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Late Pleistocene gray whales (*Eschrichtius robustus*) offshore Georgia, U.S.A., and the antiquity of gray whale migration in the North Atlantic Ocean

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ABSTRACT

Living gray whales (*Eschrichtius robustus*) are key consumers in benthic communities of the North Pacific Ocean. Gray whales, however, also inhabited the North Atlantic Ocean until recent historical times (~1600 AD), leaving open questions about their historical ecology in nearshore communities of this basin. Here we report the discovery of fossil remains from two individual gray whales recovered from underwater excavations at separate localities of JY Reef, an offshore reef situated approximately 32 kilometers (km) offshore of St. Catherine's Island, Georgia, U.S.A. Both mandibles are diagnostic to the living *E. robustus*. Radiometric dating of shells from JY Reef suggests an approximate age range of these two specimens between 42 and 30 thousand years before present (ka). Morphological measurements of the preserved elements indicate that both of the mandibles likely belonged to immature and possibly yearling individuals. Collectively, these findings are among the oldest occurrences of gray whales in the North Atlantic basin, and their presence at temperate latitudes provides limited support for the hypothesis that Atlantic gray whales used a southerly breeding area at the end of a migratory pathway, by analog with lagoonal breeding environments of Baja California, Mexico, for the extant California gray whales, and the breeding areas for the extant North Atlantic right whales (*Eubalaena glacialis*) off the Georgia coast today. Stronger support for this latter contention may stem from future fossil discoveries in the region, as well as ancillary lines of evidence, such as the remains of species-specific ectoparasites and/or ancient DNA (aDNA).

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1. Introduction

Gray whales (*Eschrichtius robustus*) are abundant members of modern cetacean communities in the eastern North Pacific Ocean. Their current population size (~22,000 individuals) represents the legacy of successful conservation practices during the mid-late 20th century, which protected this population after it was decimated by pelagic whaling in the late 19th and early 20th centuries (Rice and Wolman, 1971; Clapham et al., 1999; Reeves and Smith, 2006; Alter et al., 2007). Eastern or Californian gray whales range in the North Pacific along their migratory path from Baja California to the Bering and Chukchi seas near Alaska (Rice and Wolman, 1971), where they feed on seasonally abundant benthic invertebrate communities. A much smaller population of western gray whales, numbering <200 individuals, occurs between the coast of China and the Sea of Okhotsk, in the Western Pacific Ocean. Calculations of the gray whale pre-whaling abundances,

however, conflict by an order of magnitude with estimates of population size based on genetic evidence (Alter et al., 2007; Palsbøll et al., 2007).

Interestingly, gray whales were not always limited to coastal habitats of the North Pacific basin. The type specimen of *Eschrichtius robustus* is based on a partial skeleton excavated from Holocene sand deposits in Gräsö, Sweden (Liljeborg, 1867). At the time of its discovery, this skeleton was unique among the known morphological diversity of large cetaceans because the first comprehensive natural history accounts of cetaceans from the North Pacific Ocean did not yet exist (Scammon, 1874). Once the osteology of living gray whales from the western and eastern gray whales was documented, the identity of the Gräsö specimen became clear (van Deinse and Junge, 1937; Cederlund, 1938). After this morphological elucidation, the former distribution of gray whales in the North Atlantic basin has been substantiated by historical accounts and Holocene remains from Florida, New Jersey, Iceland, and coastlines around the North and Baltic seas (Mead and Mitchell, 1984; Bryant, 1995; Lindquist, 2000; Post, 2005). This broad, largely post-glacial range suggests that Atlantic gray whales migrated long distances to feed and breed, in an analogous fashion to the well-documented migration of gray whales in the North Pacific

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basin. Rice and Wolman (1971:20) proposed that Atlantic gray whales used temperate latitudes for breeding, and migrated northward, especially to coastal areas of the Baltic Sea, which possesses the same benthic shelf prey items (e.g., ampeliscids) that North Pacific gray whales feed on in the Bering and Chukchi seas (Nerini, 1984). It is likely that human hunting played a significant role in the extirpation of North Atlantic gray whales, based on the youngest written accounts from several hundred years ago (Mead and Mitchell, 1984), although the timing and pattern of their demise have not been elucidated.

Beyond the historical (i.e., written) records and isolated Holocene remains of Atlantic gray whales, the antiquity of gray whales in the fossil record is sparsely represented. Fossils belonging to the genus Eschrichtius have been reported from middle Pleistocene and late Pliocene of California and Japan, respectively, but they both consist of single individual specimens represented by crania and associated postcranial elements (Barnes and McLeod, 1984; Ichishima et al., 2006; respectively). Fossils referred to the family Eschrichtiidae have been reported from the late Pliocene Lee Creek mine (Whitmore and Kaltenbach, 2008), late Pliocene of the San Diego Formation (Deméré et al., 2005), as well as described material re-classified as belonging to Eschrichtiidae from the Mio-Pliocene of Italy, in the Mediterranean basin (Bisconti and Varola, 2006; Bisconti, 2008). These fossils broadly confirm that the nearest extinct relatives of living gray whales had geographic distributions far outside the North Pacific basin, although they reveal little about the evolution of their very specialized feeding ecology in Eschrichtius (Johnston et al., 2010).

Given the reported stratigraphic range for Eschritius (~3.9–2.6 Ma to present), it is clear that this lineage survived drastic changes in the availability and distribution of benthic prey resources. The eustatic sea-level at glacial maxima during the Pleistocene likely resulted in prey-switching and restricting their migration routes (Pyenson and Lindberg, 2011). In this view, fossil remains that pre-date the Last Glacial Maximum (LGM; ~18–20 ka) are especially important for testing such ecological hypotheses. Here, we report new fossil material belonging to Eschrichtius robustus, based primarily on two specimens recovered from different localities of a late Pleistocene deposit below JY Reef, approximately 32 kilometers (km) offshore of St. Catherine's Island, Georgia, U.S.A., in 2008 and 2010 (Noakes et al., 2009).

In 2008, our project team members recovered an incomplete gray whale left mandible embedded in a Pleistocene shell bed, requiring extensive underwater excavation prior to recovery. In 2010, additional mandibular fragments were recovered at a separate locality at JY Reef, near the original mandible locality, later identified as another left mandible, which thus belonged to a different individual. Recently, Garrison et al. (2012) described some of the Pleistocene material from JY Reef, but they provided an equivocal assessment of its morphology and taxonomic identification. Here we provide a robust diagnosis of the identity of the 2008 specimen, describe additional material recovered in 2010, and discuss the implications for their age on understanding the paleoecology of gray whales.

2. Materials and methods

2.1. Institutional abbreviations

GMNH, Georgia Museum of Natural History, Athens, Georgia, U.S.A.; USNM, Division of Mammals, Department of Vertebrate Zoology and Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, U.S.A.

2.2. Locality and discovery

Fossil material derives from JY Reef (31° 36.11′N and 80° 47.47′W; Fig. 1), an active benthic reef community located approximately 18 km north of Gray's Reef National Marine Sanctuary (GRNMS) and about 32 km east of St. Catherine's Island, offshore Georgia, U.S.A. This material was recovered as part of a multi-year collaborative effort to study the surficial geology, invertebrate and vertebrate paleontology and the effects of erosion at GRNMS, organized by researchers from the University of Georgia, Athens (UGA) and National Oceanic and Atmospheric Administration (NOAA). Whereas the seafloor of GRNMS is composed of dolomitic sandstone outcrops approximately 2–3 million years old (Ma), JY Reef is located on an exposure of the Pleistocene age Satilla Formation, a partially cemented reddish brown to gray quartz sand (Huddleston, 1988; Leeth, 1999). JY Reef is formed by a relatively small ledge and hard bottom system oriented along a north–south axis, at a water depth of approximately 20 m. The reef structure was once a thriving shell bed that has been dated by accelerator mass spectrometry (AMS) and optical stimulated luminescence (OSL) to a range of 30 k–42 k ka. The reef structure is at least 1 m thick and consists mainly of sea scallops (Placopecten magellianicus) that represent a more near shore setting than the current water depth (Garrison et al., 2008). The shell bed at JY Reef is lightly cemented from the seafloor surface, down to approximately 0.3 to 0.5 m, below in which it is more readily eroded. Bottom currents sweeping along the reef have undercut the softer layers of the shell bed, leaving the harder cemented shell bed as exposed ledges. In some cases, sections of these ledges have broken and fallen to the seafloor. Ongoing erosion at JY Reef has uncovered objects buried in the reef structure, including small, unidentifiable bone fragments that have been collected at random in the past. Noakes et al. (2009) reported a rostral fragment referred to Tursiops truncatus (bottlenose dolphins). Larger bone fragments and diagnostic cetacean vertebrae (GMNH 27370 and GMNH 27373) have been recovered, but remain taxonomically indeterminate. The largest vertebra (GMNH 27370) recovered from JY Reef, likely a mysticete post thoracic vertebra, was 19.2 cm in length, 19.0 cm in width and 18.0 cm in height.

The fossil material reported here was first discovered by our project team in 2006, when divers observed a long (>1 m), slightly curved bony element (now GMNH 27372) that was mostly embedded in the compacted silt and shell (Fig. 2A). Initial light excavation by hand revealed that this element did extend solidly into the reef bed, and it was preliminarily identified as belonging to a large baleen whale (crown Mysticeti), based on the known occurrences of modern Eubalaena glacialis (North Atlantic right whales) in the reef's waters. From 2007 to 2008, excavation of this site was conducted by scientific divers from UGA, NOAA, Georgia Institute of Technology (GT), and Georgia Southern University (GSU), under permits from the United States Army Corps of Engineers. A team of 9 divers completing a total of 124 dives removed fossil material by hand from beneath the overhanging ledges and hard reef substrate that covered skeletal material. GMNH 27372, a left mandible, was recovered in 2008, in several sections, after the discovery site was documented using photographs and video. Each section of the mandible was carefully removed and placed in a mesh bag, attached to a line, and then floated to the NOAA vessel at the water surface.

In 2010, the team discovered more fossil material (GMNH 27375, Fig. 2B) approximately 170 m northwest of the original mandible site and approximately 100 m from the nearest ledge outcrop. These three fragments were resting at a water depth of 21.5 m on a sandy seafloor. The first two fragments, which were long (each ~50–100 cm by 13–15 cm), but narrow were found in a linear arrangement and later reassembled by matching the breakpoints. The fragments were loosely buried by sand, which was swept away by hand fanning and excavated using light tools, before being placed in a mesh bag and carried to the surface. Later, a third fragment, buried in compact sand and silt, was discovered partially protruding into the trench of the first two fragments, resting horizontally in the sand and turned approximately 90° from where the first fragments were recovered. As with the other fragments, it was excavated in pieces, placed in a mesh bag and sent to the surface. We searched a 20 m² area around the site where GMNH 27375 was discovered and we found no additional bone fragments.
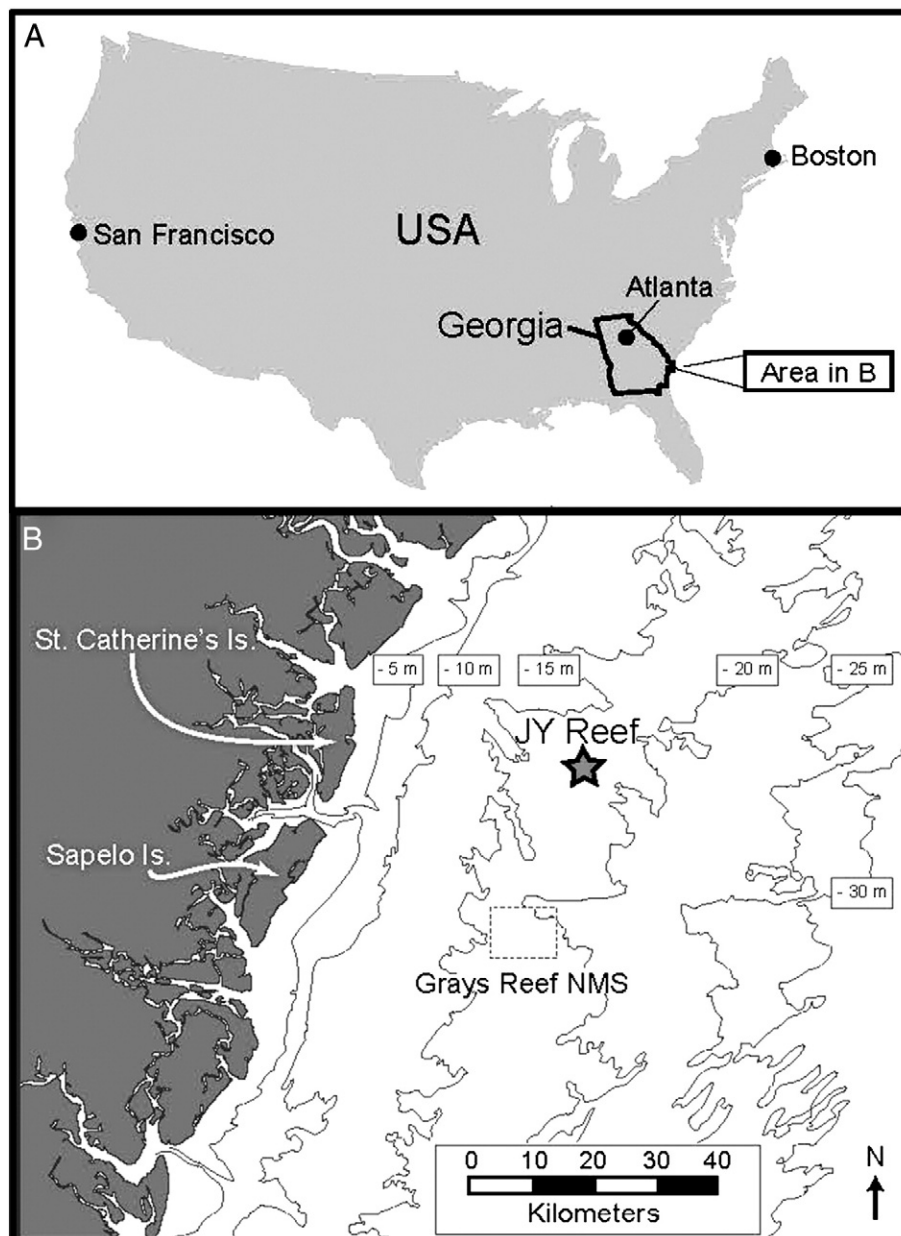
Fig. 1. Localities off-shore Georgia, U.S.A., for fossil gray whale specimens described herein.

Both discovery sites were documented using photographs and video prior and subsequent to excavation and these records were archived at the University of Georgia. Once back at the laboratory, all bone fragments were soaked for approximately 1 month in fresh water to remove the chloride salts from the saturated bone. The fresh water was replaced regularly and residual sediment was removed from the bone revealing the natural surface. Once cleaned, the bones were allowed to air dry prior to fitting in a sandbox with Acryloid B-72. See Noakes et al. (2009) for further discussion of permitting jurisdiction and excavation techniques.

3. Results

3.1. Radiometric dating and age

Previously, Garrison et al. (2008) collected *in situ* shell bed material from JY Reef, which yielded accelerator mass spectrometry (AMS) radiometric dates of 30–42 ka. The 500 kilovolt (kV) AMS at the University of Georgia's Center for Applied Isotope Studies (CAIS) is capable of

processing milligram sample weights with a typical precision of $\pm 0.5\%$. In order to remove contaminants introduced by the marine environment, samples from both mandibles were treated with acetic acid. Further treatment with hydrochloric acid was required to release carbon dioxide from the bioapatite in the sample. The carbon dioxide was then converted to graphite which was analyzed by AMS. The first mandible discovered at JY Reef, GMNH 27372 was determined to be 41,030 years old (calibrated date utilizing CALIB, Rev 6.0.0; 95% confidence at 2 sigma; Stuiver and Reimer, 1993; see also Garrison et al., 2012: Table 1 for radiometric age). The second mandible, GMNH 27375, was covered in multiple oyster shells that had grown on the bone surface. These shells were also prepared using dilute hydrochloric acid to remove contamination. The shell was then treated with phosphoric acid to produce carbon dioxide which was then converted into graphite and analyzed. Although the specimen itself was too permineralized to permit AMS dating, the oyster shells were AMS dated to 48,340 years old (calibrated date utilizing CALIB, Rev 6.0.0; 95% confidence at 2 sigma; Stuiver and Reimer, 1993). The latter dated age is nearing the upper range of AMS capabilities, but the CAIS AMS is capable of accurately dating upwards of 55 ka.
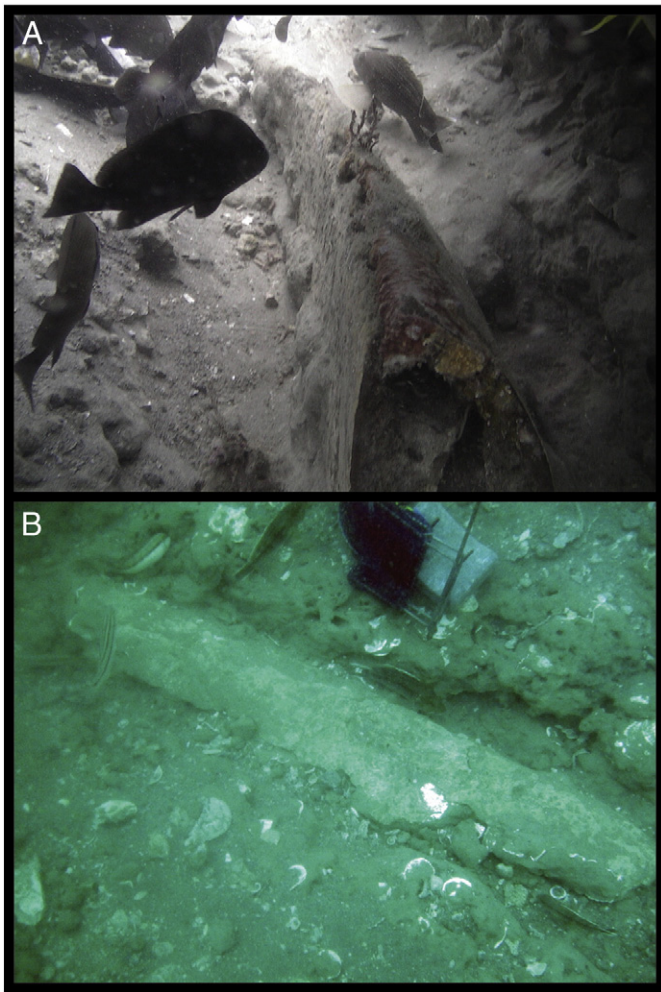
Fig. 2. Underwater photographs of A) GMNH 27372 and B) GMNH 27375 during excavation in 2008 and 2010, respectively.

3.2. Taphonomic observations

The decay and decomposition of marine mammals have been topics of study since Weigelt (1989)'s seminar work in the early twentieth century, although there have only been a handful of case studies that have investigated the actualistic taphonomy of marine mammals in a quantitative or operational manner (Schäfer, 1972; Liebig et al., 2003, 2007; also see discussion in Pyenson, 2010). In a landmark work, Schäfer (1972) outlined a general pathway for the drift, decay and final burial of cetacean carcasses in a nearshore environment, based on observations of small odontocetes in the North Sea. Allison et al. (1991) provided a primary account of the fate of cetacean carcasses on the seafloor at bathymetric depths, but this depositional setting is distal from the shallow shelf that preserved the gray whale specimens herein. Following Schäfer (1972), we surmise that the skeletal elements from both individual gray whales recovered from different localities at JY Reef were disarticulated from their source carcasses.

The postmortem encrustation of Pleistocene oysters on the bone surface of GMNH 27375 indicates a prolonged period of exposure on seafloor prior to burial. The absence of such oysters for the geochronologically younger GMNH 27372 suggests that it rested for a shorter duration of seafloor exposure prior to burial by a protective sediment layer. The bone surfaces of GMNH 27375 and 27372 are both highly abraded and weathered (see Behrensmeyer, 1978; Fiorillo, 1988, respectively), which broadly correspond to those for mammalian bone in terrestrial settings. For example, the posterior or proximal end

of the GMNH 27372 is missing the angular and articular condyles, along with much of the periosteum, leaving exposed cortical bone in posterior view (Fig. 3). However, the rounded and highly fragmented surfaces of GMNH 27375 provide further evidence that these remains were exposed for a longer period of time on the seafloor.

3.3. Comparative morphology

Although the material is abraded, worn and fragmentary, we diagnose GMNH 27372 and GMNH 27375 as belonging to *Eschrichtius* based on primarily the lack of prominent lateral curvature in the mandibular ramus anterior of the coronoid process, which typifies both extant Balaenopteridae and Balaenidae (Pyenson et al., 2013). Although both abraded and fragmentary, there is no evidence on either specimen for a tabular or projecting coronoid process, observed in Balaenopteridae (Pyenson et al., 2013). Also, the aperture of the mandibular foramen in GMNH 27372 is an exact match for USNM *Eschrichtius* specimens in side-by-side comparisons, and GMNH 27375 possesses anterior margin of the elongate lingual surface of the angular condyle, which extends to the level of the coronoid process (Fig. 5B). Lastly, as Garrison et al. (2012) noted, GMNH 27372 lacks a patent, J-shaped mylohyoid sulcus on ventrolingual surface of mandible, which is a diagnostic feature in all Balaenidae (Bisconti, 2008; Deméré et al., 2008), and GMNH 27375 lacks these features as well. Because extant *Eschrichtius* is monotypic, there is no *a priori* reason to exclude the assignment of this material to the extant species, *Eschrichtius robustus*.

GMNH 27372, the specimen recovered in 2008, is an incomplete left mandible, consisting of a mandibular corpus that is missing its anterior termination, but it is relatively complete posteriorly through the mandibular foramen, despite missing the cortical surfaces of the angular and articular condyles (Fig. 3). Its preserved but incomplete chord length along the ventral margin is 137.5 cm. An alveolar groove of about 60 cm is patent along the dorsal margin of the mandibular corpus, although it is slightly wider from postmortem expansion, as compared with extant examples. A plaster cast of the specimen is deposited in the Department of Paleobiology at the National Museum of Natural History, Smithsonian Institution as USNM 546122.

In mysticetes, the maximum cross-sectional dimension of the mandibular corpus is located roughly at the midpoint along its anteroposterior axis, which is preserved in GMNH 27372. At this plane, the maximum dorsoventral distance for GMNH 27372 is 19 cm, the maximum lingual–lateral distance is 10 cm, and the circumference is 51.1 cm. Because of its diagnostic morphology, we compared its morphometrics with those of extant gray whales, and we conducted a simple linear regression using a dataset of complete gray whale mandibles with total length (TL; see Pyenson and Sponberg, 2011, for a discussion) against circumference using JMP Version 9 (SAS Institute Incorporated 2010). Specimens included a range of ontogenetic stages, from juvenile and immature individuals to mature adults, following methods outlined by Pyenson et al. (2013). The resultant linear regression produced a high R^2 value (0.92; see Fig. 4), which permitted us to estimate that GMNH 27372 was 9.51 m in total length, forgoing detailed analyses of error (Pyenson and Sponberg, 2011; Pyenson et al., 2013). Given that newborn calves are 4.9 m and this total length value falls below those of sexually mature males and females (generally, >10–11 m in TL; see Rice and Wolman, 1971:46–51), it suggests that GMNH 27372 was older than a newborn, but sexually immature when it died.

GMNH 27375, the second specimen, which was recovered in 2010, consists of the incomplete and non-overlapping lingual and lateral cortical surfaces of a left mandible (Fig. 5). A 20 m diameter area was searched around the discovery site with no other bone fragments discovered. This led the team to believe that these fragments were that of a mandible that had broken apart over time. A defining fragment (Fig. 5C), which preserves the left lateral surface, is approximately
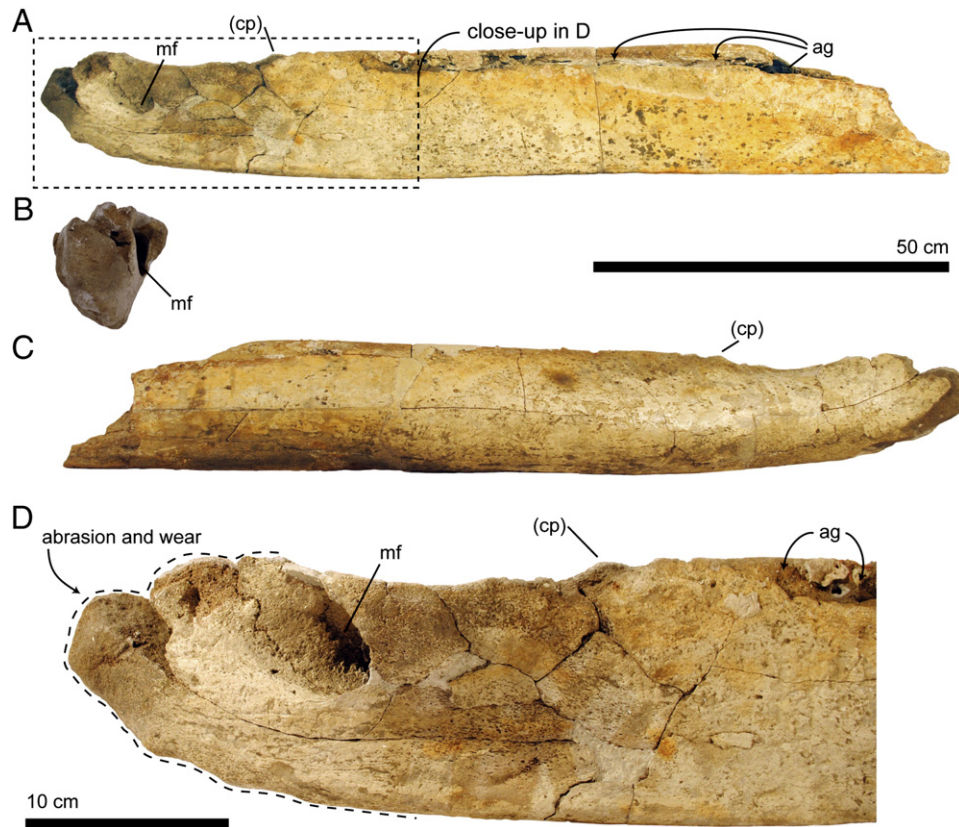
Fig. 3. GMNH 27372, an incomplete left mandible referred to *Eschrichtius robustus*, in A) medial, B) posterior, and C) lateral views, with D) showing a close-up of the posterior end of the mandible in medial view. The mandible was recovered from the JY Reef locality. Anatomical abbreviations: ag, alveolar groove; (cp), position of the coronoid process, which is not preserved; mf, mandibular foramen.

91 cm in anteroposterior length and 18 cm in maximum dorsoventral extent. This specimen consists of a mandibular corpus from roughly the transverse position of the coronoid process to the anteromedial curvature of the distal end of the mandible. A separate, unconnected fragment of this specimen, roughly 105 cm in length, preserves a lingual counterpart to the aforementioned lateral surface, and its broadly sinusoidal surface appears to preserve the more posterior aspect of this mandible (Fig. 5B). Additional fragments represent elements that surround the latter portion of the mandible, as the most diagnostic

features of the bone reflect the internal surface of the mandibular foramen. Given these overall similarities, and the lack of additional fragments in the vicinity, we assume that they all belong to the same individual. GMNH 27375 does not preserve sufficiently intact morphological features for measurements, but the aggregate of its fragment broadly falls within the same size range as the GMNH 27372, which suggests that this second, geochronologically older individual gray whale was also sexually immature at the time of its death, and measured between 9 and 10 m in total length.

4. Discussion

With Pleistocene eustatic sea-level changes, the physical locality of JY Reef has experienced multiple submergence and subaerial exposure over the past 1 Ma (Miller et al., 2005; Rohling et al., 2009; Thomas et al., 2009), and these changes also altered the depositional setting at JY Reef. The two gray whale specimens reported here, radiometrically aged to 41 ka and 48 ka, provide two separate indications that the general area of JY Reef was submerged at this time. The strong differences in Plio–Pleistocene climatic eustatic sea-level change models (Stocker and Marchal, 2000; Müller et al., 2008; Rohling et al., 2009) show a wide range of possible sea-level ranges during the late Pleistocene. While some models show sea-level at JY Reef to be very similar to that of today (Chabreck, 1988), others show JY Reef to be a dry land (Dodge et al., 1983; Cutler et al., 2003). In all likelihood, based on current models, we think that JY Reef was a shallow shell bed, located very near the shore at the times that the two gray whales died.

It seems unlikely that random attrition would account for the preservation of two Atlantic gray whales living approximately 7 k years apart, in the same general vicinity (approximately 170 m apart). Grays Reef National Marine Sanctuary, located approximately 20 km south of JY Reef and within the same approximate water depths has been
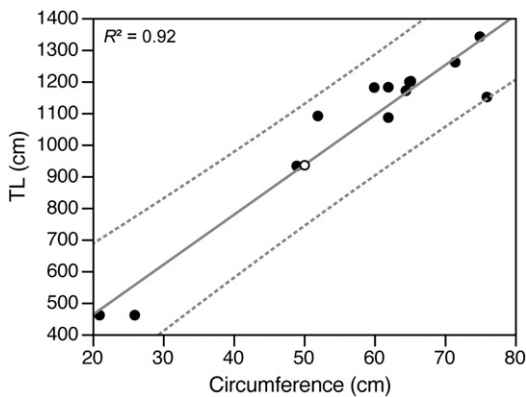
Fig. 4. Bivariate plot of total length (TL) versus mandibular circumference (IR) at its maximum diameter along the mandibular corpus for selected specimens of gray whales (black dots). Plot of GMNH 27372 (white dot) along the regression is based on its IR value. Dashed lines represent the 95% confidence level. See Pyenson and Sponberg (2011) for a discussion of TL. Data source from a large unpublished dataset for extant mysticete mandibular morphometrics (Goldbogen and Pyenson, unpublished observations).
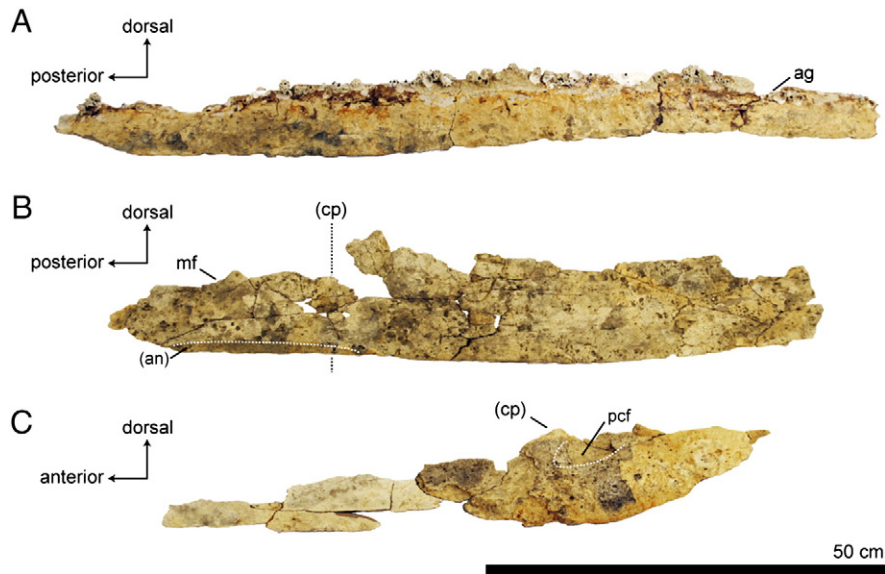
Fig. 5. GMNH 27375, representing non-articulating fragments of the corpus of a separate left mandible, referred to *Eschrichtius robustus*. A) Dorsal fragment, viewed lingually, preserving the dorsal margin of the alveolar groove; B) posterior fragment from the lingual surface, viewed lingually; C) posterior fragment from the lateral surface, viewed laterally. Anatomical abbreviations: (an), surface of the angular condyle; ag, alveolar groove; (cp) position of the coronoid process, which is not preserved, denoted by a dashed line; mf, mandibular foramen.

extensively mapped by research divers. The sanctuary covers approximately 35.5 km^2 with no whale remains having been discovered at this site. Is it possible that these fossils represent a terminus record of Atlantic gray whale migration at JY Reef or at least an area of importance to the whales? Extant eastern or California gray whales migrate approximately 8000 km annually from the lagoonal embayments of western and eastern Baja California to the Bering and Chukchi seas, and rarely departing from a few kilometers offshore (Rice and Wolman, 1971; Russell, 2001; Barrett-Lennard et al., 2011). Presumably, extinct populations of Atlantic gray whales had similar migratory routes along the eastern North American coast. If so, this migratory route may be inferred from Pleistocene and Holocene sites that extend, in maximum geographic range, from Jupiter Island, Florida to Southampton, New York (Mead and Mitchell, 1984), excluding anecdotal accounts of putative gray whales further northward to Canada and Iceland (Ellis, 2003). In this regard, JY Reef would have been close to the southern end of the western Atlantic gray whale migratory path.

Given annual mortality rates (~5%) of extant gray whales along the eastern Pacific migratory route (Wade and DeMaster, 1996), it is not surprising to find accounts of gray whale remains along their migration route. For example, gray whales feature prominently among the large mysticete carcasses that have been documented from the abyssal seafloor (Smith, 2006), where they serve as the foundation for deep-sea whalefall communities, although human hunting during the 19th and 20th centuries likely reduced the rate and extent of annual attrition (Alter et al., 2007). Based on mortality and strandings rates, Smith (2006) argued that the seafloor will be the end destination of the majority of gray whale mortalities, although the persistence of such carcasses may differ based on scavenging, depositional environment, and whalefall community turnover. The notion that the seafloor adjacent to long coastlines samples cetacean diversity is reinforced by recent studies of the stranding record by Pyenson (2010, 2011), who demonstrated that the richness and abundances of cetacean strandings at decadal-scale temporal and continental-scale geographic sampling regimes can provide faithful measures of diversity in living communities.

Sanchez Pacheco (1998) and Le Boeuf et al. (2000) both noted that extant gray whale mortalities do occasionally accumulate, on an annual basis, in breeding lagoons of Baja California, although the causal mechanism for such a concentrated abundance of carcasses is not entirely clear, if at all singular (Gulland et al., 2005). Equally, not all

extant gray whales undertake the long-range annual migration: a non-migratory sub-population (~1% of the total population) persists near Washington State and Vancouver Island (Pike, 1962; Darling, 1984). Given these two examples, could JY Reef have represented a hub for resident Atlantic gray whales or, potentially, a southerly calving ground? In the former instance, the lack of benthic prey items associated with northern Bering and Chukchi feeding grounds would not have prevented gray whales from alternatively employing feeding modes observed by the resident gray whales of Vancouver Island (Pyenson and Lindberg, 2011). In the latter instance, there is currently insufficient data to properly evaluate why more than one gray whale was preserved at JY Reef, over the course of ~7 k years. The highly endangered North Atlantic right whales still use the coastal waters of Georgia as a southerly breeding ground (Kraus and Rolland, 2007), providing at least one modern analog for a migratory, large cetacean species along this same pathway today.

Mead and Mitchell (1984) reviewed the historical records of putative or cryptic gray whale sightings and strandings from North America and Iceland, and they argued that Atlantic gray whales persisted in the North Atlantic until the 17th century. This argument was bolstered by the addition of the youngest radiometric ages (275 ± 35 years old as dated in 1977) from vouchered Atlantic gray whale material (see also Bryant, 1995). The oldest radiocarbon dates for the collection reported by Mead and Mitchell (1984) was ~10 ka. Thus, the new material reported here, and that in Garrison et al. (2012), are the oldest documented occurrences of gray whales in the western Atlantic, and among the oldest diagnostic remains in the Atlantic Ocean Basin. Post (2005) and Aaris-Sørensen et al. (2010) both reported Pleistocene remains of gray whales from several localities in the eastern Atlantic that have been radiocarbon dated as old as ~42–45 ka, but the museum vouchers representing these records are isolated vertebrae (especially post-cervical ones) that may be undiagnostic for *Eschrichtius*, or may belong to other large mysticetes. Interestingly, fossil remains assigned to the family Eschrichtiidae have been reported from older marine deposits of late Pliocene and late Miocene age in Italy (see Introduction), extending the evolutionary history of this clade in the North Atlantic basin further back in geologic time than in the North Pacific basin, where the oldest diagnostic remains of *Eschrichtius* are from late Pliocene rocks on the island of Hokkaido, Japan (Ichishima et al., 2006).

Additional insights into the paleoecology of marine mammals – especially large cetaceans – may stem from two additional lines of evidence. First, advances in high output gene sequencing for molecular phylogenetics offer the possibility of analyzing genomic evidence from ancient DNA (aDNA) of Pleistocene and Holocene age mammals (de Bruyn et al., 2011). Marine mammals are especially promising in this regard because the depositional conditions of their remains include cold, oxygen-poor or very dry environments, unlike those for many terrestrial mammals. Although a novel field of investigation, thus far aDNA marine mammal studies have mostly focused on retrieving estimates for genetic diversity of extinct or extirpated populations concomitant with human exploitation and/or environmental change (Foote et al., 2012).

Second, some species of large baleen whales possess unique ectoparasites, including crustaceans whose hard parts do preserve well in the fossil record. Gray whales, for example, are the unique hosts of the barnacle species *Cryptolepas rhachianecti* (Bradford et al., 2011). Thus far, this taxon has no fossil record, but remains of this barnacle might be recovered from JY Reef with further investigation. Interestingly, Pleistocene fossils of another barnacle parasite, *Coronula diadema*, which is preferentially hosted (but not uniquely) by humpback whales (*Megaptera novaeangliae*), have been used to trace ancient migratory routes along South America and in the Mediterranean Sea (Bianucci et al., 2006). The inference that *Coronula* detaches from their hosts along migratory routes or in breeding areas (Bianucci et al., 2006) holds promise for finding such proxies at JY Reef and other localities.

5. Conclusion

In this paper, we provided a full account of late Pleistocene fossil material belonging to various cetaceans, including the remains from at least two individual gray whales discovered at JY Reef, offshore Georgia, U.S.A. Two localities at JY Reef yielded the remains of at least two individuals, both of which are diagnostic to extant gray whales, which are the first known examples of this taxon from the state of Georgia. This discovery of two individual gray whales, ~7 ka apart in geochronologic age, is unusual; the only other known location in the entire North Atlantic Ocean that has produced multiple individual gray whale remains is Corolla, North Carolina (see Mead and Mitchell, 1984: 77–78 for provenance history). Given that extant gray whales migrate from northern feeding areas to southern breeding sites, we argue that the Georgia coast possibly served as such breeding areas for now extinct Atlantic gray whales, in a manner analogous to the pathways used by North Atlantic right whales along the US eastern seaboard, from Florida to Maine. The geochronologic difference in the age of the two specimens suggests some persistence to such a breeding ground. We outline several lines of evidence that may test this suggestion more thoroughly in future studies. Overall, the age of these specimens implies the persistence of gray whales at temperate latitudes along eastern North America prior to the LGM.

Acknowledgments

References

Aaris-Sørensen, K., Rasmussen, K.L., Linze, C., Petersen, K.S., 2010. Late Pleistocene and Holocene whale remains (Cetacea) from Denmark and adjacent countries: species, distribution, chronology, and trace element concentrations. Mar. Mammal Sci. 26, 253–281.

Allison, P.A., Smith, C.R., Kukert, H., Deming, J.W., Bennett, B.A., 1991. Deep-water taphonomy of vertebrate carcasses: a whale skeleton in the bathyal Santa Catalina Basin. Paleobiology 17, 78–89.

Alter, S.E., Rynes, E., Palumbi, S.R., 2007. DNA evidence for historic population size and past ecosystem impacts of gray whales. Proc. Natl. Acad. Sci. U. S. A. 104, 15162–15167.

Barnes, L.G., McLeod, S.A., 1984. The fossil record and phyletic relationships of gray whales. In: Jones, M.L., Swartz, S.L., Leatherwood, S. (Eds.), The Gray Whale, *Eschrichtius robustus*. Academic Press, New York, pp. 3–28.

Barrett-Lennard, L.G., Matkin, C.O., Durban, J.W., Saulitis, E.L., Ellifrit, D., 2011. Predation on gray whales and prolonged feeding on submerged carcasses by transient killer whales at Unimak Island, Alaska. Mar. Ecol. Prog. Ser. 421, 229–241.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4, 150–162.

Bianucci, G., Landini, W., Buckeridge, J., 2006. Whale barnacles and Neogene cetacean migration routes. N. Z. J. Geol. Geophys. 49, 115–120.

Bisconti, M., 2008. Morphology and phylogenetic relationships of a new eschrichtiid genus (Cetacea: Mysticeti) from the Early Pliocene of northern Italy. Zool. J. Linnean Soc. 153, 161–186.

Bisconti, M., Varola, A., 2006. The oldest *Eschrichtius mysticete*: and a new morphological diagnosis of Eschrichtiidae (gray whales). Riv. Ital. Paleontol. Stratigr. 112, 447–457.

Bradford, A.L., Weller, D.W., Burdin, A.M., Brownell Jr., R.L., 2011. Using barnacle and pigmentation characteristics to identify gray whale calves on their feeding grounds. Mar. Mammal Sci. 27, 644–651.

Bryant, P.J., 1995. Dating remains of gray whales from the Eastern North Atlantic. J. Mammal. 76, 857–861.

Cederlund, B.A., 1938. A subfossil gray whale discovered in Sweden in 1859. Zool. Bidrag. Uppsala 18, 269–286.

Chabreck, R.H., 1988. Coastal Marshes: Ecology and Wildlife Management. University of Minnesota Press, Minneapolis (138 pp.).

Clapham, P.J., Young, S.B., Brownell Jr., R.L., 1999. Baleen whales: conservation issues and the status of the most endangered populations. Mammal Rev. 29, 35–60.

Cutler, K.B., Edwards, R.L., Taylor, F.W., Cheng, H., Adkins, J., Gallup, C.D., Cutler, P.M., Burr, G.S., Bloom, A.L., 2003. Rapid sea-level fall and deep-ocean temperature change since the last interglacial period. Earth Planet. Sci. Lett. 206, 253–271.

Darling, J.D., 1984. Gray whales off Vancouver Island, British Columbia. In: Jones, M.L., Swartz, S.L., Leatherwood, S. (Eds.), The Gray Whale *Eschrichtius robustus*. Academic Press, San Diego, pp. 267–287.

de Bruyn, M., Hoelzel, A.R., Carvalho, G.R., Hofreiter, M., 2011. Faunal histories from Holocene ancient DNA. Trends Ecol. Evol. 26, 405–413.

Deméré, T.A., Berta, A., McGowen, M.R., 2005. The taxonomic and evolutionary history of fossil and modern balaenopteroid mysticetes. J. Mamm. Evol. 12, 99–143.

Deméré, T.A., McGowen, M.R., Berta, A., Gatesy, J., 2008. Morphological and molecular evidence for a stepwise evolutionary transition from teeth to baleen in mysticete. Syst. Biol. 57, 15–37.

Dodge, R.E., Fairbanks, R.G., Benninger, L.D., Maurrasse, F., 1983. Pleistocene sea level from raised coral reefs of Haiti. Science 219, 1423–1425.

Ellis, R., 2003. Grays Whales in the Atlantic (Introduction). The Empty Ocean, Island Press, Washington, D.C.1-55963-974-1.

Fiorillo, A.R., 1988. Taphonomy of hazard homestead quarry (Ogallala Group), Hitchcock County, Nebraska. Contributions to Geology, 26. University of Wyoming, pp. 57–97.

Foote, A.D., Hofreiter, M., Morin, P.A., 2012. Ancient DNA from marine mammals: studying long-lived species over ecological and evolutionary timescales. Ann. Anat. 194, 112–120.

Garrison, E.G., McFall, G., Noakes, S.E., 2008. Shallow marine margin sediments, modern marine erosion and the fate of sequence boundaries, Georgia Bight (USA). Southeast. Geol. 45, 127–142.

Garrison, E.G., McFall, G., Cherkinsky, A., Noakes, S.E., 2012. Discovery of a Pleistocene mysticete whale, Georgia Bight (USA). Palaeontol. Electron. 15, 10p.

Gulland, F.M.D., Perez-Cortes, M., Urgan, R., Rojas-Bracho, R.L., Ylitalo, G., Weir, J., Norman, S.A., Muto, M.M., Rugh, D.J., Kreuder, C., Rowles, T., 2005. Eastern North Pacific gray whale (*Eschrichtius robustus*) unusual mortality event, 1999–2000. NOAA Technical Memorandum NMFS-AFSC-150. U.S. Department of Commerce, National Marine Fisheries Service (33 pp.).

Huddleston, P.F., 1988. A revision of the lithostratigraphic units of the coastal plain of Georgia—Miocene through Holocene. Georgia Geol. Surv. Bull. 104, 162 pp.

Ichishima, H., Sato, E., Sagayama, T., Kimura, M., 2006. The oldest record of Eschrichtiidae (Cetacean: Mysticeti) from the Late Pliocene, Hokkaido, Japan. J. Paleontol. 80, 367–379.

Johnston, C., Deméré, T.A., Berta, A., Yonas, J., St. Leger, J., 2010. Observations on the musculoskeletal anatomy of the head of a neonate gray whale (*Eschrichtius robustus*). Mar. Mammal Sci. 26, 186–194.

Kraus, S.D., Rolland, R.M., 2007. The Urban Whale: North Atlantic Right Whales at the Crossroads. Harvard University Press, Cambridge, MA (576 pp.).

Le Boeuf, B.J., Perez-Cortes, H.M., Urban, R.J., Mate, B.R., Ollervides, U.F., 2000. High gray whale mortality and low recruitment in 1999: potential causes and implications. J. Cetacean Res. Manage. 2, 85–99.

Leeth, D.C., 1999. Hydrogeology of the surficial aquifer in the vicinity of a former landfill, Naval Submarine Base Kings Bay, Camden County, Georgia. U.S. Geological Survey, Water-Resources Investigations Report 98-4246 (26 pp.).

Liebig, P.M., Taylor, T.-S.A., Flessa, K.W., 2003. Bones on the beach: marine mammal taphonomy of the Colorado Delta, Mexico. Palaios 18, 168–175.

Liebig, P.M., Flessa, K.W., Taylor, S.A., 2007. Taphonomic variation despite catastrophic mortality: analysis of a mass stranding of false killer whales (*Pseudorca crassidens*), Gulf of California, Mexico. Palaios 22, 384–391.

Liljeborg, W., 1867. On two subfossil whales discovered in Sweden. Nova Acta of the Royal Society of Sciences at Uppsala, Series III, VI (48 pp.).

Lindquist, O., 2000. The North Atlantic gray whale (*Escherichtius* [sic] *robustus*): an historical outline based on Icelandic, Danish–Icelandic, English and Swedish sources dating from ca 1000 AD to 1792. Occasional Papers 1. Universities of St. Andrews and Stirling, Scotland (50 pp.).

Mead, J.G., Mitchell, E., 1984. Atlantic gray whales. In: Jones, M.L., Swartz, S.L., Leatherwood, S. (Eds.), The Gray Whale, *Eschrichtius robustus*. Academic Press, Inc., New York, pp. 33–53.

Miller, K.G., Kominz, M.A., Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E., Sugarman, P.J., Cramer, B.S., Christie-Blick, N., Pekar, S.F., 2005. The Phanerozoic record of global sea-level change. Science 310, 1293–1298.

Müller, R.D., Sdrolias, M., Gaina, C., Steinberger, B., Heine, C., 2008. Long-term sea-level fluctuations driven by ocean basin dynamics. Science 319, 1357–1362.

Nerini, M., 1984. A review of gray whale feeding ecology. In: Jones, M.L., Swartz, S.L., Leatherwood, S. (Eds.), The Gray Whale, *Eschrichtius robustus*. Academic Press, New York, pp. 423–450.

Noakes, S.E., Garrison, E.G., McFall, G.B., 2009. Underwater paleontology: recovery of a prehistoric whale mandible offshore Georgia. In: Pollack, N.W. (Ed.), Diving for Science. Proceedings of the American Academy of Underwater Sciences, Dauphin Island, AL, pp. 245–251.

Palsbøll, P.J., Bérubé, M., Larsen, F., 2007. Could genetic diversity in eastern North Pacific gray whales reflect global historic abundance? Proc. Natl. Acad. Sci. U. S. A. 104, E2.

Pike, G.C., 1962. Migration and feeding of the gray whale (*Eschrichtius gibbosus*). J. Fish. Res. Board Can. 19, 815–838.

Post, K., 2005. A Weichselian marine mammal assemblage from the southern North Sea. Deinsea 11, 21–27.

Pyenson, N.D., 2010. Carcasses on the coastline: measuring the ecological fidelity of the cetacean stranding record in the eastern North Pacific Ocean. Paleobiology 36, 453–480.

Pyenson, N.D., 2011. The high fidelity of the cetacean stranding record: insights into measuring diversity by integrating taphonomy and macroecology. Proc. R. Soc. B: Biol. Sci. 278, 3608–3616.

Pyenson, N.D., Lindberg, D.R., 2011. What happened to gray whales during the Pleistocene? The ecological impact of sea-level change on benthic feeding areas in the North Pacific Ocean. PLoS ONE 6 (7), e21295.

Pyenson, N.D., Sponberg, S.N., 2011. Reconstructing body size in extinct crown Cetacea (Neoceti) using allometry, phylogenetic methods and tests from the fossil record. J. Mamm. Evol. 18, 269–288.

Pyenson, N.D., Goldbogen, J.A., Shadwick, R.E., 2013. Mandible allometry in extant and fossil Balaenopteridae (Cetacea: Mammalia): the largest vertebrate skeletal element and its role in rorqual lunge-feeding. Biol. J. Linn. Soc. 108, 586–599.

Reeves, R.R., Smith, T.D., 2006. A taxonomy of world whaling. Operation and eras. In: Estes, J.A., Demaster, D.P., Doak, D.F., Williams, T.M., Brownell Jr., R.L. (Eds.), Whales, Whaling, and Ocean Ecosystems. University of California Press, Berkeley, pp. 82–101.

Rice, D.W., Wolman, A.A., 1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). Am. Soc. Mammal. Spec. Publ. 3, 1–142.

Rohling, E.J., Grant, K., Bolshaw, M., Roberts, A.P., Siddall, M., 2009. Antarctic temperature and global sea level closely coupled over the past five glacial cycles. Nat. Geosci. 2, 500–504.

Russell, D., 2001. Eye of the Whale, Epic Passage from Baja to Siberia. Simon and Schuster, New York (662 pp.).

Sanchez Pacheco, J.A., 1998. Gray whale mortality at Ojo de Liebre and Guerrero Negro lagoons, Baja California Sur, Mexico: 1984–1995. Mar. Mammal Sci. 14, 149–155.

Scammon, C.M., 1874. The Marine Mammals of the North-western Coast of North America, Described and Illustrated: Together with an Account of the American Whale-fishery. John H. Carmany, San Francisco.

Schäfer, W., 1972. Ecology and Palaeoecology of Marine Environments. The University of Chicago Press, Chicago (568 pp.).

Smith, C.R., 2006. Bigger is better: the role of whales as detritus in marine ecosystems. In: Estes, J., DeMaster, D.P., Doak, D.F., Williams, T.M., Brownell Jr., R.L. (Eds.), Whales, Whaling and Ocean Ecosystems. California University Press, Berkeley, CA, pp. 286–302.

Stocker, T.F., Marchal, O., 2000. Abrupt climate change in the computer: is it real? Proc. Natl. Acad. Sci. U. S. A. 97, 1362–1365.

Stuiver, M., Reimer, P.J., 1993. Extended 14C database and revised CALIB radiocarbon calibration program. Radiocarbon 35, 215–230.

Thomas, A.L., Henderson, G.M., Deschamps, P., Yokoyama, Y., Mason, A.J., 2009. Penultimate deglacial sea-level timing from Uranium/Thorium dating of Tahitian corals. Science 324, 1186–1189.

van Deinse, A.B., Junge, G.C.A., 1937. Recent and older finds of the California gray whale in the Atlantic. Temminckia 2, 161–188.

Wade, P.R., DeMaster, D.P., 1996. A Bayesian analysis of eastern Pacific gray whale population dynamics. Unpublished doc. Submitted to International Whale Commission (SC/48/AS3), 21 pp.

Weigelt, J., 1989. Recent Vertebrate Carcasses and Their Paleobiological Implications (transl. by J. Schaefer). University of Chicago Press, Chicago, IL.

Whitmore Jr., F.C., Kaltenbach, J.A., 2008. Neogene Cetacea of the Lee Creek Phosphate Mine, North Carolina. In: Ray, C.E., Bohaska, D.J., Koretsky, I.A., Ward, L.W., Barnes, L.G. (Eds.), Geology and Paleontology of the Lee Creek Mine, North Carolina, IV. Virginia Museum of Natural History Special Publication, 14, pp. 181–269.