the list of m/z markers for marine mammals presented in Kirby *et al*. 2013 and Buckley et al. 2014.

3. Results

Paleontology

Based on the paleontological analyses of the smaller vertebra (4024; GMNH-27373), we provisionally assign this element to the thoracic portion of the spinal column. Both vertebrae have many attributes that suggest they are eschrichtiid in origin.

We compared the two Florida gray whale skulls to descriptions and photographs of *Eschrichtius robustus* (True 1983; 1904, plate 47; Barnes and McLeod 1984, figs. 1, 2, 5A). Because both Florida skulls consist only of the braincase, our comparisons are limited to characters present in this anatomical region (Fig. 3; Table 1). Characters the Florida skulls share with *E. robustus* include: small and steep occipital shield with prominent paired tuberosities; large occipital condyles; large and posteriorly oriented paroccipital processes; and short, massive zygomatic processes of the squamosals.

Table 1. Cranial measurements (in cm) of Quaternary gray whale (*Eschrichtius robustus*) skulls from Florida (this study).

On the basis of these similarities, we confidently refer the two Florida skulls to *E. robustus*. The Hobe Sound skull was previously identified as a gray whale by several cetacean specialists, including Robert Bonde, James Mead, Dan Odell, and Charles Potter. Both Florida gray whale skulls represent immature individuals based on the unfused basioccipital-basisphenoid suture (Table 1). The Hobe Sound skull (UF 69000) is most likely a newborn calf, whereas the larger Jacksonville Beach skull (UF 99000) was probably several years old.

A juvenile fossil gray whale cranium from Cape Lookout, North Carolina measured 80 cm in width across the zygomatic processes (Mead and Mitchell, 1984). This compares to a width across the zygomatic processes in the two juvenile skulls from Florida of 76 cm in UF 99000 and 60 cm in UF 69000 (width of squamosals in Table 1). An adult fossil gray whale cranium from Corolla, North Carolina measured between 130 and 140 cm across the zygomatics (Mead and Mitchell, 1984). The width of the occipital condyles in the adult from Corolla is 31 cm, compared to 24 cm in UF 99000 and 22 cm in UF 69000 (Table 1).

Our diagnoses, together with earlier studies, are in line with that of two recently reported Holocene-aged gray whale finds in the western Pacific, off Taiwan (Tsai *et al*. 2014). That study identified the paired tuberosities on the occipital shield as ontogenetically diagnostic of Eschrichtiidae sp. (*supra*). Both Florida gray whale skulls demonstrate these paired tuberosities, in particular UF 99000 (Fig. 3).

Furthermore, the collagen peptide mass fingerprinting results confirm the anatomical identification of Gray Whale for the two Florida skulls (Fig. 4). Both skulls exhibited diagnostic gray whale specific markers presented in Kirby et al. 2013 (specifically, the presence of diagnostic collagen peptide F at 2899).

Figure 4. MALDI-ToF Collagen peptide mass fingerprints for specimens UF69000 and UF99000, labelled according to Buckley et al. 2014 and Kirby et al. 2013 modern; inset displays unique gray whale peptide marker at 2899 for both specimens.

Radiocarbon (^{14}C) dates

We dated the samples using the organic fraction and mineral fraction of bioapatite. The overall morphology of the bones was very well preserved, however, the collagen fraction was almost completely destroyed and the concentration of organic carbon was about 0.1% or lower. In all four cases the bioapatite fraction radiocarbon age estimate was older (33-37.5 ka) than that from the organic, collagen-like, fractions (8.3 to 23 ka). The per mil [‰] values of $\delta^{13}C$ reported against VPDB and $\delta^{18}O$ reported against VPDB and VSMOW and are shown in Table 2, and the AMS dates are displayed in Table 3.

Table 2. Isotopic results for Georgia Bight and Florida specimens of *Eschrichtius robustus*.
Table3. Radiocarbon ages for Georgia Bight and Florida Specimens

Without doing a full statistical analysis, the results shown in Table 2 for the $\delta^{13}C$ of sample A (-5.11 ± 0.04 ‰) and sample B (-5.04 ± 0.04 ‰) seem to be more strongly related and are probably from the same whale, while sample C (-4.80 ± 0.04 ‰) differs slightly from the other samples. Sample C could also be from another individual, but because the difference from the other samples is not more than 1‰ it is likely that all three of the mysticete whale bone fragments are from the same individual.

4. Discussion

Our results identify the presence of gray whale in the Georgia Bight and along the Atlantic Coast of Florida, in both the Pleistocene and late Holocene. These observations, in particular the two late Holocene records of juveniles from Florida, potentially provide insight into this species migration route and calving grounds. The eastern Pacific population of gray whales annually migrates from summer grounds in the Bering Sea and Chukchi Sea between Alaska and Russia to winter/calving grounds in Mexico along the western coast of Baja California and the southern Gulf of California. The best known calving sites of *Eschrichtius robustus* in the eastern Pacific are located in shallow lagoons along the coast of Baja California between 24° and 29° North latitude, including Laguna Ojo de Liebre (also known as “Scammon’s Lagoon”), Laguna San Ignacio, and Bahia Magdalena (Rice and Wolman, 1971). The presence of a fossil skull (UF 69000) representing a newborn gray whale calf from Jupiter Island along the southeastern coast of Florida suggests the possibility that this region may have been used as a calving ground by the now-extinct western Atlantic population of gray whales. Along the Atlantic coast of southeastern Florida between 24° and 29° N there are numerous shallow bays and protected lagoons, including Florida Bay, Biscayne Bay, Lake Worth, Hobe Sound, Indian River, Banana River, and Mosquito Lagoon, that would seem to have provided ideal calving grounds for gray whales.

Our results also provide new insight into the ecological history of this enigmatic species. Current Atlantic Arctic species have evolved over periods whereby adaptation to profoundly different climate regimes was required, such as ca. 12 ka when the Bering land bridge closed the western Arctic to Pacific water intrusion (Walsh 2008) or during the retreat of the great ice sheets and the opening continental shelves at the onset of the Holocene (Harington 2008).

Climatic changes of the glacial cycles are thought to have been a major driver of arctic population declines and species extinctions, however, there is still not a full understanding of how marine species responded to past climate change.

It has been suggested that some Pleistocene cetacean lineages survived into the Holocene and their effective female population size increased rapidly, concurrent with a threefold increase in core suitable habitat (Evans, 1987). For example, using ancient DNA analysis, Foote *et al*. (2005; 2013) show that the bowhead whale (*Balaena mysticetus*), shifted its range and tracked its core suitable habitat northwards during the rapid climate change of the Pleistocene–Holocene transition. The case for this type of habitat tracking in Late Pleistocene Atlantic gray whale is not as straightforward. Pyenson and Lindberg (2011) argue for the adaptability of gray whales, suggesting that gray whales survived Pleistocene glacial maxima (e.g. LGM) and maintained substantial population sizes by employing a diverse set of feeding modes, similar to those seen in seasonal resident whales found today between northern Washington State and the coast of Vancouver Island. Molecular data, however, do not support a widespread (maternal) continuity in gray whale lineages across the LGM. In their analysis of Atlantic gray whale fossils, Alter *et al* (2015) detected little genetic continuity between the late Pleistocene and Holocene populations – within the dataset, only a single sample displayed a lineage that survived post-LGM. The remaining Holocene samples from both the Western and Eastern basins shared a most recent common ancestor with Pacific gray whales dating to the early to mid-Holocene, suggesting that the majority of the Atlantic Holocene population were the result of a second colonization event when warming temperatures, sea-level rise, and decreases in sea ice permitted passage through the Bering Strait (Alter *et al*. 2015).

We examine these two hypotheses in light of the range and distribution of the 53 radiocarbon dates for all available Atlantic gray whale finds (Fig. 5). There are 15 late Pleistocene ages that range from >45,200 to 35,520 BP and 38 Holocene ages that range from 10,400 BP to 340 BP (Table 4, Fig.5). These ages are clearly bimodal in their distribution suggesting either that: (1) any population surviving post-LGM is geologically "invisible", due to a lack of fossil evidence; or (2) the lack of finds reflects their true absence, indicating a significant decline or even the effective extirpation of gray whales across the north Atlantic Ocean in the period between ~40 ka and ~11 ka. The argument in favor for the latter may be further supported by geologic evidence for a much-reduced habitat in the north Atlantic during LGM due to the subaerial exposure of both the North Sea/Baltic and the Georgia Bight and Florida continental shelves (Alter et al. 2015; Garrison et al. 2008; 2012; Harris et al. 2013). Fossil evidence for the gray whale, however, may yet be found for the post- 40 ka – 11 ka interval on areas of the Atlantic continental shelf that were inundated at or during the last low stand. Nevertheless, the dates produced in our study for recent western Atlantic Ocean finds are in good alignment with these (predominantly Eastern basin) dates and, likewise, suggest a bi-modal distribution for Atlantic gray whales in the Western basin.

Figure 5. Scatter plot of 53 radiocarbon ages for Atlantic Basin gray whale finds, with gap between ~35,000 and ~11,000 BC (Logarithmic scale, base 10).

Table 4 **Pleistocene and Holocene eastern and western North Atlantic gray whale specimens**

5. Conclusions

In our results, collagen peptide mass fingerprinting and paleontological diagnoses confirm the two Florida finds to be the Atlantic gray whale, *Eschricthius robustus*. While unable to report direct biomolecular findings, paleontological diagnoses support our identification of the Georgia Bight specimens as gray whale as well. Thus, the existence of both Pleistocene and Holocene gray whale populations in the western Atlantic Ocean are supported by these radiocarbon dates for recent, fossil discoveries in the Georgia Bight of the western Atlantic Ocean. The results of our study may help explain the Late Quaternary occurrences of gray whales in the Georgia Bight and along the Atlantic Coast of Florida, in particular the two late Holocene records of juveniles from Florida.

The presence of newborn gray whale calf's skull from Jupiter Island as well as a juvenile gray whale's dentary from the Georgia Bight suggests that the region between 24° and 29° N may have been used as a calving ground by the now-extinct western Atlantic population of gray whales.

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Figure 1(on next page)

The Georgia Bight and Florida Peninsula.

The Georgia Bight and Florida Peninsula, showing the locations of the gray whale specimens discussed in the text. These records include specimens from the JY Reef and Gray's Reef National Marine Sanctuary in the Georgia Bight and Jacksonville Beach and Hobe Sounds on the Atlantic coast of Florida.

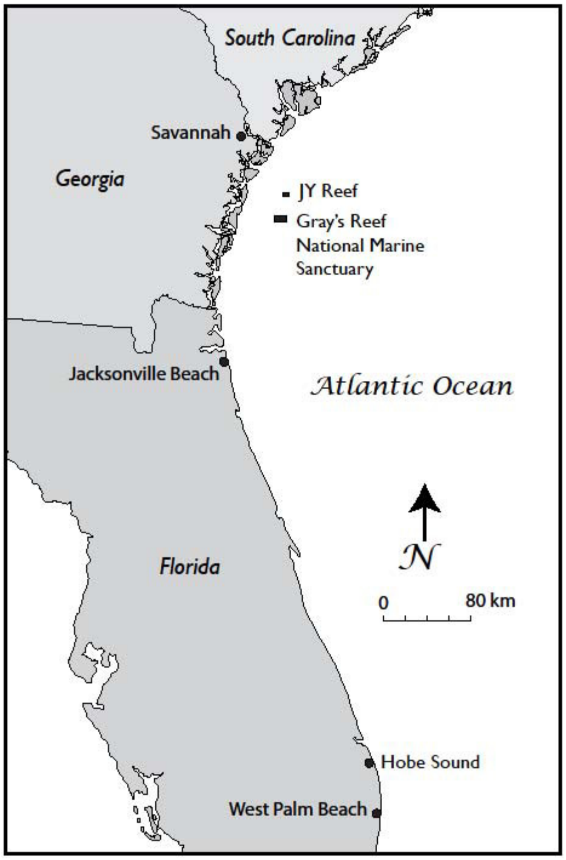


Figure 1. The Georgia Bight and Florida Peninsula, showing the location of the gray whale specimens discussed in the text. These records include specimens from the JY Reef and Gray's Reef National Marine Sanctuary in the Georgia Bight and Jacksonville Beach and Hobe Sound on the Atlantic Coast of Florida.

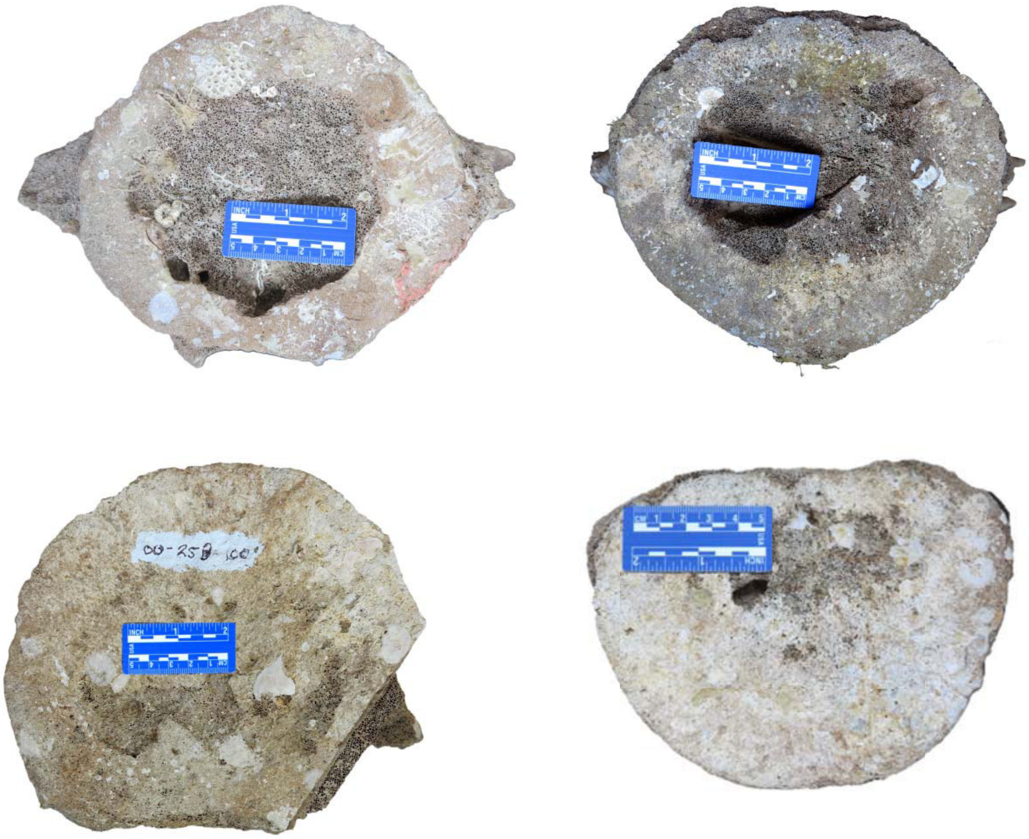
Figure 2 (on next page)

The late Pleistocene and Holocene specimens of the gray whale.

The late Pleistocene and Holocene specimens of the gray whale (*Eschrichtius robustus*), Research Ledge site, JY Reef, Georgia Bight used in this study. A: Lateral views of the three dentary fragments (GNMH accession numbers, 00-28-09, 00-28-10,00-28-13), B: Lateral view of the right dentary, (GNMH 4281) with comparison to North Sea specimen (top), Rotterdam Museum of Natural History collections, scale is 20 cm; D: anterior (top) and posterior (bottom) views of thoracic vertebrae, C: (GNMH 4024), D: (GNMH 4215). Measurements of these specimens in Table 1.

A.

B.



C. **D.**

Figure 2. The late Pleistocene and Holocene specimens of the gray whale (*Eschrichtius robustus*), Research Ledge site, JY Reef, Georgia Bight used in this study. A: Lateral views of three dentary fragments (GMNH accession numbers, 00-28-09, 00-28-10, 00-28-13), B: Lateral view of right dentary, (GMNH 4281) with comparison to North Sea specimen (top), Rotterdam Museum of Natural History collections, scale is 20 cm; D: anterior (top) and posterior (bottom) views of two thoracic vertebrae, C (number 4024), D. (GMNH 4215). Measurements of these specimens are in Table 1.

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Figure 3(on next page)

Two partial Holocene skull of gray whales.

Two partial Holocene skulls of gray whales (*Eschrichtius robustus*) from Florida (USA). Top row (A-C), Jacksonville Beach (UF 99000), A. posterior view, B. right lateral view, C. ventral view; Middle row (D-F) Hobe Sound National Wildlife Refuge (NWR) (UF 69000), D. posterior, E. right lateral and F. ventral views); Bottom row, two views of the left periotic (internal ear bone) of the Hobe Sound skull. Both braincases are relatively intact from the condyles to the broken frontals. All scale bars are 10 cm; overall dimensions in Table 1.

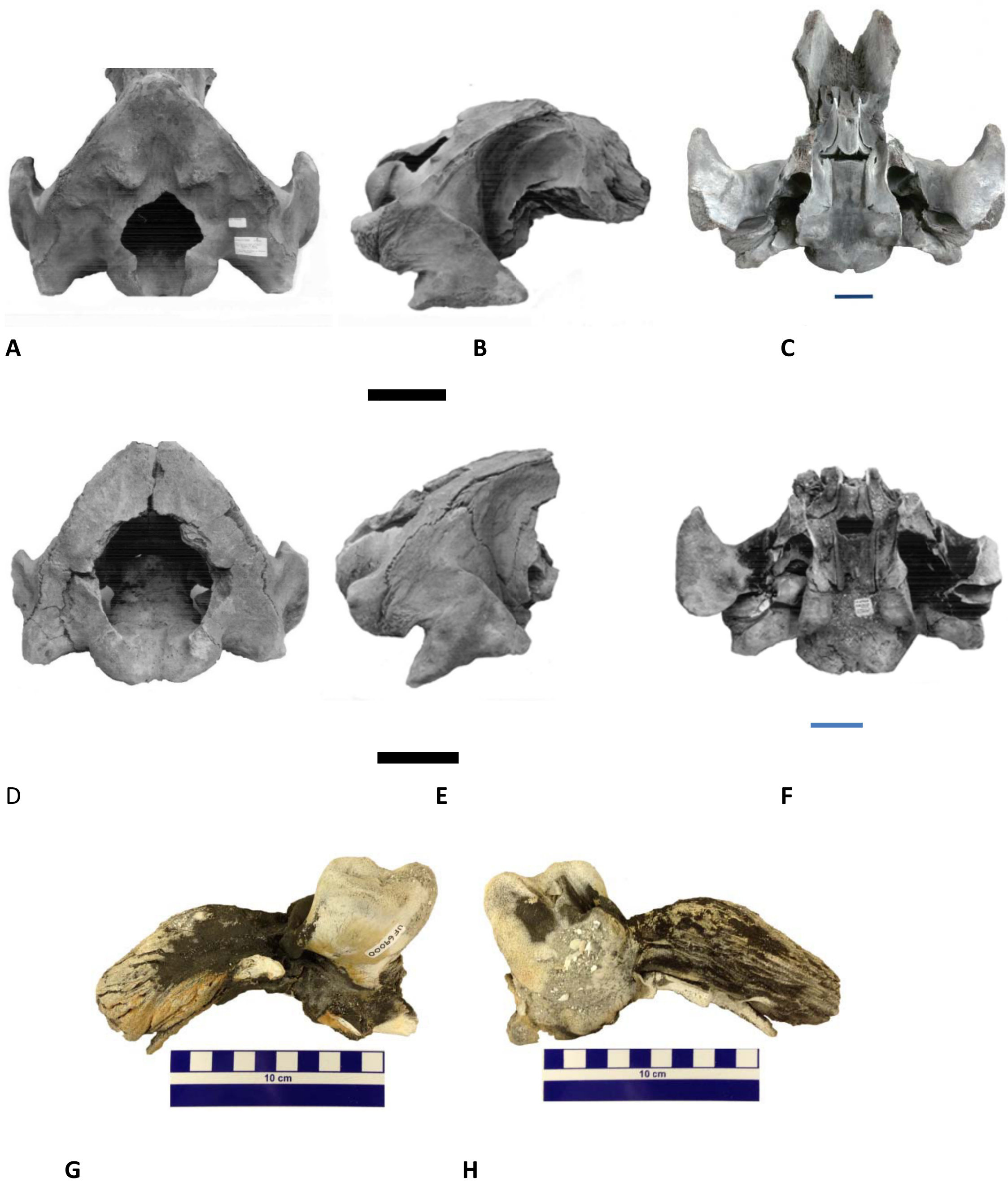

Figure 3. Two partial Holocene skulls of gray whales (*Eschrichtius robustus*) from Florida (USA). Top row (A-C), Jacksonville Beach (UF 99000), A. posterior view, B. right lateral view, C. ventral view; Middle row (D-F) Hobe Sound National Wildlife Refuge (NWR) (UF 69000), D. posterior, E. right lateral and F. ventral views); Bottom row, two views of the left periotic (internal ear bone) from the Hobe Sound skull. Both braincases are relatively intact from the condyles to the broken frontals. All Scale bars are 10 cm; overall dimensions in Table 1.

Table 1 (on next page)

Cranial measurements of Quaternary gray whale skulls

Cranial measurements (in cm) of Quaternary gray whales (*Eschrichtius robustus*) skulls from Florida (this study).

Table 1. Cranial measurements (in cm) of Quaternary gray whale (*Eschrichtius robustus*) skulls from Florida (this study).

Locality & Catalogue #	width of squamosals	width of paraoccipitals	width of supraoccipitals	width of occipital condyles	height of skull
Hobe Sound NWR UF 69000	60	45	39	22	41
Jacksonville Beach UF 99000	76	59	51	24	51

Figure 4(on next page)

MALDI-ToF Collagen peptide fingerprinst for specimens UF69000 and UF99000.

MALDI-ToF Collagen peptide mass fingerprints for specimens UF69000 and UF99000, labelled according to Buckley et al. 2014 and Kirby et al 2013 modern; inset displays unique gray whale peptide marked at 2899 for both specimens.

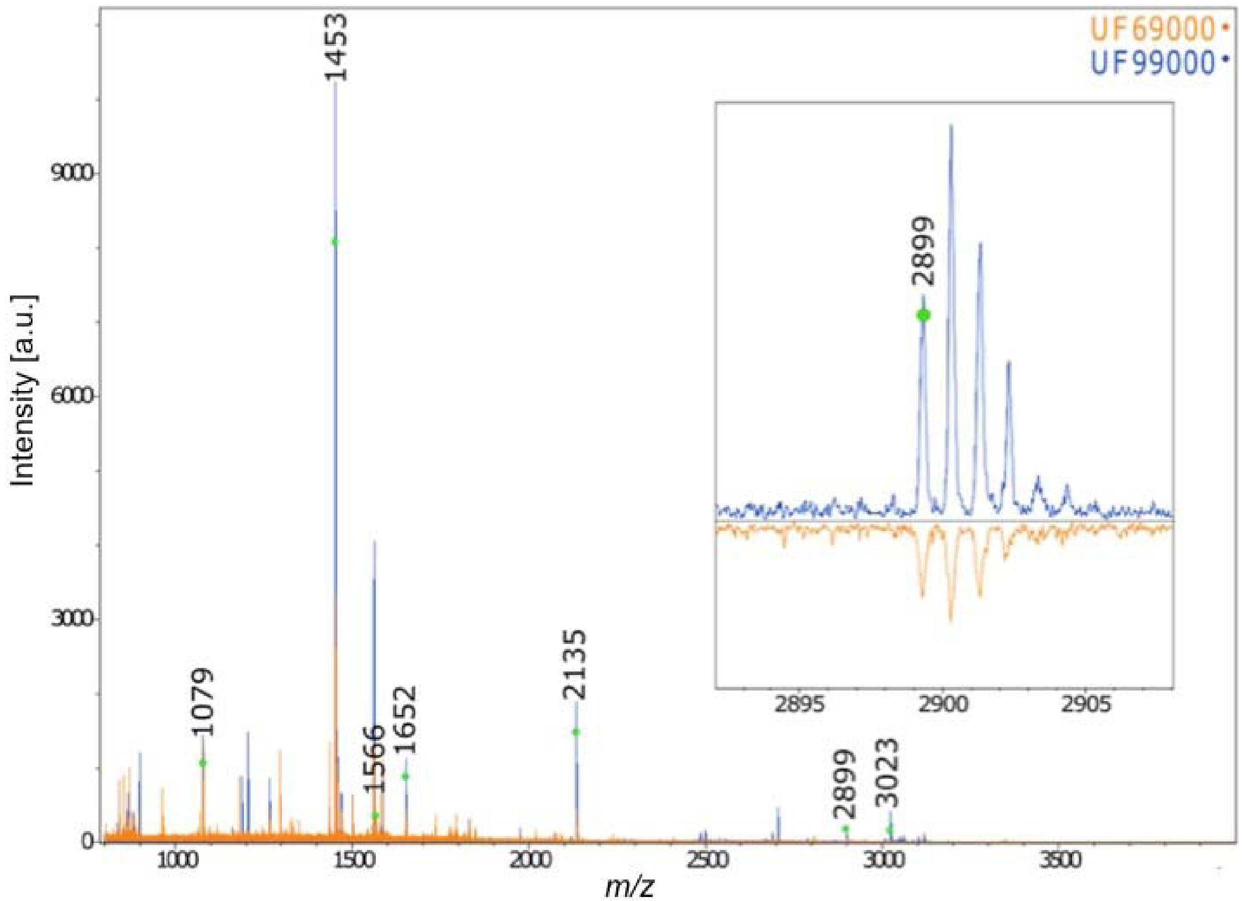

Figure 4. MALDI-ToF Collagen peptide mass fingerprints for specimens UF69000 and UF99000, labelled according to Buckley et al. 2014 and Kirby et al. 2013 modern; inset displays unique gray whale peptide marker at 2899 for both specimens.

Table 2(on next page)

Isotopic results for Georgia Bight secimens.

Isotopic results for the Georgia Bight and Florida specimens of *Eschrichtius robustus*.

Table 2. Isotopic results for Georgia Bight and Florida specimens of *Eschrichtius robustus*.

Laboratory #	$\delta^{13}C$ ‰ vs. VPDB	$\delta^{18}O$ ‰ vs. VPDB	$\delta^{18}O$ ‰ vs. VSMOW
Dentary A (00-28-09)	-5.11	0.22	31.14
Dentary B (00-28-10)	-5.04	0.14	31.05
Dentary C (00-28-13)	-4.80	0.92	31.86
4024 (vertebra)	-7.66	-9.65	20.96
4281 (dentary)	-6.62	-10.34	20.25
4215 (vertebra)	-6.67	-9.41	21.21
UF 69000 (cranium)	-9.5	-	-
UF 99000 (cranium)	-10.3	-	-

Table 3 (on next page)

Radiocarbon ages for specimens.

Radiocarbon ages for Georgia Bight and Florida specimens.

Table 3. Radiocarbon ages for Georgia Bight and Florida Specimens

UGA #	Element	Condition	Find Location	^{14}C age, yr BP	Reservoir effect, ΔR	Calendar age, BP 95.4% probability
4024	Vertebra	fossil	J-Reef	37,580±120	-120±78	41490-42070
4281	Dentary	fossil	J-Reef	36,570±300	-120±78	40230-41550
4215	Vertebra	fossil	J-reef	34,520±160	-120±78	38350-39140
4214	Dentary?	fossil	J-reef	33,520±160	-120±78	36240-37460
7742a	Shell	fossil	J-reef	46190±340	-120±78	48550-50000
UF 69000	Cranium	fossil	Jacksonville Beach, Florida	2130+/-25	-90±131	1500-2150
UF 99000	Cranium	fossil	Hobe Sound, Florida	2190+/-20	-90±131	1570-2220

Figure 5(on next page)

Scatter plot of 53 radiocarbon ages for Atlantic basin gray whales.

Scatter plot of 53 radiocarbon ages for Atlantic basin gray wahles finds, with gap between ~35,000 and ~11,000 BC (Logarithmic scale, base 10).

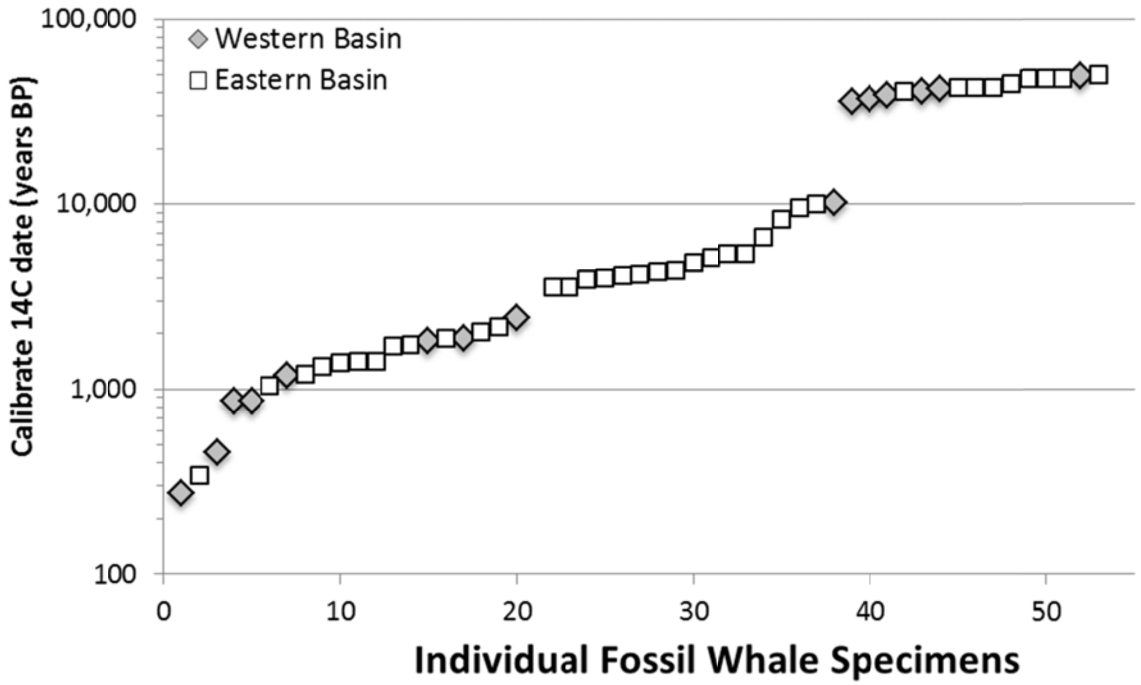

Figure 5. Scatter plot of 53 radiocarbon ages for Atlantic Basin gray whale finds, with gap between ~35,000 and ~11,000 BC (Logarithmic scale, base 10).

Table 4(on next page)

Pleistocene and Holocene Atlantic gray whale specimens.

Pleistocene and Holocene eastern and western Atlantic gray whale spoecimens.

Table 4. **Pleistocene and Holocene eastern and western North Atlantic gray whale specimens**

Region	***Date found***	***Cal yr BP***	***Citation***	***Current Location***
Gray whale - Eastern Atlantic Basin				
Pentuan, England	1829	1,329 ± 195	Flower 1872; Bryant 1995; Alter et al. 2015	unknown
Gräsö, Sweden	1859	4,395 ±155	Lilljeborg 1861; Persson 1986	unknown
Babbacombe Bay, England	1861		Gray 1864	unknown
Babbacombe Bay, England	1865	340 ±260	Gray 1866; Pengelly 1865, 1878; Bryant 1995; Alter et al. 2015	unknown
Ijmuiden, Netherlands	1879	8,330 ± 85	Van Deinse and Junge 1937; Bryant 1995	National Natural History Museum Naturalis, Leiden
Ijmuiden, Netherlands	1916	1,400	Van Deinse and Junge1937; Bryant 1995	National Natural History Museum Naturalis, Leiden
Wieringermeer-Polder,Netherlands	1935	4,195 ± 45	Van Deinse and Junge1937; Bryant 1995	National Natural History Museum Naturalis, Leiden
Oostduinkerke-Koksijde,Belgium	1978	2,024 ± 110	Asselberg 1981; Bryant 1995	Unknown
North Sea, Netherlands	2005	42,800 ±4100-2700	Post 2005	Natural History Museum, Rotterdam
North Sea, Netherlands	2005	>45,200	Mol *et al.* 2006	Natural History Museum, Rotterdam
North Sea, Netherlands	2001	1150–1270	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	No Data	1350–1500	Alter et al. 2015	Unknown
North Sea, Netherlands	1997	1350–1500	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	2003	2650–2730	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	No data	>48 000	Alter et al. 2015	Unknown
North Sea, Netherlands	2005	>48 000	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	2003	42 500–43 300	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	1879	9470–9550	Alter et al. 2015	National Natural History Museum Naturalis, Leiden
North Sea, Netherlands	1916	1600–1800	Alter et al. 2015	National Natural History Museum Naturalis, Leiden
North Sea, Netherlands	1935	4760–4850	Alter et al. 2015	National Natural History Museum Naturalis, Leiden
North Sea, Netherlands	No data	4950–5250	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	1954	3830–3960	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	1994	960–1120	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	1995	4230–4420	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	1996	>48 000	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	2005	1820–1950	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	2005	>50 000	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	2005	3480–3630	Alter et al. 2015	Natural History Museum, Rotterdam

North Sea, Netherlands	2005	10 000–10 180	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	2005	5280–5430	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	2005	6620–6700	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	No data	5320–5470	Alter et al. 2015	Unknown
North Sea, Netherlands	No data	3470–3620	Alter et al. 2015	Unknown
North Sea, Netherlands	No data	40 200–41 400	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	No data	1680–1800	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	No data	42 400–43 600	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	2007	3930–4070	Alter et al. 2015	Natural History Museum, Rotterdam
North Sea, Netherlands	No data	4020–4270	Alter et al. 2015	Unknown
Gray whale - Western Atlantic Basin				
Tom's River, New Jersey	**1850s**	455 ± 90	Mead and Mitchell1984	Smithsonian National Museum of Natural History, Washington D.C
Myrtle Beach, South Carolina	1959	865 ± 165	Mead and Mitchell1984	unknown
Chesapeake Bay, Virginia	1969	10,140 ± 125	Mead and Mitchell1984	unknown
Nags Head, North Carolina	1970's	865 ± 50	Mead and Mitchell1984	Smithsonian National Museum of Natural History, Washington D.C
Corolla, North Carolina	1976	2415 ± 90	Mead and Mitchell1984	unknown
Southampton, New York	1977	275 ±35	Mead and Mitchell1984	unknown
Corolla, North Carolina	1977		Mead and Mitchell1984	unknown
Rehobeth, Delaware	1978		Mead and Mitchell1984	Smithsonian National Museum of Natural History, Washington D.C
Cape Lookout, North Carolina	1979	1190 ±245	Mead and Mitchell1984	unknown
Jupiter Island, Florida	1983s	~1500-2150	this study	Florida Museum of Natural History (UF69000)
Jacksonville Beach, Florida	1970s	1570-2220	this study	Florida Museum of Natural History (UF99000)
South Atlantic Bight, Georgia	2006	~36,000 yBP	Noakes *et al.* 2009;Cherkinsky *et al.*2009; Garrison *et al., this study*	Georgia Museum of Natural History (No. 4032)
South Atlantic Bight, Georgia	2006	41490-42070	This study	Georgia Museum of Natural History (No. 4024)
South Atlantic Bight, Georgia	2006	40230-41550	This study	Georgia Museum of Natural History No. 4281)
South Atlantic Bight, Georgia	2006	38350-39140	This study	Georgia Museum of Natural History (No. 4215)
South Atlantic Bight, Georgia	2006	36240-37460	This study	Georgia Museum of Natural History (No. 4214)
South Atlantic Bight, Georgia	2006	48550-50000	This study	Georgia Museum of Natural History (No. 7742a)