A review of Mediterranean whale species

Supplementary materials to:

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Introduction

We follow the common usage of the term “whale” to refer to large marine mammals in order Cetacea, including all of those in sub-order Mysticeti (baleen whales) and the larger species in sub-order Odontoceti (toothed whales). The latter sub-order also includes dolphins and porpoises, which are not treated here.

We review eight species of whale that are currently found in the Mediterranean Sea (including the Strait of Gibraltar area; Supplementary Figure 1) and two which might have plausibly regularly occurred there in the past. The eight species are those classified by Reeves & Notarbartolo di Sciara (2006) as either “regular” (with year-round populations: fin whale, long-finned pilot whale, sperm whale, Cuvier’s beaked whale, and killer whale,) or “visitors” (that do not reproduce in the Mediterranean but which regularly occur within its boundaries: common minke whale, humpback whale, false killer whale). In contrast, (Coll et al. 2010) classified only the first four species (fin whale, long-finned pilot whale, sperm whale, Cuvier’s beaked whale) as “residents” and all others (killer whale, common minke whale, humpback whale, false killer whale) as “transients”, since killer whales are regularly found only in the Strait of Gibraltar. Two additional species that we consider likely to have occurred in the past are the gray whale (currently absent from the Mediterranean) and the North Atlantic right whale (classified by Reeves & Notarbartolo di Sciara 2006 as “vagrant”, i.e., found only occasionally; and by (Coll et al. 2010] as “transient”).

There are six other whale species that have been recorded very sporadically in the Mediterranean (classified as “vagrants” by Reeves & Notarbartolo di Sciara 2006)] and as “transients” by (Coll et al. 2010), which we do not treat here: the Sei whale (Balaenoptera borealis), a rorqual of intermediate size between the minke and the fin whales; the dwarf sperm whale (Kogia sima), a small relative of the sperm whale; and four species of beaked whales (family Ziphiidae), the northern bottlenose whale (Hyperoodon ampullatus), Sowerby’s beaked whale (Mesoplodon bidens), Blainville’s beaked whale (Mesoplodon densirostris), and Gervais’ beaked whale (Mesoplodon europaeus). All of these are pelagic species, i.e., that use open, offshore waters (Wilson & Mittermeier 2014) and therefore unlikely to have been exploited in antiquity other than the rare stranded individual.

The ten species reviewed here are organised into three types, corresponding to three main sections in this document:

Section 1. Species that could have been actively exploited (if regularly present in reasonable abundances)

1.1. Humpback whale, Megaptera novaeangliae

1.2. North Atlantic right whale, Eubalaena glacialis

1.3. Gray whale, Eschrichtius robustus
Section 2. Species that could have been occasionally or locally exploited

2.1. Sperm whale, *Physeter macrocephalus*

2.2. Killer whale, *Orcinus orca*

2.3. Long-finned pilot whale, *Globicephala melas*

Section 3. Species unlikely to have been actively exploited

3.1. Fin whale, *Balaenoptera physalus*

3.2. Common minke whale, *Balaenoptera acutorostrata*

3.3. False killer whale, *Pseudorca crassidens*

3.4. Cuvier’s beaked whale, *Ziphius cavirostris*

For each species, we provide a brief overview of their appearance, ecology, behaviour, history of exploitation, and presence in the Mediterranean Sea, finishing by discussing the likelihood that the species was the focus of ancient exploitation. We focus on details that may be particularly useful to historians and archaeologists. Information on appearance, ecology and behaviour was mainly obtained from Wilson & Mittermeier (2014); data on current presence in the Mediterranean Sea comes mainly from Reeves & Notarbartolo Di Sciara (2006) and (Coll et al. 2010).
Supplementary Figure 1. Mediterranean Sea, showing the locations mentioned in the text: 1) Strait of Gibraltar; 2) Gulf of Cadiz; 3) Sea of Alborán; 4) Balearic Islands; 5) Gulf of Lyon; 6) Ligurian Sea; 7) Corsica; 8) Sardinia; 9) Thyrrenian Sea; 10) Sicily; 11) Sicily Channel; 12) Strait of Messina; 13) Adriatic Sea; 14) Ionian Sea; 15) Crete; 16) Aegean Sea; 17) Levantine Sea; 18) Black Sea. Map image courtesy of the National Geophysical Data Center, NOAA (created by J. Varner and E. Lim, CIRES, University of Colorado at Boulder) from the ETOPO1 Ice Surface data (Amante & Eakins 2008). Shades of blue represent ocean depths and shades of green and brown represent dry land areas.
Section 1. Species that could have been actively exploited (if regularly present in reasonable abundances)

1.1. Humpback whale, Megaptera novaeangliae

Description

With a body length up to 17 meters and weighting up to 34 tonnes, it is shorter and stouter than the fin whale. The back is uniformly black whereas the ventral surface can be variably coloured, from black to white to moulted black and white. Its most distinctive features are the very large pectoral fins, up to 5 meters in length (Supplementary Figure 2A). These are white on the ventral surface and variably coloured (from black to white) in the dorsal surface, and have scalloped leading edges marked by fleshy tubercles incrusted with large barnacles. The dorsal fin is relatively small, located on a low fleshy lump that gives it its “humpback” nickname. The tail flukes are large, with the trailing edge visible serrated and incrusted by barnacles, often marked by scars (thought to result from unsuccessful attacks by killer whales), very visible when the whales dive. Ventral grooves are fewer and deeper than in other rorquals. The head has fleshy tubercles and barnacle incrustations (Wilson & Mittermeier 2014). Baleen plates are relatively short and broad, up to 100 cm in length, usually dark gray to black with white longitudinal strikes. The barnacles most usually found on humpback whales are Coronula diadema (up to 5 cm in diameter) and Conchoderma auritum; an individual humpback may carry as much as 450 kg of barnacles (Ford & Reeves 2008).

Ecology and behaviour

A cosmopolitan species, the humpback whale is found in all ocean basins (Supplementary Figure 2B). Like other rorqual species, it feeds by filtering prey from the water using its baleen plates, captured by gulping huge quantities of water into its extensible throat pouch. Favoured prey include small schooling fish (e.g., herring, capelin), planktonic crustaceans (e.g. krill) and, less commonly, benthonic species (amphipods). Feeding may be cooperative, with individuals using bubbles and calls to concentrate schooling fish (“bubble-net feeding”) before ascending to the surface in a synchronized “collective gulp”. The humpback whale is well known for its acrobatic displays that can involve full breaches, making it a favourite of whale-watching tourism. Reproductive behaviour involves visible water trashing and audible singing (Wilson & Mittermeier 2014).

Most populations are migratory, spending the summer in productive high-latitude feeding areas and the winters in warm breeding grounds. They are more coastal than fin and minke whales, particularly in the breeding grounds (usually near islands, banks and reefs) but also in the feeding grounds (usually near shelf-slope breaks, marine embankments and channels) and during near-coastal migrations. In the North Atlantic, their feeding grounds go as far north as the Labrador Sea, Greenland Sea, and Barents Sea and as far south as the Gulf of Maine and Ireland. The main breeding grounds are in West Indies, around Hispaniola (Wilson & Mittermeier 2014). Whaling records

indicate that the currently smaller breeding ground around the Cape Verde Islands might have been historically as important as the West Indies ground (Reeves et al. 2002). Genetic evidence suggests there may be a third, currently unknown, breeding and birthing area in the North Atlantic (Wilson & Mittermeier 2014).

Humpback whales are not particularly fast compared to other rorquals, but they are much more manoeuvrable. Whereas other rorquals respond to killer whales by swimming fast, humpbacks can use their flippers and flukes as weapons to defend themselves and their calves against attacks (Ford & Reeves 2008).

Supplementary Figure 2. Humpback whale, *Megaptera novaeangliae*. A) Main physical characteristics (illustration ©Uko Gorter). B) Global distribution (global range map from Reilly et al. 2008; feeding, breeding and year-round regions from National Park Service 2010). C) Known records in the Mediterranean region (sightings and strandings between 1885 and 2013 as listed in Supplementary Table 1; the three records in blue correspond to a multiple sightings of a single individual, as do the two records in yellow).
**Presence in the Mediterranean Sea**

The humpback whale is an occasional but increasingly regular visitor to the Mediterranean Sea (Supplementary Table 1). Indeed, we found only two known records prior to 1990, but six from 1990 to 1999, seven from 2000 and 2009, and ten from 2010 to 2013. Although this likely also reflects higher sampling effort, it seems to indicate a real increase in the use of the Mediterranean by this species either as the colonization of a new area or the recolonization of previous grounds (Simone Panigada et al. 2014; Frantzis et al. 2004).

There are observations in all months of the year, but mainly concentrated in the spring (March, April) and summer (July, August). Most of the observations are in the northern western basin (Ligurian Sea and Gulf of Lyon), in areas favoured by fin whales (Supplementary Figure 10C). For example among the recent observations, Panigada et al. (2014) reported an individual actively feeding in a main feeding ground for fin whales (off Lampedusa, Sicily Channel), where the latter species regularly preys on very abundant euphausiids species. This suggests that the Mediterranean Sea offers suitable feeding habitat for humpback whales.

Humpback whales are one of the three species (with right and gray whales) which we consider may have been regularly present in the Mediterranean Sea in the past. Indeed, humpbacks occurred historically in coastal Western Europe (Rondelet 1558) as well as in breeding grounds in Cape Verde (Smith et al. 2012), so the Mediterranean Sea would have been well within the reach of their migratory populations. If so, the depletion of this species in the North Atlantic through intensive whaling (see below) could explain its current rarity in the Mediterranean. The current population increase could then reflect the recovery of the North Atlantic population (from about 1,000 to about 20,000 individuals) following the end of whaling (Stevick et al. 2003). Nonetheless, the current North Atlantic population is believed to be very far from its historical levels and presumed carrying capacity (Fleming & Jackson 2011; Ruegg et al. 2012).

Although we have not found conclusive evidence for the presence of humpback whales in the Mediterranean in antiquity, the fact that they use sheltered coastal areas as winter calving grounds makes them (with right and gray whales) one of the possible species described by Pliny’s *Naturalis Historia* (NH, 9:12; translation by Bostock & Riley 1855) being attacked off Cadiz by killer whales when they came in the Winter Solstice to “retire and conceal themselves in some calm capacious bay, in which they take a delight in bringing forth”. We also suggest that humpbacks may correspond to the female ram-fishes described by Aelian (De Natura Animalium, 15:2; translated by Scholfield 1959) as spending the winter between Corsica and Sardinia, their ventral groves described as reminiscent of “cock wattles”.
**Supplementary Table 1.** Review of humpback whale records in the Mediterranean. Map reference numbers as in Supplementary Figure 2C.

<table>
<thead>
<tr>
<th>Ref.</th>
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<th>Location</th>
<th>Notes</th>
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</thead>
<tbody>
<tr>
<td>1</td>
<td>1885 (Nov)</td>
<td>Toulon (France)</td>
<td>A 6.8m individual by-caught</td>
<td>Aguilar (1989)</td>
</tr>
<tr>
<td>2</td>
<td>1986 (14 Mar)</td>
<td>Majorca, Baleares (Spain)</td>
<td>Sighting of two individuals, possibly a female with calf</td>
<td>Aguilar (1989)</td>
</tr>
<tr>
<td>3</td>
<td>1990 (Mar)</td>
<td>Bay of Aiguablava, Catalonia (Spain)</td>
<td>Sighting of one possible adult</td>
<td>Personal comm. from A. Aguilar to (Frantzis et al. 2004)</td>
</tr>
<tr>
<td>6</td>
<td>1993 (Aug)</td>
<td>Toulon (France)</td>
<td>Sighting of two individuals</td>
<td>Personal comm. from R. Sears to (Frantzis et al. 2004)</td>
</tr>
<tr>
<td>7</td>
<td>1998 (24 Jan)</td>
<td>Gulf of Oristano, W. Sardinia (Italy)</td>
<td>Sighting of a 7-8 m individual</td>
<td>(Frantzis et al. 2004)</td>
</tr>
<tr>
<td>8</td>
<td>1999 (12 Dec)</td>
<td>off Marbella, Málaga (Spain)</td>
<td>An individual ca. 10m, by-caught and released</td>
<td>Bellido et al. (2006)</td>
</tr>
<tr>
<td>9</td>
<td>2001 (17 Apr)</td>
<td>Bay of Tolo, Myrtoon Sea (Greece)</td>
<td>Sighting of a 8-11 m individual</td>
<td>Frantzis et al. (2004)</td>
</tr>
<tr>
<td>14</td>
<td>2004 (2 Apr)</td>
<td>Siracusa, Sicily (Italy)</td>
<td>A ca. 10m individual, by-caught alive and released</td>
<td>Centro Studi Cetacei (2006), in Reeves &amp; Notarbartolo Di Sciara (2006)</td>
</tr>
<tr>
<td>15</td>
<td>2009 (10 Feb – mid April)</td>
<td>Gulf of Trieste (Italy, Slovenia)</td>
<td>Young individual (ca. 10-12 meters) observed repeatedly (photographed)</td>
<td>Genov et al. (2009)</td>
</tr>
<tr>
<td>16</td>
<td>2010 (27 Aug)</td>
<td>Ligurian Sea (Italy)</td>
<td>Individual sighted during several days</td>
<td>Rosso &amp; Tepsich (2003)</td>
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<tr>
<td>17</td>
<td>2010 (Sept)</td>
<td>San Antonio Cape, Jávea, Alicante (Spain)</td>
<td>Two individuals, sighted (photographed)</td>
<td>Anon. (2010)</td>
</tr>
<tr>
<td>19</td>
<td>2011 (13 Jun)</td>
<td>Port of Carry-le-Rouet (France)</td>
<td>Young female (7.40 m) stranded dead (photographed)</td>
<td>GECEM (2011)</td>
</tr>
<tr>
<td>20</td>
<td>2012 (28 Jun)</td>
<td>20 miles off Nice (France)</td>
<td>Individual 8-10 meters; same as in references 22 and 25</td>
<td>Panigada et al. (2014); GECEM (2012)</td>
</tr>
<tr>
<td>21</td>
<td>2012 (2 Aug)</td>
<td>Off Cerbère, Gulf of Lyon (France)</td>
<td>Two individuals sighted (photographed)</td>
<td>BREACH (2012)</td>
</tr>
<tr>
<td>22</td>
<td>2013 (Mar)</td>
<td>Off Lampedusa (Italy)</td>
<td>Sighting; same individual as in refs 20 and 24 (photographed)</td>
<td>Panigada et al. (2014); GECEM (2013)</td>
</tr>
<tr>
<td>23</td>
<td>2013 (16 Jun)</td>
<td>Canet port, Perpignan (France)</td>
<td>Sightings; same individual as in ref. 24 (photographed)</td>
<td>PixWhale (2013)</td>
</tr>
<tr>
<td>24</td>
<td>2013 (10 Jul)</td>
<td>Strait of Gibraltar</td>
<td>Sightings; same individual as in ref. 23 (photographed)</td>
<td>PixWhale (2013)</td>
</tr>
<tr>
<td>25</td>
<td>2013 (27 Jul)</td>
<td>Between Nice and Calvi (43°19' N, 7°50'E; France)</td>
<td>A young animal following a minke whale; same individual as refs. 20 and 22 (photographed)</td>
<td>Panigada et al. (2014; GECEM (2013)</td>
</tr>
</tbody>
</table>
**History of exploitation**

The humpback whale is much more coastal than the other rorqual species, which would have rendered it accessible to early whalers even with relatively limited technology. Accordingly, it was one of the first species targeted by active whaling worldwide (Reeves & Smith 2007), for example by the Nuu-chah-nulth people in Vancouver Island (Pacific Northwest coast of Canada) for which evidence of capture of this species goes back 2500 years (Monks et al. 2001). Siberian and Canadian Artic Eskimos (Somerset Island, Nunavut, Canada; and Chukchi Peninsula, Siberia, Russia; from 1500 BP) selectively targeted juveniles, which were easier to catch and to process, as well as tastier (Krupnik 1993). In the eastern North Atlantic, Rondelet (1558, p.353) presents a very realistic description of this species (“gibbar”) in his Ichthyology treatise, explicitly stating that it was caught in a similar way to the right whale, and that it was found in Saintoge (in Southwestern France). A reference to whaling of humpback whales (“jibartes”) in the Gulf of Biscay can also be found in a 1690 Basque document (Barkham 2000).

Whales captured off coastal areas were transformed locally and the entire carcass (oil, meat, bones) potentially exploitable. However, once the Basques and others started whaling in distant regions (Newfoundland, the Arctic), the only parts of the whale they kept for transport and trade were the blubber (rendered into oil and transported in casks) and the baleen (for right and bowhead whales); the rest of the carcass was discarded (Duhamel du Monceau 1782). In these conditions, the humpback whale was a much less interesting target to whalers, as it produced much less oil than some of the other species (bowhead, right, sperm whales) and its baleen had little value (Edge 1905). Furthermore, unlike right and sperm whales, humpbacks sink once dead, and if found outside their calving grounds they are faster and more difficult to approach. As a result, up to the 19th century humpbacks were generally avoided by whalers (Richards 2010) except in some coastal regions, particularly their low latitude breeding grounds, including the Cape Verde islands (Smith et al. 2012). Nonetheless, as the stocks of the most desirable whales (bowhead, right, gray, sperm) were successively extirpated, and as technology evolved (steam-powered boats, explosive harpoons, better methods for processing the whales), humpbacks changed from secondary to main targets of whaling (Reeves & Smith 2007), and their overexploitation accelerated across the North Atlantic (Reeves & Smith 2002). By 1955, when the International Whaling Commission banned whaling in the North Atlantic, the population had been reduced to less than 1000 individuals. After many decades of legal protection, humpback whales have increased in numbers (estimated at near 20,000 in the North Atlantic) but remain far from recovery (Ruegg et al. 2012).

**Likelihood of ancient exploitation in the Mediterranean region**

If humpbacks were regularly present in the Mediterranean Sea in the past, their coastal habits would have made them a tempting target to fishing communities. This would have been particularly so if the Mediterranean was a calving area, as not only the whales would have been found even closer to the coastline, the young would have been easier targets. If they migrated in and out of the Mediterranean through the Gibraltar Strait, they would have been particularly vulnerable in this region. Any bones of humpback whales found in the Mediterranean archaeozoological record
therefore deserve careful consideration, as they may correspond to individuals that were actively taken.

Also of interest to zooarchaeologists should be the presence of barnacles that are typically associated with this species (*Coronula diadema*; *Conchoderma auritum*). Humpbacks naturally shed barnacles, most noticeably in warm waters associated with breeding grounds, and the presence of Pliocene-Pleistocene fossils of *Coronula* spp. in Italy has been interpreted as a possible evidence of a past migration route of humpback whales or related species between feeding areas in the North Atlantic and breeding areas in the Mediterranean sea (Bianucci *et al.* 2006). Barnacle shells found associated with humans are more likely to attest to pieces of whale skin having been transported for consumption of the underlying blubber and/or meat, given that live barnacles are embedded deep in the whale epidermis and can only be removed by cutting the skin (Kandel & Conard 2003). It is for example the case of *Coronula diadema* plates found in middle Magdalenian deposits at Las Caldas Cave, in the Cantabrian coast of Spain (Álvarez-Fernández 2011).

1.2. North Atlantic right whale, *Eubalaena glacialis*

*Description*

The North Atlantic right whale is a very large species, reaching over 16 meters in length and 70 tonnes in weight, with a stout body (girth may be 60% of total length) thanks to its thick blubber layer (c. 15-20 cm). The very large head (about one third of its length), and pronounced arched lips, enclose on average 250 pairs of dark baleen plates, up to 3 meters long. Right whales (and their relative the bowhead whale) are the only whale species with a smooth back, i.e., without any dorsal fin or ridge (Supplementary Figure 3A). Flippers are large and paddle-shaped. Blowhole openings are widely separated and point outwards, generating a characteristic V-shape spout up to 5 meters high. Skin is shiny black, sometimes with a white ventral region. The head has pale patches of thick skin called “callosities”, commonly covered in whale lice (*Cyamus sp.*; Wilson & Mittermeier 2014). In the Southern right whale (*E. australis*), large barnacles (*Tubicinella major* and *Cetopirus complanatus*) are encrusted in these callosities (Hayashi 2013). These same two barnacle species have been found in upper Magdalenian layers in the Nerja Cave (Málaga, southern Spain) (Álvarez-Fernández *et al.* 2014), which may indicate the previous presence of the North Atlantic right whale.

*Ecology and behaviour*

This species occurs in temperate waters in the North Atlantic (Supplementary Figure 3B). Currently, its small population (ca. 500 individuals) is concentrated found off eastern United States, between the main feeding grounds in the Gulf of Maine and Bay of Fundy and the birthing areas off Florida and Georgia, but historically it occurred across the Atlantic (Monsarrat *et al.* 2015). Feeds through skim-feeding, i.e., by swimming slowly with the mouth open through densely concentrated swarms of prey, mainly calanoid copepods (*Calanus finmarchicus*), either at the water’s surface or deep below (in dives lasting 10-20 minutes). Pregnant females and many sub-adults leave higher-latitude feeding grounds in late autumn and move southwards to the warmer birthing grounds; non-reproducing females and adult males seem to remain in the northern grounds throughout the year.
Births occur in calm coastal areas, mostly from December through March, with a peak in early January. Known historical calving grounds included the Gulf of Biscay and Cintra Bay in Western Sahara, as well as the current breeding ground off Florida and Georgia in the United States. Neonates are about 5 meters long and weight about 800 kg. Female adult whales do not eat during this period, living off their fat reserves, whereas calves grow quickly on the mother’s milk. Lactation lasts for 8-17 months, with most calves weaned in the first year. In the spring, the females with newborns (and subadults) migrate northwards along the coast of North America to the summer feeding grounds (Wilson & Mittermeier 2014).

Supplementary Figure 3. North Atlantic right whale, *Eubalaena glacialis.* A) Main physical characteristics (illustration ©Uko Gorter). B) Global distribution (including the current as well as the historical range; map from Reilly et al. 2008c). C) Known records in the Mediterranean region (as listed in Supplementary Table 2).
Presence in the Mediterranean Sea

There are only five confirmed or possible records of right whales inside the Mediterranean Sea, plus three near Gibraltar (Supplementary Figure 4C). The oldest of these records is indirect: in the Upper Magdalenian deposits in Nerja Cave (Málaga) Álvarez-Fernández et al. (2014) recovered 167 plates (fresh and burnt) of two species of barnacle (*Tubicinella major*, *Cetopirus complanatus*), that are only found on the skin of right whales (Hayashi 2013). *Tubicinella major* has only been reported from the southern right whale (*E. australis*), whereas *Cetopirus complanatus* has been found both in the southern right whale and the North Pacific right whale (*E. japonica*) (Hayashi 2013). Álvarez-Fernández et al. (2014) concluded that given that the southern right whale is the only whale species where both barnacle species are known to occur, their finding is evidence that *E. australis* previously occurred north of the Equator too. We consider it more likely that *E. glacialis* previously hosted these species. In any case, these barnacles suggest the past utilisation of the blubber or meat of right whales (Kandel & Conard 2003). The barnacle plates were recovered from four stratigraphic layers, suggesting a long-term use of this resource. Climate was however quite different in the Upper Magdalenian and the presence of right whales in the Mediterranean in this period does not necessarily mean that conditions would have been suitable for right whales in the Mediterranean later during the Holocene.

Among the more recent records, three correspond to the winter period (January, February) consistent with the calving season, and two with the spring (April, May) that may have corresponded to individuals migrating north to the feeding grounds (for the other two, the month is not known). The historical calving ground in Cintra Bay (Western Sahara) (Reeves 2001) means that North Atlantic right whales migrated past the entrance of the Gibraltar Strait yearly. The three records outside Gibraltar may therefore simply correspond to individuals following this migratory route. However, entering the Mediterranean would have been well within the normal migratory distances of right whales, and it is possible they calved there in the past.

As mentioned above, right whales are (with humpback and gray whales) one of the three species which we consider as possibly regularly present in the Mediterranean Sea in the past, and one of the candidates for the whale species attacked by killer whales off Cadiz described by Pliny (NH, 9:14). We also hypothesise that right whales may correspond to the male ram-fishes that according to Aelian spent winter between Corsica and Sardinia (De Natura Animalium, 15:2; translated by Scholfield 1959), if we interpret their white callosities to correspond to the white head ornaments (tiara-like) described. The long and highly flexible baleen of right whales fit particularly well Aelian’s description that “the hairs which grow from the nostrils of the Ram-fish serve many purposes”.

Supplementary Table 2: Review of North Atlantic right whale records in the Mediterranean and Strait area adjacent to the Strait of Gibraltar. Map reference numbers are those in Supplementary Figure 3C.

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<tr>
<td>1</td>
<td>Upper Magdalenian, ca. 14,000 BP</td>
<td>Nerja Cave, Málaga (Spain)</td>
<td>167 plates of two whale barnacle species (<em>Tubicinella major</em>, <em>Cetopirus complanatus</em>), indicative of right whale bubble and/or meat use.</td>
<td>Álvarez-Fernández et al. (2014)</td>
</tr>
<tr>
<td>2</td>
<td>1620</td>
<td>Corsica (France)</td>
<td>Lacepede (p. 116) reports that a right whale was taken in Corsica in 1620, but provides no other details.</td>
<td>Lacépède (1826)</td>
</tr>
<tr>
<td>3</td>
<td>1808</td>
<td>Cadiz (Spain)</td>
<td>Graells (p.27) mentions that the 1817 work “Peces del Mar de Andalucía” (Cabrera et al.) there is a reference to a whale identified as “Balaena Mysticetus” that stranded dead in 1808 in the Cadiz beach. It had an enormous head, occupying a third of its body (which was 20 &quot;varas&quot; long, about 16 m) had a huge mouth, a black back and white belly.</td>
<td>Cabrera et al. (1817; “Peces del Mar de Andalucía”) cited by Graells (1889)</td>
</tr>
<tr>
<td>4</td>
<td>1877 (9 Feb.)</td>
<td>Gulf of Taranto (Italy)</td>
<td>Captured in the Taranto beach, it was painted from life in watercolour by Alejandro Hueber (see Supplementary Figure 4), leaving no doubt about the species.</td>
<td>Graells (1889)</td>
</tr>
<tr>
<td>5</td>
<td>1888 (20 Jan)</td>
<td>Between Castiglione (Bou Ismail) and Tipaza (Algeria)</td>
<td>Two right whales were seen in the waters of Alger. One got entangled in the tuna traps and stranded on the sand, being captured by fishermen. It measured about 11m of length and 6.6 mof girth. The skeleton was recovered by the Paris Museum.</td>
<td>Pouchet &amp; Beauregard (1888)</td>
</tr>
<tr>
<td>6</td>
<td>1921 (May, or April?)</td>
<td>Strait of Gibraltar region</td>
<td>Only known from the report of a technical visit (by Rodríguez Santamaría) to the Getaires factory (Algeciras), which was supplied by whaling boats (Condesa del Moral de Calatrava; Pepita Maura) operated by Norwegian whalers. Rodríguez Santamaría mentions baleen plates of two meters which can only have come from (one or more individuals of) right whales.</td>
<td>Valdés Hansen (2010)</td>
</tr>
<tr>
<td>8</td>
<td>1995 (3 Feb)</td>
<td>Off Cape St Vicent (Portugal): 37°07'N, 08°58'W.</td>
<td>Sighting of an adult and calf. Calf estimated to be very young (2 months) based on size in relation to adult.</td>
<td>Martin &amp; Walker (1997)</td>
</tr>
</tbody>
</table>
Rights whales (Eubalaena sp.) were one of the earlier targets of whaling (Reeves & Smith 2007). The North Pacific species was captured by the Makah Indians of Washington State, USA (Huelsbeck 1988) using harpoons and floaters, and by Japanese 17th century whalers using nets and harpoons (Takahashi et al. 1989). The North Atlantic species was the main target of Basque whaling from at least the 11th century (Aguilar 1986), first in the Gulf of Biscay where it was sighted and approached from the shore as it either calved in this area or passed in migration. Calves were particularly targeted, serving as bait to the accompanying mother. From the 16th century onwards, the Basque expanded their exploitation into Newfoundland and Ireland, first still capturing whales from coastal stations, but subsequently (from 1635) developing the methods for capturing and processing whales in the high seas (Duhamel du Monceau 1782). The Dutch, English, Americans and other nationalities joined the Basques in exploiting North Atlantic right whales as one of the most desirable targets of the 17th- to 19th-century whaling industry (Reeves et al., 2007), and by 1750 they were considered commercially extinct (Allen, 1908). The few remaining individuals continued to be opportunistically taken by whalers, and the species became close to biological extinction before it was given full legal protection in 1935 (Reeves et al., 2007).

Right whales have several characteristics that made them a preferred target of the early whaling industry: their coastal habits made them accessible to human populations, particularly during the winter calving season and the spring migration of mothers and calves back to the feeding grounds. Being relatively slow swimmers they could be approached by rowing boats after having been spotted.

Supplementary Figure 4. North Atlantic right whale captured in Taranto (Southern Italy) on the 9th of February 1877. Originally from a watercolour drawing by Alejandro Hueber, reproduced by Graells (1889).
from lookout towers. Also, unlike most other species, they float when dead, meaning that they could be towed back to land. Their very thick blubber layer made them highly productive in terms of oil. For example, a 1611 description of whaled species (Edge 1905) listed the North Atlantic right whale (“Sarda”) as yielding between 80 and 100 hogsheads of oil, only superseded by its relative the bowhead whale (“bearded whale”, 100-120 hogsheads) and far more than the Sperm whale (“Trumpa”, 40 hogsheads plus spermaceti), the gray whale (“Otta Sotta”, 30 hogsheads), the humpback (“Gibarta”, 12 hogsheads), and the fin whale (“Sedeva”, producing “little or no oil”). The right whale also has very long baleen plates, up to 3 meters long, which were a highly valuable and versatile material.

Likelihood of ancient exploitation in the Mediterranean region

The right whale is (with the humpback and the gray whale) one of the species that could plausibly have been exploited in antiquity in the Mediterranean if it becomes clear that it was previously regularly found in this region. In particular, if it came to the Mediterranean region to calve it would have predictably been found close to the coast, and the calves would have been particularly tempting targets. As a bottleneck to their migration routes, the Gibraltar region would have been especially suitable as an area for their exploitation, in the same way that it has served for millennia as a preferred area for the exploitation of migratory tuna. Any bones of right whales found in the Mediterranean archaeozoological record deserve therefore careful consideration, as they may correspond to individuals that were actively taken. Zooarchaeologists should also be interested in the presence of barnacle species associated with right whales (Tubicinella major, Cetopirus complanatus) as found in the Nerja Cave by Álvarez-Fernández et al. (2014).

1.3. Gray whale, *Eschrichtius robustus*

*Description*

Gray whales can grow up to 15 meters long and weight up to 35,000 kg. The single species of family Eschrichtiidae, their unusual grey appearance comes from the fact that in adult individuals the skin is mostly covered by commensal barnacles (*Cryptolepas rhachianecti*) and whale lice (*Cyamus* sp.) and marked by the pale scars left by previously attached barnacles, especially on the head (Supplementary Figure 5A). Newborns (up to 5 meters, 800 kg) have no barnacles, being dark grey to black. Gray whales have no dorsal fin, but a series of 6 to 12 bumps (“knuckles”) on the midline of their rear quarters. Their 130-180 baleen plates are short (5-40 cm long) and pale yellow. They have a blubber layer ca. 12 cm thick and 2-7 throat pleats (less conspicuous than in rorquals). They produce a characteristic heart-shaped spout through their blowhole (Jones *et al*. 1984; Wilson & Mittermeier 2014).
Ecology and behaviour

Today the gray whale is only found in the North Pacific ocean, but in the past it also occurred in the North Atlantic (Mead & Mitchell 1984; see below). In the North Pacific, it is found primarily in shallow water along the edges of continental shelves, very rarely in deep water. It was previously common on both coasts but the western (Asian) population is currently very small and may be extinct (Mate et al. 2015).

It is the only whale species that is extremely coastal all year round. In summer, they are found at high latitude feeding grounds (Gulf of Alaska, Bering Sea, Chukchi Sea, Beaufort Sea, East Siberian Sea and
Sea of Okhotsk) where they feed mainly on invertebrates on the sea floor. They have a unique suction feeding behaviour whereby they scoops up mouthfuls of sediment (sand, mud), using their baleen plates to sieve the small invertebrates found there, leaving long trails of mud behind them and forming "feeding pits" in the sea floor. This behaviour explains their common names of “mud digger” and “mussel digger” given by 19th century whalers (Jones et al. 1984) as well as “sand eater” given by the 13th century Norse (Lindquist 2000). Occasionally, it also feeds at the surface, skimming invertebrates from the water.

In the late autumn, they migrate southwards along the continental shelf to Baja California (Mexico), concentrating during winter in low-depth coastal bays and lagoons where they give birth (December to early March), rear their young and mate. They do not eat during this period but live off their fat reserves. They migrate northwards again in spring, first the newly pregnant females and last the female with young of the year (Wilson & Mittermeier 2014). The latter migrate particularly close to the coastline, probably to avoid predation by killer whales (Ford & Reeves 2008): 97% of gray whale cow-calf pairs were found to pass within 800 meters of shore, often just beyond the surf zone (Losey & Yang 2007).

In their calving and feeding grounds, as well as during migration, individuals can be found in astonishingly shallow waters. Scammon (1874; p. 34) describing them in the calving lagoons of Baja California, stated that “About the shoals […] we saw large numbers of the monsters. […] To our surprise we saw many of the whales going through the surf where the depth of water was barely sufficient to float them […] they must be near or touching the bottom”. In their feeding grounds, Russian whalers mentioned that “The whales entered the lagoons and dozens of them filled the shallow lakes connected with the sea. Some whales were just lying on the sand bars; […] Some whales would lie immobile at the surface not paying attention to the approaching boats or even prods of the oars, as if they were sleeping” (Yahlokov & Bogoslovskaya 1984, p. 479). Another of its Norse names was Sandlægja, meaning “one lying in the sand” (Lindquist 2000).

**Presence in the Mediterranean Sea**

The only confirmed records of gray whale in the Mediterranean are the astonishing observation of the same individual in May 2010, first off Israel and then 22 days later off Barcelona, very likely a vagrant from the eastern North Pacific population (Scheinin et al. 2011). Bones attributed to this species have been found in Lattes, southern France (Macé 2003) but this identification is not considered reliable and awaits verification by genetic analyses (A. Gardesein, pers. comm.).

Despite the lack of past records, this species is (with the humpback and right whales) one of those we believe should be considered as potentially having previously occurred in the Mediterranean. Given that the living population in the North Pacific makes extremely long migrations and calves in warm waters off Mexico, it seems feasible that the extinct Atlantic population could have migrated along the European coast to warmer waters off Africa or within the Mediterranean. Their preference for sheltered coastal areas for calving in the winter makes it one of the species that Pliny NH, 9:4) could be referring to when describing an attack of killer whales to whales and calves coming to a “calm capacious bay, in which they take a delight in bringing forth”. 


Gray whales, with their habit of using very shallow waters, could also be the species at the origin of Oppian's statement (*Haliaeutica*, book 1:390; translation by Mair 1928) that “*even the shameless Whale, they say, leaves the sea for the dry land and basks in the sun*”.

**History of exploitation**

Gray whales have been hunted for millennia for their blubber/oil, meat and bone, as their coastal habits brought them within reach of human populations even with limited technology. In the North Pacific, aboriginal groups extending from Washington State to Aleutian islands used poisoned lances or harpoons attached to floaters (O’Leary 1984). In the North-western Pacific (e.g. Okhotsk Sea, Kamchatka Peninsula), aboriginal groups specialised in the capture of young whales, including by driving them into shallow waters and then killing them with lances, arrows and darts, or by catching them in shallow waters with nets (Krupnik 1984). In Japan, from the 1600s onwards they were taken using nets (Omura 1984). The eastern population collapsed in the second half of the 19th century due to American whaling in the calving lagoons in Baja California (Scammon 1874), on their migration route from coastal stations along the California coast (Sayers 1984), and also occasionally in their high-latitude summer feeding grounds (Smith *et al.* 2012). Small numbers continued to be taken until the species was protected by the United States in 1936. This population has since recovered spectacularly and it is now estimate to exceed 20,000 individuals (Reilly *et al.* 2008b). The western population was nearly extirpated by American, Russian, Korean and Japanese commercial whalers (late-19th and early-20th centuries), and has never recovered. It is believed to be a very small population or even extinct (Mate *et al.* 2015).

Archaeological records as well as historical evidence testify that gray whales were previously present in the Atlantic, but that is no longer the case (Mead & Mitchell 1984). The little available evidence indicates that this species was taken by the Norse in Iceland (Lindquist 2000), and off the United States coast (Dudley 1725). It was known to the Basque, as it appears in a 1611 list of potentially exploitable whale species, where it is presented fourth in desirability (after the bowhead, right and sperm whales) but having the best oil (Edge 1905). It is presumed to have disappeared by the late 18th century as it is not recorded since despite an increase in the available documentation on whaling. The only North Atlantic record after this period is of a presumed vagrant individual in the Mediterranean in 2010 (Scheinin *et al.* 2011).

**Likelihood of ancient exploitation in the Mediterranean region**

Any material evidence of the past presence of gray whales in the Mediterranean region – including bones as well as barnacles (*Cryptolepas rhachianecti*) – should be analysed with particular interest. Indeed, if this species occurred in the Mediterranean in the past it would have likely been within easy reach of human populations, and hence likely to have been actively exploited at least in some regions (e.g. calving bays, strategic points in its migration route).
Section 2. Species that could have been occasionally or locally exploited

2.1. Sperm whale, *Physeter macrocephalus*

*Description*

A large whale species, exhibiting strong sexual dimorphism, males (up to 19.2 meters and up to 70,000 kg) being substantially larger and heavier than females (up to 12.5 meters and 24,000 kg). Their enormous block-shaped head gives them a characteristic appearance. Skin is dark grey (appearing dark brown in some conditions) and they have a series of ridges on the midline of their rear quarter, the largest of which may appear like a fin. Their paddle-like flippers are relatively small. The single blowhole is located asymmetrically on the left side of the front end of the rostrum, resulting in a forward-facing left-angled spout. They have 20-26 pairs of conical teeth, erupting only on the lower jaw.

*Ecology and behaviour*

It is a cosmopolitan species, found in deep, ice-free ocean waters across the world, including the Mediterranean (but not the Red Sea). In general, females and dependent young inhabit tropical, subtropical and temperate waters deeper than 1000 m and above 15°C, whereas sub-adult and adult males range more widely, including ice-free waters near both poles close to 0°C (the Mediterranean is an exception; see below). They feed primarily on cephalopods, including giant-squid, but also bottom-dwelling fish. Prey are located through sonar and captured in foraging dives usually to depths of 300-1200 m (lasting 30-45 mins) but up to 1000-2000 m (lasting more than 60 mins). Sperm whales in the Northern Hemisphere typically breed from January to August, more intensely between March and June. Highly social and nomadic, they travel in long-term social units consisting of c. 11 individuals, including adult females with and without offspring. Pubertal males leave their natal units at 4-21 years old and gather in loosely grouped bachelor groups. Mature males travel with fewer individuals. The largest males are often solitary and found near the polar ice edges (Wilson & Mittermeier 2014). This species is sometimes found in mass strandings, particularly in geographic areas such as the North Sea and in the Southern Australian and New Zealand waters. The strong social links of sperm whales may prompt healthy animals to follow sick or disordered members of a pod, exacerbating the risk of mass strandings (Mazzariol et al. 2011).

*Presence in the Mediterranean Sea*

Sperm whales are widely distributed in the Mediterranean Sea from the Gibraltar Strait to the Levant Basin. Known in the past to have been predictably present in parts of the Gibraltar Strait area, around the Balearic Islands, between the Algerian coast and the Ligurian Sea, in the Tyrrhenian Sea, in the deep waters to the north, east and southeast of Sicily, in the Ionian Sea and in parts of the Aegean Sea. It is still fairly predictable in the Gibraltar Strait and along the Hellenic Trench (from the NE Ionian Sea to the NW Levantine Sea). They are rare in the Sicilian Channel, vagrant in the Adriatic
Sea and absent from the Black Sea. They prefer continental slope waters, with deeper offshore waters also inhabited but perhaps to a lesser degree (Reeves & Notarbartolo di Sciara 2006 and references herein).

Genetic data, sound analyses and photo-identification data all indicate that sperm whales in the Mediterranean constitute a separate population from that in the Atlantic (Reeves & Notarbartolo di Sciara 2006; Carpinelli et al. 2014). All age classes are present all year-round, and the occurrence of neonates confirms that calving takes place here. The total current population is estimated to be in the hundreds (rather than in the thousands) of individuals, but it seems to have been more abundant.
even in the recent past, at least until the 1950s. For example, there are reports of large “aggregations” of as many as 30 individuals in the Strait of Messina in the late 1940s and early 1950s, compared to just 9 individuals in the same region detected by an intensive programme of survey in the same area. Stranding records in France and Italy also suggest a population decline in the past few decades. This is likely the result of entanglement in high-seas swordfish driftnets that has caused considerable and ongoing mortality since the 1980s (Reeves & Notarbartolo di Sciara 2006 and references herein).

Mass strandings are extremely rare in the Mediterranean, but in the Adriatic Sea, five events involving 3-8 animals have been reported since 1555. Sperm whales are absent or only present as vagrants in this relatively shallow Sea, and it has been proposed that the Eastern South Adriatic coastline may be a potentially dangerous natural trap for this species (Mazzariol et al. 2011).

**History of exploitation**

Sperm whales were highly desired for several reasons (Edge 1905): a high oil yield, including that produced from their blubber layer but also *spermaceti*, a particularly fine type of oil found in their head cavity; ambergris, a valuable waxy product used in perfumes and ancient medicine, only produced in sperm whale intestines (found in some dead whales, but it can also be expelled and hence also found floating or washed up on beaches); and their teeth, up to 1 kg each, which could be carved into ivory ornaments (scrimshaw). Sperm whales also have the advantage that they generally float when dead (like right whales, but unlike other species), preventing them from sinking out of reach of whalers. However, given that they are mainly found in deep waters, they were not easily accessible to early whalers. An exception is aboriginal sperm whaling documented in the Indonesian islands of Lembata, Solor and Lamakera, adjacent to the deep and highly productive waters of the Savu Sea (up to 3500 km). Here, for centuries (and prior to European influence) harpooners have killed sperm whales by jumping off a boat, adding their weight to the force of the thrust (Reeve 2002). In other parts of the world, sperm whales only appear to have become a main target of whaling once more coastal species (right whales) had been depleted and methods for whaling in the high seas had developed. They were certainly well-known to 16th century Basque whalers (Edge 1905) and were taken in the Gulf of Biscay (Rondelet 1558) but seem to have been an occasional catch (Barkham 2000). Intensive sperm whaling started with 18th century New England whalers (Macy 1835), first in the north-western North Atlantic and then expanding into all seas of the world (Smith et al. 2012) well into the 20th century until the 1985 international moratorium on commercial whaling (Reeves & Smith 2007).

In the Mediterranean region, Duhamel du Monceau (1782) mentions that sometimes small sperm whales were caught (presumably accidentally) in the nets of fishermen in the Adriatic Sea. A few individuals were taken in the Gulf of Cadiz by 19th century American pelagic whalers (Smith et al. 2012) and a few hundreds were taken in the Gibraltar region in the 20th century particularly by Norwegian whalers operating from Getares (Aguilar 2013).
Likelihood of ancient exploitation in the Mediterranean region

Even considering that sperm whales were surely more abundant in the Mediterranean in antiquity than they are today, their deep-sea habitat makes it unlikely that they would have been found predictably near the shore and hence a target of organised whaling. However, given the above-mentioned precedent in the Indonesian islands near the Savu Sea (proving that sperm whales can be captured from coastal areas with very simple technology), it cannot be discounted that sperm whale capture could have taken place in particular areas of the Mediterranean coastline that are adjacent to deep trenches with high productivity (e.g., south of the Strait of Messina, where sperm whales were apparently relatively common until recently; Reeves & Notarbartolo di Sciara 2006). The reference in Duhamel du Monceau (1782; p. 34) to small sperm whales sometimes being caught in the nets of fishermen in the Adriatic Sea (fishing “à la Tartane”, i.e. with sailboats, in relatively high seas; Nicolò 2012) seems to refer to by-catch (or maybe opportunistic catches) but it reinforces the idea that sperm whales could have sometimes appeared within reach of coastal communities.

In some regions of the world (e.g. Gulf of Biscay, New England), the capture of coastal right whales seems to have served as a stepping-stone to the capture of the more oceanic sperm whales. So if organised whaling of coastal species was in place in the Mediterranean then it would have been more likely that sperm whales were captured too.

2.2. Killer whale, Orcinus orca

Description

A distinctive and easily recognised species, thanks to its characteristic black-and-white pattern, its tall dorsal fin and its large paddle-like flippers (Supplementary Figure 7A). Males can reach nearly 10 meters in length and weight 6.6 tonnes (females are smaller). Each jaw has 10-14 pairs of large, conical teeth (up to 10 cm long). Although currently considered a single species, genetic, morphological and ecological evidence suggest the existence of multiple ecotypes, which may represent separate species or subspecies (Wilson & Mittermeier 2014).

Ecology and behaviour

The killer whale is cosmopolitan species found across the world’s oceans (Supplementary Figure 7B), but more abundant at higher latitudes and in near-shore waters (usually <800 meters from the shoreline), particularly in regions of high productivity. Highly social, it is often found in groups. It is a top predator, with a diverse diet including small and large fish, cephalopods, marine mammals (from seals to large whales), seabirds and marine turtles. Some populations are specialised in particular prey, for example on salmon, marine mammals, or on sharks. Such dietary specialisation can involve particular forms of cooperative hunting behaviour, culturally transmitted. For example, the killer whales of the Strait of Gibraltar feed on Atlantic bluefin tuna (Thunnus thynnus), taken by chasing the tuna schools at high speed until they are exhausted (Wilson & Mittermeier 2014).
**Presence in the Mediterranean Sea**

It is an infrequent visitor to the Mediterranean Sea (Supplementary Figure 7C). In a review of known occurrences, Reeves & Notarbartolo Di Sciara (2006) found less than 30 records, decreasing progressively eastward. Given this species’ distinctive and conspicuous appearance, such scarcity of records likely reflects a true rarity, suggesting that individuals in the Mediterranean are occasional wanderers from a North Atlantic population (Notarbartolo di Sciara 2006). A small population is however regularly found in the spring and summer in the Gibraltar region and adjacent waters to the west (Gulf of Cadiz, southern Portugal), where they specialise in the capture of migratory Atlantic bluefin tuna (Esteban et al. 2014). These individuals belong to the same population found in the Canary Islands, which is genetically different from other populations in the north-east Atlantic (Foote et al. 2011).
There is however evidence from historical texts that in the past, killer whales in the Mediterranean followed a somewhat different (or broader?) pattern of spatial and temporal presence. Aelian in his *De Natura Animalium* (NA 15.2) referred to “ram-fishes” (interpreted by Thompson [1947] as corresponding to killer whales) that “spend the winter near the Strait between Corsica and Sardinia” (Scholfield 1959). Even though the fantastic physical description does not match killer whales (and we propose it may instead refer to right whales and humpback whales; see above) the description of seals hunting behaviour is realistic. Pliny, in his *Naturalis Historia* (NH 9.14) describes the capture of an “orca” that had entered the port of Ostia and was assailed by the Emperor Claudius. Pliny also described a very realistic attack by “orca” (the “form of which cannot be in any way adequately described, but as an enormous mass of flesh armed with teeth”) on whales and their calves, in the Cadiz Bay, “in some calm capacious bay, in which [the whales] take a delight in bringing forth” (NH 9.12-13). The description matches very well the behaviour of killer whale pods attacking coastal baleen whales (Ford & Reeves 2008) and the timing (“before the winter solstice”) agrees perfectly with the calving season of gray, right or humpback whales. Finally, Rondelet, in his *Histoire Entière des Poissons* (Rondelet 1558) lists several species of whale, among which the “Espaular” or “Orca” (Supplementary Figure 8). Rondelet’s book is not specific to the Mediterranean (even if he was based in Montpellier) but he states that this species was known as “Dorque” in Languedoc (southern France), suggesting that it was well-known in the Mediterranean coast of France. Together, these records suggest that killer whales were found with some regularity inside in the western Mediterranean, that they occurred in the winter, and that the preyed on whales and seals. This is biologically plausible as these are natural prey of some populations/ecotypes of killer whales in other parts of the world, and that both seals and whales (as well as tuna) were likely substantially more abundant in the Mediterranean Sea in the past than today.

**Supplementary Figure 8.** Rondelet’s “Espaular” or “Orca”, known as “Dorque” in the Languedoc region. The drawing shows the tall dorsal fin, large flippers and menacing teeth on both jaws. The description mentions “a tail like that of the dolphin, but the body twenty times larger [...] very large and pointy teeth [...] with which it seriously wounds the whale” (Rondelet 1558).

**History of exploitation**

Killer whales do not seem to have been main targets of whaling, but were taken at least in low frequencies in several regions around the world (Taylor et al. 2008). For example, after describing the way Basque captured right whales in the Gulf of Biscay, Rondelet (1558) stated that killer whales were taken in a similar way. Scammon (1874; p. 92) mentioned that they “seldom captured by the civilized whaleman” given the difficulty to capture them and relatively low yields, but were occasionally taken by the Makah Indians (Washington State, USA) who considered their flesh and fat...
more luxurious than that of the larger whales. Killer whales were also taken in small numbers during the 20th century, by Norwegian, Japanese and Soviet whalers, and are still taken in some coastal fisheries off Japan, Greenland, Indonesia, and the Caribbean islands (Taylor et al. 2008).

Killer whales had however strong interactions with whalers, both negative and positive. They were often seen as competitors and nuisances, as they attacked the carcasses of captured whales (e.g., Andrews 1916; Scammon 1874). There are however multiple independent accounts of killer whales cooperating with whalers by driving whales to shore (e.g., in the New World, Rondelet 1558; in Norway, Lindquist 1994; in Australia, Clode 2002; in Korea, Andrews 1916). In a well-documented example of the latter, killer whales in southern Australia actively drove baleen whales towards a bay where they were harpooned and killed by whalers, reportedly even warning the humans of the presence of trapped whales. In exchange, the whalers allowed the killer whales to feed on the tongue and lips of the captured whales (Clode 2002). This behaviour is reminiscent of the cooperation between dolphin and fishermen reported by Pliny in Southern France (NH 9.9; Bostock & Riley 1855).

**Likelihood of ancient exploitation in the Mediterranean Sea**

It seems likely that killer whales were previously more abundant in the Mediterranean than today, which affects the possibility of ancient whale exploitation in three ways. Firstly, killer whales themselves might have been subject to exploitation, given that they can be found in coastal waters. Secondly, as feared predators of all species of whales, they may have increased the likelihood of natural strandings by panicking individuals of other whale species. Third, they may have cooperated with humans by driving whales to shore to be killed by whalers, as described above.

### 2.3. Long-finned pilot whale, *Globicephala melas*

**Description**

This is a small whale, up to 6.7 meters in length and 2.3 tonnes in weight, having as a distinctive feature a large bulbous head (Supplementary Figure 9A). The skin is dark (gray, brown or black), except for white or pale-gray ventral patches. The dorsal fin is falcate, with a wide base, located closer to the head than to the tail. It has proportionately long flippers, with a characteristic shape (forming an “elbow”). Both jaws have 8-13 pairs of teeth (Wilson & Mittermeier 2014).

**Ecology and behaviour**

Long-finned pilot whales are found in temperate and subpolar seas in the North Atlantic and the southern Hemisphere (Supplementary Figure 9B), although there is some evidence that these correspond to different species. They occur both in coastal and oceanic waters, with their preferred habitat being over continental shelf breaks and slopes. They can dive to depths of 300-1800 m, using echolocation to find prey, mainly small cephalopods and small to medium-sized fish. Their foraging activity is often nocturnal as it preys on squid migrating closer to the surface. Highly social, they typically travel in groups of 20-100 individuals, with groups up to 1000 individuals recorded, and
sometimes found in mixed-species groups with other delphinids. Births mainly take place in the Spring and Summer. This species is commonly associated with mass strandings of unknown cause (maybe as a group follows a confused, diseased or injured individual that has made a navigational mistake) (Wilson & Mittermeier 2014). This is not a new phenomenon, with regular strandings having been recorded in the North Atlantic for hundreds of years (Abend & Smith 1999).

**Supplementary Figure 9.** Long-finned pilot whale, *Globicephala melas*. A) Main physical characteristics (illustration ©Uko Gorter). B) Global distribution (map from Taylor et al. 2008e). C) Distribution in the Mediterranean region (as reviewed and mapped by Reeves & Notarbartolo di Sciara 2006).

**Presence in the Mediterranean Sea**

Long-finned pilot whales are regularly found in the Mediterranean Sea, being very common in the Alborán Sea and adjacent waters and relatively common to scarce in the rest of the western Mediterranean (Supplementary Figure 9C). They have not been recorded in the eastern basin. Their
population in the Alborán Sea is believed to reach from several hundred to a few thousands, with 250-270 in the Strait of Gibraltar. They are mainly found offshore, over deep waters seaward of the continental shelf and slope, in water deeper than 500 m (Reeves & Notarbartolo di Sciara 2006; Cañadas & Sagarminaga 2000). Most strandings have been reported from the western Mediterranean (Spain and France) (Univ. Valencia 2011).

History of exploitation

This species has been exploited for hundreds of years through drive fisheries, whereby fishermen surround and scare pods towards land, taking advantage of their social behaviour to prompt mass strandings before killing the whales on the shore with large knives. The best-known example is the pilot whale drive in the Faeroes Islands, actively pursued since the 9th century and still ongoing (Landt 1810; Lindquist 1994; Taylor et al. 2008d). They were also historically taken through whale drives off Shetland, Orkney, the Hebrides, Ireland, Iceland, and eastern United States (particularly off Cape Cod, Massachusetts) (Abend & Smith 1999; Goode 1887; Lindquist 1994). While not a major target of pelagic whalers, they were harpooned when the more desirable whale species were not found (Whitecar 1860), and considerable numbers were taken on the whaling grounds east of the Grand Banks of Newfoundland. In the North Pacific, a previously existing population disappeared (Taylor, Baird, Barlow, Dawson, Ford, Mead, Notarbartolo di Sciara, et al. 2008c). Pilot whales were valued for their meat and oil.

Pilot whale driving is technically simple, requiring only a concentration of fishing boats working in coordination to drive the whales to land, plus a group of people on the shore ready to kill the stranded individuals. In places where the occurrence of whale pods near the shore was very occasional, whale driving must have occurred only opportunistically. If on the other hand such occurrences were reasonably regular, whale driving could develop into an active fisheries operation with a certain level of preparedness. In the Faeroes and in Cape Cod, alarm systems were in place to alert fishermen in the sea as well as men inland to the presence of a pod (Landt 1810; Goode 1887), since this endeavour required large numbers of people to drive and kill the whales as well as to process the meat and blubber. In these regions, whale driving was strongly seasonal, as a function of the months when whales mostly approached the shores, likely driven by the distribution of their prey species.

Likelihood of ancient exploitation in the Mediterranean region

Whether or not whale driving could have occurred in the Mediterranean in the past, either opportunistically or even as an organised operation, depends on whether pilot whales approached the coast regularly. Currently, although considered common in the Alborán Sea, pilot whales seem to use mainly deep waters (Cañadas & Sagarminaga 2000), although this may have been different in the past. Any archaeological findings of pilot whales may therefore be associated with either natural strandings, opportunistic capture or organised whaling. In all of these cases, the number of individuals killed could be high, and therefore not necessarily indicative of organised whaling activity.
Section 3. Species unlikely to have been actively exploited

3.1. Fin whale, *Balaenoptera physalus*

*Description*

The world’s second largest whale species (after the blue whale, *B. musculus*) and the largest in the Mediterranean Sea, it can reach 27 meters and weigh 90 tonnes. Has a long and slender body (Supplementary Figure 10A), of a uniform dark gray to brownish-black on back and sides, grading into white on belly. The head is asymmetrically coloured (dark on the left side, with a complex pattern of dark and light markings on the right). The baleen plates (up to 90 cm long) match this asymmetry, with the left baleen plates being dark-blue gray and right baleen plates partially dark and partially pale. Like other rorquals, it has a series of ventral grooves that allow its throat to expand when feeding. Its distinctive dorsal fin justifies the nickname “razorback”, being very prominent in the arched back when individuals begin to dive. Pectoral fins are relatively small and slender (Wilson & Mittermeier 2014). Mediterranean individuals are sometimes afflicted by ectoparasites such as copepods *Pennella sp.* (Notarbartolo di Sciara et al. 2003), but like other *Balaenoptera* species their skin is mainly free of barnacle encrustations (Ford & Reeves 2008).

*Ecology and behaviour*

A cosmopolitan species, it is found in temperate and colder waters in all ocean basins (Supplementary Figure 10B), usually in the open seas. Like other baleen whales, it feeds by filtering small prey from the water using its baleen plates. Like for other rorquals, prey are captured by gulping huge quantities of water through the extension of the throat pouch, with water subsequently expelled and sieved through the baleen plates. Favoured preys include planktonic crustaceans (e.g. krill) and small schooling fish (e.g., herring). Fin whales generally migrate between high-productivity, high-latitude summer feeding grounds and lower-latitude winter breeding and birthing areas. Conception takes place in the winter, in the high seas. A fast swimmer, it breaches (i.e., leaps out of the water) only occasionally (Wilson & Mittermeier 2014).

*Presence in the Mediterranean Sea*

The fin whale is the most common whale species currently found in the Mediterranean Sea (Supplementary Figure 10C), and the only commonly observed mysticete. It occurs all over the basin, mostly in deep, offshore waters of the western and central portion of the region, from the waters north and east of the Balearic Islands to, and including, the Ionian Sea. Although it has a marked preference for deep waters (> 2000 m), in some years it can be found unusually close to the coast, following the distribution of its prey (Notarbartolo di Sciara et al. 2003).

The total current population estimate for the Mediterranean Sea is less than 5,000 individuals (Panigada & Notarbartolo di Sciara 2012). Abundance is highest (by far) in the Ligurian Sea and Gulf of Lyon. It is extremely rare in the Adriatic and Aegean Seas, Levantine Sea, and Black Sea. Records show particularly high summer concentrations in highly productive portions of the Corsican, Ligurian
and Tyrrhenian seas. Similar concentrations may occur in the less studied eastern Ionian Sea. Late winter feeding aggregations have been recorded in the Sicily Channel (Panigada & Notarbartolo di Scia 2012; Reeves & Notarbartolo di Scia 2006). Stranding records are also concentrated in the western Mediterranean, particularly in the Ligurian Sea and Gulf of Lyon, as well as in the Strait of Gibraltar area (Univ. Valencia 2011), with isolated strandings recorded in the Eastern Mediterranean – Greece, Turkey, Israel (Frantzis 1998; Kerem et al. 2012).

There is a resident subpopulation in the Mediterranean that is genetically separated from the North Atlantic population, but individuals from the latter cross the Strait of Gibraltar to winter in the Alborán Sea (Castellote et al. 2012). Breeding and calving grounds have yet to be identified. Records of neonates suggest that births may occur throughout the year (with a peak in November) and over a wide geographic area (Notarbartolo di Scia et al. 2003).
Whaling in the Gulf of Cadiz and Strait of Gibraltar (see below) substantially depleted the population in this area. A 1921 testimony recorded that whales were at the time often captured less than two miles from the factory in Getares (Algeciras), and that in a single afternoon up to 22 individuals were observed from land, something unthinkable today (Aguilar 2013). Hence, in this area at least, fin whales were historically more abundant than today.

**History of exploitation**

Being an open water species, the fin whale was not easily accessible to human populations, and was therefore not a common target of subsistence whaling (Reeves & Smith 2007). Medieval Norse whalers occasionally exploited a wide diversity of species, including rorquals, by enclosing individuals that wandered into bays, and/or darting them and waiting for them to die and be brought to shore. However, they legally protected the fin whale given the belief that it was a “fish driver”, that helped fishermen by bringing fish (particularly herring) to them (Lindquist 1994).

The commercial exploitation of the fin whale started only in the late 19th century, when whaling technology developed sufficiently to allow its capture and efficient processing. Before then, several characteristics of this species contributed to protect it from major whaling efforts, as summarized by an American whaler: “The great speed and activity of the physalis, render it a difficult and dangerous object of attack; while the small quantity of inferior oil it affords makes it unworthy the general attention of the fishers” (Scoresby 1820). Hence, the fin whale was very difficult to approach, being much faster than the main targets of earlier whaling efforts (right, gray, and sperm whales). If harpooned using the traditional hand-held harpoons developed by Basque whalers, it escaped at high speed, either breaking the line or forcing the crew to do so to save themselves from being dragged and sunk (Scoresby 1820). Furthermore, once killed in sink out of reach. Fin whales therefore only became easily and predictably accessible with the invention of steam-powered whaling boats (that could approach faster species), explosive harpoons (that killed quickly) and methods for pumping air into dead whales to keep them afloat while being secured to the whaling boats, a method developed by the Norwegians in the 1860s (Reeves & Smith 2007). The fin whale was also much less desirable than right, gray or sperm whales. With a relatively thin blubber layer (15 to 20 cm thick; Scoresby 1820), it produced much less oil than the more desirable right, gray or sperm whales. Its short and low quality baleen plates had little commercial value. The commercialization of the fin whale only became economically reasonable with the development of processing methods that used not only the blubber layer (as in Basque-style offshore whaling) but made use of the full whale as sources of oil, meat, and fertilizers (Jackson 1978).

Fin whales were heavily exploited in the early 20th Century in the Strait of Gibraltar and adjacent Atlantic waters, being the main target (>90% of the catches) of whaling operating from land stations (the most important being in Getares, Algeciras) and floating factories (Notarbartolo di Sciara et al. 2003). About 4,500 individuals were captured in just seven years (1921 to 1926), resulting in the collapse of the population. Whaling continued in subsequent decades at much lower levels (much higher catch-per-unit effort) before it ceased in the 1960s (Aguilar 2013). Whaling took place all year round, suggested that it targeted a sub-population resident in that area, which has possibly been extirpated (Notarbartolo di Sciara et al. 2003).
**Likelihood of ancient exploitation in the Mediterranean region**

Given the difficulties inherent to the exploitation of fin whales (not coastal, difficult to capture, sinks when killed), this species is highly unlikely to have been actively exploited by Mediterranean societies in antiquity. It is the most commonly found species of whale found stranded in the Mediterranean today (Univ. Valencia 2011) and this is likely to have been true in antiquity as well. Bones in the zooarchaeological records are therefore likely to reflect an opportunistic use of naturally stranded (dead or dying) whales rather than active pursuit of healthy individuals.

### 3.2. Common minke whale, *Balaenoptera acutorostrata*

**Description**

Has a similar body plan to the fin whale, but much smaller (not exceeding 9 meters or 3 tonnes), a bluish-dark grey back with a variable pattern of lighter shading areas, and an ivory-white belly. Its most distinctive feature is a brilliant white band or patch on the flippers (Supplementary Figure 11A). The scientific epithet *acutorostratum* comes from prominent rostral ridge extending from the blowholes to the tip of the snout. The dorsal fin is relatively large, with a falcate form. It has ventral grooves, like the other rorqual species. Baleen plates are yellowish white, up to 21 cm in length (Wilson & Mittermeier 2014).

**Ecology and behaviour**

A cosmopolitan species, found in all oceans, in virtually all latitudes (Supplementary Figure 11B). It prefers open waters, but may occasionally be found in inshore coastal waters such as bays or even large rivers. Feeds mainly on small schooling fish (e.g. herring, capelin) but also on planktonic crustaceans (e.g. krill), filtering prey through the baleen plates. Generally migrates between high-productivity, high-latitude summer feeding grounds and lower-latitude winter breeding and birthing areas, but the latter are poorly known. Births taking place in the open seas, peaking in December and June for the North Atlantic population (Wilson & Mittermeier 2014).

**Presence in the Mediterranean Sea**

It is an occasional visitor to the Mediterranean, and a vagrant in the Black Sea. Reeves & Notarbartolo Di Sciara (2012) found only 30 known records of live or stranded individuals between 1771 and 2006 (21 post 1950; Supplementary Figure 11C). These strandings were mostly in the western Mediterranean, and primarily in spring, even if spread throughout the year. This species does not seem to have been captured by 20th-century whalers off Gibraltar (Aguilar 2013), suggesting that it was not common.
**History of exploitation**

Being mainly an open water species, minke whales were not a main target of subsistence whaling worldwide, but their smaller size and propensity to come closer to shore might have made them more accessible than fin whales. They may have been occasionally killed through poison whaling by North Pacific native Americans, which consisted of darting a whale with a poisoned or infected spear, and then waiting for it to strand after the effects of the poison or septicemia to kill or debilitate the animal (Reeves & Smith 2007). Like fin whales, they were respected as “fish drivers” and fishermen helpers by medieval Norse whalers, but contemporary historical records refer to it as occasionally running live ashore and “well edible” (Lindquist 1994).

Because of their small size and their low oil productivity, they were not a focus of dedicated commercial whaling until quite late, after the stocks of the more desirable larger species had been exhausted. In the North Atlantic, it was intensively whaled between 1952 and 1983. Catches were
then phased out by 1987 but whaling then resumed (at a lower lever) in 1993 and is still ongoing (Reilly et al. 2014b).

**Likelihood of ancient exploitation in the Mediterranean region**

This species’ commercial exploitation only started in the mid-20th century and yet we did not find evidence that it was taken in the Mediterranean (off Gibraltar) at the time (Aguilar 2013), which suggests that it was already uncommon by then. It seems therefore improbable that this species would have been much more abundant in the Mediterranean in the past than today. Although it occasionally approaches coastal areas, such events are not predictable. From the combination of rarity and low accessibility, we consider it unlikely that it would have been exploited in Antiquity, other than the occasionally stranded animal.

### 3.3. False killer whale, *Pseudorca crassidens*

**Description**

It is a small whale, up to 6 meters and 2.2 tonnes, with a slender body and a round head. Its skin is uniformly dark gray to black, except for a lighter patch on chest. The dorsal fin is small and falcate, and flippers have a characteristic (slight “S”) shape (Supplementary Figure 12A). Both jaws have 7-12 pairs of large conical teeth (Wilson & Mittermeier 2014).

**Ecology and behaviour**

False killer whales are found worldwide in tropical and warm oceanic waters, mainly between 50°N and 50°S (Supplementary Figure 12B). They prefer deep offshore waters, with depths > 3000, although they can occasionally be found at lower depths. They feed mainly on cephalopods (e.g. oceanic squid) and large fish (e.g. salmon, tuna). Like killer whales, they can attack other cetaceans, mainly small dolphins but occasionally Mysticets such as Humpback whales. Highly social, they often travel in groups of 20-100 individuals. The ecology of the species is poorly known, including regarding breeding seasonality. It is one of the cetacean species known to mass strand (occasionally >1000 individuals) (Wilson & Mittermeier 2014).

**Presence in the Mediterranean Sea**

It is an occasional visitor to the Mediterranean, unknown from the Black Sea. Reeves & Notarbartolo di Sciara (2012) found only 32 records of live or stranded individuals between 1787 and 2006 (20 since 1950), extending across the Mediterranean and spread throughout the year (Supplementary Figure 12C).

**History of exploitation**

Records of historical catches of this species are not easy to find, as it was not formally described until 1862, but it does not seem to have been a common target of whaling efforts. It was included among a number of mid-sized Odontocete species generally called “blackfish” (Stacey & Baird 1994), that
also including pilot whales, which were occasionally exploited by whalers as sources of meat and bait. False killer whales were taken as a direct catch off Japan and in the Caribbean for meat and cooking oil, and were the target of a drive fishery (where pods are channelled to shore forcing them to strand) off Taiwan. In recent times, captures of this species have mainly been incidental (by-catch of other fisheries), but fishermen also kill them to reduce competition for fish such as tuna (Wilson & Mittermeier 2014).

**Likelihood of ancient exploitation in the Mediterranean region**

The tendency of this species to stay in deep waters means that it would not have been easily accessible to humans in antiquity, even if it was then more common than today. It is therefore very unlikely that it was exploited during antiquity other that through the use of stranded individuals.
3.4. Cuvier’s beaked whale, *Ziphius cavirostris*

**Description**

A small whale, usually 6 to 7 meters in length and 2.5 to 3.5 tonnes in weight. Like in all beaked whales, the rostrum and jaw form a beak, which in this species is relatively short (Supplementary Figure 13A). The skin is typically dark brown or dark gray, with a paler head. Adult males often have pale linear scars, believed to originate from aggressive interactions with other males (males have a pair of conical tusks at the tip of the lower jaw). The dorsal fin is small and located much closer to the tail than to the head (Wilson & Mittermeier 2014).

**Ecology and behaviour**

This species inhabits warm temperate to tropical waters of the world, perhaps also in cooler waters of the Southern Ocean and the North Pacific (Supplementary Figure 13B). It is a deep diving species, spending two thirds of its life at depths greater than 1000 m (Wilson & Mittermeier 2014). Cuvier’s beaked whale holds the current record for the deepest known dive by a marine mammal, up to nearly 3000 m, and the longest, up to 137 minutes (Schorr et al. 2014). Accordingly, it is typically found in waters deeper than 500 m, particularly over areas with complex seabed topography (canyons, seamounts). They primarily feed on deep-water squid, in some regions also on deep-water crustaceans. Prey are located through echolocation and apparently captured by suction feeding, resulting from the expansion of two throat grooves. This species is rarely seen at the surface, and it is usually alone or in small groups of up to five individuals.

**Presence in the Mediterranean Sea**

It is a regular species, likely resident, in the Mediterranean (the Mediterranean population is genetically different from neighbouring eastern North Atlantic populations), but poorly known given its inconspicuous and infrequent appearance at the surface. Most information on the distribution and abundance of this species comes therefore from stranding records, which are mainly concentrated in regions with steep bathymetry (Podesta et al. 2006). These records show that Cuvier’s beaked whales are found in both the western and eastern basins of the Mediterranean. They seem to be relatively abundant in the eastern Ligurian Sea, off Southwestern Crete, over the Hellenic Trench and in the eastern Alborán Sea (Reeves & Notarbartolo di Sciara 2006) (Supplementary Figure 13C). The absence of records from much of the Adriatic sea, despite consistent recording effort in the Italian coast, suggests that the area (of shallow water) is not used by beaked whales; in contrast, the absence of records from much of the North African coast possibly reflect a lack of data recording rather than real absence (Podesta et al. 2006). Individuals usually strand alone, with recent mass strandings (>2 individuals) being apparently a recent phenomenon and suspected to result from military activity (Podesta et al. 2006).
**History of exploitation**

Cuvier’s beaked whales seem to be relatively common in some regions, but given their infrequent and inconspicuous presence at the surface they have never been the target of full scale commercial fisheries (Wilson & Mittermeier 2014).

**Likelihood of ancient exploitation in the Mediterranean region**

This species is highly unlikely to have been exploited in the Mediterranean in antiquity, other than through the use of stranded individuals. Any bones found in the zooarchaeological records should be interpreted accordingly.
Supplementary references


(Physeter macrocephalus) movements within the western Mediterranean Sea through photo-identification.


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