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What's in a whale bone? Combining new analytical methods, ecology and history to shed light on ancient human-whale interactions

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Abstract

Ancient human-whale relationships are difficult to study because, counterintuitively, whales have been virtually invisible in the archaeological record despite the immense quantities of valuable products they provide. In this review, we explain the reasons for this invisibility, and we also show how an interdisciplinary approach combining archaeological and ethnographic studies with new biomolecular and isotopic techniques is yielding new insights, allowing a broader perspective on what whale bones found in archaeological sites or collections can tell us.

Until recently, the rare whale bones found in archaeological sites were often overlooked or misidentified. The recent development of biomolecular methods, including ancient DNA analyses and collagen peptide mass fingerprinting (ZooMS), has enabled reliable identification of whale species from even small bone fragments. In addition, stable isotope analyses can provide information about ancient whale diets, feeding habits, migrations, or even environmental changes. Combined with radiocarbon dating, these approaches provide valuable ecological and historical context for whale conservation.

The results obtained from these new analytical methods can be contextualised by historical and ethnographic information to shed light on ancient uses of whales. Indeed, ethnographic records from maritime cultures around the world reveal that in addition to the bones, whales were valued for their blubber, meat, baleen, intestines, nerves or even veins. Previously undetectable in the archaeological record, recent advances in the analysis of lipid and protein residues, trapped in ceramics or charcoal, can reveal the processing of marine mammal blubber oil in stone pits, the transport of whale products in containers, or the use of blubber for lighting.

The identification of the whale species, thanks to ZooMS or ancient DNA analyses, is also essential to consider whether the bone may have originated not simply from scavenging, but through an active capture of the whale, as only some species could be caught with pre-industrial methods. Nonetheless, historical and ethnographic records reveal that a wide diversity of pre-industrial whaling techniques existed throughout the world, beyond the traditional boat and harpoon hunting. The tools they employed, such as natural traps, stone or wooden dams, nets, spears, arrows, and ropes leave few or no artefacts, or artefacts not specific to whaling. Therefore, the absence of unequivocal evidence of whaling should not be confused with evidence that it did not exist.

Key words Ancient DNA, archaeology, ethnography, exploitation, stable isotopes, whale, ZooMS

1. Introduction

Whales have been important resources to coastal communities for millennia (e.g. Álvarez-Fernández et al., 2014; Clark, 1947; Grier, 1999; Huelsbeck, 1988; Jacob and Snoeijing, 1984), each individual providing a bounty of food and other valuable products (D'Auteroche, 1768; Vazquez de Espinosa, 1862). Whale stranding can happen along all coastlines, and their opportunistic exploitation is undoubtedly the earlier form of close contact between humans and whales (Savelle, 2005). However, stranding events are unpredictable, and so whales observed alive in the sea must have been tantalizing to coastal dwellers. In a wide diversity of regions across the world, humans developed the cooperative methods and technology that enabled them to drive or bring to shore some of those whales (Reeves 2002; Reeves and Smith 2007). Approaching such huge animals was fraught with danger, but came with substantial rewards, not only in terms of resources but also personal prestige (Arima and Hoover, 2011; Drucker, 1951; Losey and Yang, 2007). Judging from ethnographical records, whaling was associated with complex cultural practices, involving many individuals (Bodenhorn, 1990), not only for the whaling act itself but also in its preparation as well as subsequent butchering and processing of the captured whales (Grier, 1999).

Ancient relationships between humans and whales are however difficult to study, because whales can be quite invisible in the archaeological record (Smith and Kinahan, 1984). Indeed, given their enormous size, they were necessarily processed on the shore (Figure 1), their skeleton then broken down and dispersed by the action of the waves, leaving few or no archaeological traces. Even though whale bones can provide a valuable material, they are so large that they are seldom brought inland intact, being instead found as highly fragmented or transformed remains that are impossible to identify through traditional anatomical approaches. Other valuable whale resources - such as meat, blubber, and baleen - leave few or no archaeological records. This invisibility likely results in an underestimate of the value of whales to coastal populations, leaving many gaps in our understanding of ancient interactions between humans and the world's largest animals.

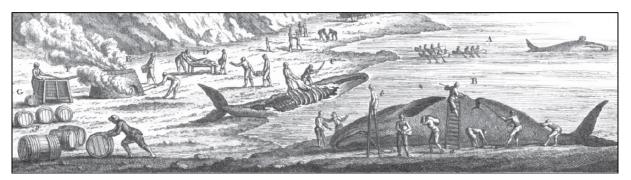


Figure 1 : Whale processing by Basques in Spitzbergen, showing a whale being towed to shore (A), blubber extraction (B and C), blubber chopping (D), oil rendering in ovens (E) and storage in wood casks (G) (Duhamel du Monceau, 1782).

Yet, a revolution in analytical methods is now making ancient whales more visible than ever, sometimes even in surprising contexts. For example, analyses of environmental DNA in Greenlandic midden deposits suggest that intensive use of whale products started 4,000 years ago, far earlier than presumed from zooarchaeological remains (Seersholm et al. 2016). Chemical analysis of cemented organic residues and charcoal samples in Late Iron Age slab-lined pits in Norway revealed their purpose for rendering oil from the blubber of marine mammals, rather than as graves or turf houses as initially presumed (Heron et al. 2010).

We present here a multidisciplinary review of the literature, focused on supporting archaeologists confronted with whale bones. By bringing together sources from archaeology, ethnography, history, ecology, and molecular and isotopic techniques our goal is to help these researchers better contextualize and thus interpret their findings, by presenting the most recent methodological advances and discussing the remaining challenges. We structured this review into three sections. The first section is devoted to the whale bones themselves, and the information that can potentially be extracted directly from them: species identity, bone age, evidence of use, and information on the whale population. The second section reviews the type of evidence that can be obtained from other types of archaeological records besides bones: whale barnacles, lipid and protein residues, environmental DNA, baleen, and the bones of potential human consumers. In the third section, we discuss how the whale may have been obtained (i.e., whether it was scavenged or captured), reviewing traditional methods of whale exploitation, the evidence that these methods can leave, and emphasizing the importance of reliable identification of whale species, given that pre-industrial whaling focused on only a fraction of them.

Given the breadth of the disciplines studied, we have not attempted to provide a systematic literature review in each individual field, but we have focused on the most recent developments (especially with regard to methodological advances) and on the most illustrative examples we have found.

2. Information obtained directly from whale bones

Whale bone specimens have often been overlooked or misidentified, so we begin this section with a brief overview of their main osteological characteristics. We then review the main types of information that can potentially be extracted directly from the bones: species identity (using collagen and ancient DNA); bone age (based on radiocarbon dating); evidence of use; and ecological information about whale populations themselves (using stable isotope and ancient DNA).



Figure 2. Examples of Magdalenian objects made in whale bone from Ermittia – level III (Guipúzcoa, Spain), 1: projectile point, 2: indeterminate object made on rod blank, a-d: close-up of the material. The porosity of whale compact bone tissue is perceptible by the presence of alveoli evenly distributed both inside (a, c) and on the surface (b, d) of the objects (modified from Lefebvre et al., 2021).

2.1. Characteristics of cetacean bones

Most whale bone found in terrestrial archaeological contexts consists of relatively small and indistinct fragments (Buckley et al., 2014). When recovered in contexts where the use of whale bone is not documented by historic or ethnographic sources, such artefacts can easily be overlooked for lack of trained specialists. For example, Pétillon (2013) and Lefebvre et al. (2021) re-discovered over 160 artefacts of whale bone in 23 Magdalenian sites across the Pyreneo-Cantabrian region, mainly large projectile heads previously archived as antler artefacts.

In reality, whale bone - and more generally cetacean bone – is a biomaterial with singular characteristics. Long bones lack a medullary cavity and the skeleton is highly porous, reflecting cetaceans' skeletal adaptations for improved hydrostatic locomotion (buoyancy control), and deep-sea diving (de Ricglès and de Buffrénil, 2001; Gray et al., 2007) (Figure 2). Histology shows that whale bone presents no clear distinction between compact and cancellous tissues. The bone tissue is porous with an evenly-spaced network of alveoli (Campbell-Malone, 2007; Felts and Spurrell, 1965; Margaris, 2014; Pétillon, 2013; Reiche et al., 2011) (Figure 2). These characteristics help differentiate whale bone from other osseous raw materials, and often make it easy to identify the bone (or the bone object) as coming from a large cetacean. However, on highly fragmented and/or poorly preserved specimens, these characteristics are not always obvious.

2.2. Identifying the species

Even for whale bones found in coastal archaeological contexts and correctly identified as marine mammal remains, morphological observation alone seldom allowed their identification to the species level, given the frequent and extensive fragmentation of cetacean bone, the osteological similarities between species, and the scarcity of complete reference collections (Speller et al., 2016). In recent years, the development of molecular methods has allowed for the accurate taxonomic identifications of even small fragments. Collagen peptide mass fingerprinting (or ZooMS) has recently been developed and tested for archaeological cetacean identification (Buckley et al., 2014; Kirby et al., 2013; Speller et al., 2016). ZooMS can differentiate baleen whales to the genus level,

and in some cases to the species level. Closely related species - such as bowhead whales (Balaena mysticetus) and the three species of right whales (Eubalaena glacialis, E. japonica, E. australis), for example— cannot be differentiated; likewise, odontocetes can usually only be identified to broad taxonomic units (Buckley et al., 2014). ZooMS, however, is ideally suited as a taxonomic screening approach. Rapid and cost-effective, ZooMS can be used to screen a large number of samples to reconstruct species distributions within archaeological sites, or to search for particular taxa of interest, and can easily identify any non-cetacean fragments in the assemblage (e.g., Evans et al. 2016). For example, ZooMS screening has been used to identify the most northerly (Hufthammer et al. 2018) and southerly distribution (Rodrigues et al. 2018) of the Atlantic gray whale - a population that was extirpated from the North Atlantic before formal analysis could be made of its ecology, migration routes and breeding grounds. ZooMS has also been effective in documenting the diversity of cetacean species exploited in Medieval Europe (van den Hurk et al., 2021, 2020). Minimally destructive compared to other molecular analyses, ZooMS is particularly useful for highly fragmented and/or modified remains, such as artefacts and tools manufactured from whale bone. For example, Hennius et al. (2018) were able to identify the use of North Atlantic right whale (Eubalaena glacialis) bone in the manufacture of Viking age Scandinavian gaming pieces. Moreover, there are several non-destructive ZooMS methods that can be employed including the analysis of collagen adhering to the plastic bags in which artefacts were stored, or collected through gentle rubbing with a PVC eraser (e.g., McGrath et al., 2019). These minimally-invasive methods however, have yet to be systematically tested on whale bone remains. Genetic analyses can provide higher resolution taxonomic information than ZooMS, providing identifications to species or population level (Foote et al., 2012), and potentially even identifying specific ecotypes (Foote et al., 2013). DNA identifications are particularly effective in the case of odontocetes, where ZooMS lacks the taxonomic resolution to differentiate many beaked whale, dolphin and porpoise species (Biard et al., 2017).

Identification to the species level is crucial for understanding the past composition of marine mammal assemblages, as well as the spectrum of interactions that humans may have had with whales, from an opportunistic utilization of stranded or drift whales (possible for all species) to active whaling (plausible for only a few species in pre-industrial times; Rodrigues et al. 2016). This aspect is discussed in the section 4.3 species matters.

2.3. Bone age

Radiocarbon dating is crucial properly to contextualize the information obtained from whale bones. Dating requires destructive sampling (in quantities even larger than those required by genetic and collagen based analyses), which is not very appealing to museum conservators, particularly when dealing with worked artefacts. Fortuitously, continuous developments in sample preparation and radiocarbon dating techniques have considerably reduced the required sample size, making radiocarbon dating possible using tens of milligrams of bone (Cersoy et al., 2017; Cucchi et al., 2020; Rofes et al., 2020), depending on the state of bone preservation.

Accurate dating of marine animals is difficult because of the marine reservoir effect (Ascough et al., 2005; Olsson, 1980). As CO₂ from the atmosphere enters the ocean by exchange at the water surface, it takes time for it to distribute evenly across the entire water body. In the deep ocean, radiocarbon will start to decay, leading to lower ¹⁴C concentrations, while new radiocarbon is constantly added via the surface. This will inevitably result in a mixture of both young and water (i.e., waters with varying ¹⁴C old concentrations) being present in the oceans. The global average reservoir age is 400 years, although there are spatial and temporal variations. Where the animals feed (e.g., open water, at depth close to the sea floor, or in coastal areas) and what they feed on (their food sources will also display typical feeding behavior), will all have an effect on the single radiocarbon measurement produced by a bone from a marine animal. As such, knowing the whale species of a particular bone can add useful information on their feeding habitat and choice of prey. Whale species feeding in fresh or brackish water can be even more challenging to radiocarbon date, as their food sources can also include terrestrial carbon originating from specific types of bedrock, such as limestone, which can bring very old (dead) radiocarbon to the equation (Philippsen, 2013). In addition, whales can make long journeys or seasonally migrate, during which they may supplementary feed in locations with different ¹⁴C signatures (Eisenmann et al., 2017).

Additionally, when archaeological whale bone is found in close context with terrestrial material, it can be extremely useful for paleoceanographers to investigate ocean reservoir offsets in the past (Ascough et al., 2005; Reimer et al., 2002), as it enables the comparison of a fully marine with a fully terrestrial sample that should be of the same age (i.e. the samples died at roughly the same time). Thus, the difference in age can be assigned to the reservoir effect, which, for example, has been done using closely associated marine mollusks shells and terrestrial material in northern Iberia (e.g. García-Escárzaga et al., 2022; Soares et al., 2016).

2.4. Evidence of utilization

Modification and marks in whale bones (together with other contextual archaeological information) can shed light on their utilization and thus value to past communities. Some bones were used whole as structural elements, such as ribs and skulls for components of housing or fences, vertebrae as stools or tables, scapulae as shovels. For example, huts made of whale ribs, and whale vertebrae probably used as stools, were excavated at a pre-19th century seasonal pastoralist Khoisan camp on the coast of Namibia (Smith and Kinahan, 1984). In Nuu-chahnulth sites in Vancouver Island (British Columbia, Canada), whale bones architectural elements served both for retaining walls and diverting water away from the houses (Huelsbeck, 1994, 289; McMillan et al., 2012, 83-86). Eighteenth Century Kamchatka Indigenous peoples used the lower jaws to make sliders for their sledges and vertebrae as mortars (D'Auteroche, 1768). The use of unmodified bonesmostly vertebrae—of large whale species as passive tools such as anvils, mortars and cutting boards is documented in the Mediterranean Basin at least from the Bronze Age to the Antiquity (Benito et al., 2019); for example, four vertebra of sperm whale (Physeter macrocephalus), excavated at the 6th-5th century BC Phoenician site of Motya in Sicily, were used as platforms for breaking purple-dye shells with stone tools (Reese, 2005).

Other whale bones were instead processed to produce a large diversity of tools and utensils (e.g. Betts, 2007; Christensen, 2016; Clark, 1947; Cunliffe, 2013; Margaris, 2014), often related to weaponry (projectile points and harpoon heads). Sometimes their specific use can be readily identified in terms of functionality based on design, as in the case of the previously mentioned Magdalenian projectile points (Lefebvre et al., 2021; Pétillon, 2013) and other weaponry, common tools such as scrapers or wedges, or even gaming pieces (Hennius et al., 2018) and other context-specific tools such as stone pressure flakers (Christensen, 2016), wool weaving combs and peat spades (Mulville, 2002).

However, some larger artefacts can be harder to interpret, as their cut marks and reductions can be suggestive of either butchery or intentional modification, leading to more tenuous functional suggestions (Bernal-Casasola et al., 2016; Mulville, 2002). This ambiguity can potentially mean that such elements remain largely ignored in archaeological studies.

In addition, some worked whale bones are the byproducts of processing, rather than worked artefacts. For example, a large quantity of whale bone cutting fragments excavated from a 15th century Māori coastal fishing camp in New Zealand, reduced longitudinally using a chipping technique, likely reflects a first step in a bone processing industry, whereby large bones were reduced into portions that could be easily transported inland, where they could then be further manufactured into artefacts (Cunliffe and Brooks 2016). Similarly, at the McKinley Inuit sites, the large majority of the whale bone sample recovered is made of waste material from the different stages of the tool-making process (Betts, 2007).

A less known but potentially significant past use of whale bones is as fuel. Whales are unique among vertebrates because of the enormous amount of oil their bones contain. Lipid content varies depending on the species and type of bone, but can reach more than 50% of the bone composition (Higgs et al., 2011). Bones could have been broken to facilitate the release of oil they contain (by dripping) or to be used directly as fuel (e.g. Hambrecht and Gibbons, 2018; Huelsbeck, 1994 cited by McMillan, 2015; Monks, 2005, 2004).

In the case of odontocetes, teeth can also be found in the archaeological record, either whole (e.g. carved sperm and pilot whale teeth dated to the Magdalenian from Spain; Corchón-Rodríguez and Álvarez-Fernández, 2008) or carved into objects (e.g., ivory buttons from Chalcolithic Portugal, Schuhmacher et al. 2013). Scrimshaw —engraved handicrafts by mariners— frequently employed sperm whale (*Physeter macrocephalus*) teeth and bone (Pichler et al., 2001).

2.5. Information regarding the whale populations

Analyses of whale bone can also reveal information about the ancient populations of the respective whale species. Carbon and nitrogen stable isotope analyses can shed light on the animals' diet and feeding habits, with δ^{15} N values reflecting the trophic level and δ^{13} C values differing between pelagic and benthic/coastal feeding areas (Newsome et al., 2010; Riccialdelli et al., 2010; Sharp, 2017). Erreur ! Signet non défini.Carbon and nitrogen stable isotope analysis of whale teeth have also been used to investigate past nursing strategies (Walker and Macko, 1999). Oxygen stable isotope analysis on bone can in some cases shed light on population structures, and on the use of feeding grounds and migration (e.g. Vighi et al., 2016), although the latter is likely to be more informative combined with hydrogen stable isotope analysis of baleen plates (e.g. deHart and Picco, 2015).

Genetic analyses can be used to distinguish different whale populations, as well as the sex of individuals (e.g. Morin et al., 2005; Pichler et al., 2001; Szpak et al., 2020). Analysis of ancient DNA (particularly when contrasted with modern DNA) can be used to reconstruct the former genetic diversity, population demographic history, size, and including anthropogenic and/or natural bottlenecks and thus be used to understand the impacts of whaling (Alter et al., 2012; Béland et al., 2020). For example, in their analysis of Northeast Pacific humpback and gray whale populations, Béland et al. (2020) were able to demonstrate that commercial whaling had relatively little effect on the overall mitochondrial or nuclear genetic diversity indices of these two species. Nevertheless, patterns of genetic characteristics were affected, with coalescent-based modelling identifying a genetic bottleneck arising from commercial hunting of these species. These studies can inform ongoing conservation efforts, by providing baselines to inform recovery targets. In addition, quantification of distinct mtDNA haplotypes or microsatellite profiles can provide insight into the minimum number of individuals found in a given area (e.g. Arndt 2011; Béland et al. 2020; Evans et al. 2016), which is often otherwise exceedingly difficult to estimate in highly fragmentary assemblages.

3. Evidence from beyond the bones

Until recently bones, and teeth for odontocetes, were the only whale remains that could dependably be found in the archaeological record. However, advances in analytical methods are now bringing to light other direct and indirect evidence of ancient whale utilization. In this section, we start by reviewing historical and ethnological records of ancient uses, processing, storage and transportation of whale products, as context for archaeological records other than whale bones. We then review the main types of such records and the information that can be derived from them: whale barnacles; lipids and protein residues; environmental DNA; baleen; and isotopic analyses of the bones of human consumers.

3.1. The many uses of whales

Ethnological records reveal the wide diversity of whale uses. For example, Jean Chappe d'Auteroche (1768) described how the Indigenous peoples in Kamchatka took advantage of every part of the gray whales they hunted (D'Auteroche, 1768). Meat was dried and eaten, with the tongue and fins particularly appreciated. Blubber was also smoked and eaten, as well as rendered into oil for illumination and for heating. The whale skin was dried and beaten, and then transformed into shoe soles and belts. The baleen was used to sew canoes and to make nets for fishing and hunting. Intestines were used as containers, bladders as floaters, as well as to make waterproof clothing. Nerves and veins were converted into ropes. Careful reading of ancient texts can also bring these whale parts to life. Two passages could be examples of such textual evidence in the Mediterranean: Petronius (Satyricon, chapter 21, transl. Arrowsmith and Arrowsmith 1959) mentions a "whalebone-cane" plausibly made of baleen, and Aelian (On the Characteristics of Animals, book 17, section 6, transl. Scholfield 1959) explains that sinews of large sea monsters are useful for the stringing of harps and other instruments, and even for engines of war.

A single large whale provides tons or tens of tons of meat and blubber, and a main challenge is to quickly preserve these products for future consumption before they spoil. In the Arctic, cellars dug in the permafrost could have been used to freeze them year round, as is still done today by the Iñupiat whalers in Alaska (Krupnik et al. 2012). Elsewhere, available options for preserving whale products included smoke drying (e.g. in Kamchatka, 18th century; D'Auteroche 1768), salting (e.g., in Medieval Europe; Szabo 2008), and drying by burying in the sand (e.g., 17th-19th century south-western Africa; Smith and Kinahan 1984).

Blubber could also have been rendered into oil, which keeps for a long time if stored properly, and has for millennia been a major output of whale exploitation (Monks, 2005). Simple methods to render oil included letting it drip from the blubber (e.g., 18th century Olioutores, Kamtchatka; D'Auteroche 1768) and heating in the sun (e.g., 18th century Chango Indians from Northern Chile; Vazquez de Espinosa 1862). More sophisticated methods involved using hot stones (e.g., Norway Iron Age, Heron et al. 2010), boiling (e.g. 17th century Khoi, South Africa; Smith & Kinahan 1984), and furnaces (e.g. 19th century Basque whalers; Duhamel du Monceau 1782, figure 1). Oil was used directly as food (e.g., Changos, Vazquez de Espinosa 1862; Khoisan, Smith & Kinahan 1984), as fuel for illumination and heating (e.g., Kamchatka Indians; D'Auteroche 1768), in the impermeabilization of ropes, leather or boats, as well as in the manufacture of products like soap and paint (e.g. 17th century Europe, Viret, 1671). Spermaceti, a liquid wax found in the head cavity of sperm whales, was particularly prized in Medieval Europe as a lighting fuel because it burns without producing smoke and odour.

Dried blubber or meat could have been transported without particular containers, including as packs directly attached to the body (e.g., hunter-gatherers of southern South America; Bove 1883 cited by Lefèvre et al. 2003). Oil required containers, but simple options mentioned in historical texts included the intestines of whales (Olioutures; D'Auteroche 1768) or of seals (Changos; Vazquez de Espinosa 1862), dried kelp (Khoisan; Smith & Kinahan 1984), and skins (19th century Makah from the northwestern United States; Scammon 1874). Basque whalers used wooden casks for the transport and trade of oil (Duhamel du Monceau, 1782).

Baleen plates are the filtering system used by baleen whales (Mysticeti) to remove prey from the water. Consisting of long strains of keratin, they vary in size and physical properties depending on the whale species. Right whales, and even more so bowhead whales, have particularly long baleen plates (up to 4 m in the latter) that have long been appreciated as a strong and flexible material. Traditional uses of baleen by Arctic whalers included weaved baskets and mats, nets, weirs, fishing lines, and snares (Lauffenburger, 1993) but also some kinds of knives, end- and side blades, and lashing strips for tools and weapons, as well as for drying racks (Mathiassen, 1927). In historic times, baleen was a prized commodity from commercial whaling. Using heat and pressure, baleen could be fashioned into complex shapes, and was incorporated into objects like collars and corsets, buggy whips, brushes and bed springs.

The degradability of meat, blubber, oil and baleen means that evidence of their use is largely absent from the archaeological record (Smith and Kinahan, 1984). Nonetheless, direct and indirect evidence may sometimes remain, as reviewed below.

3.2. Whale barnacles

The oldest archaeological evidence for the transport and use of whale blubber is unexpectedly provided by whale barnacles, i.e., cirripede crustaceans that live deeply embedded in the skin of some whale species. Because barnacles can only be removed by cutting the skin, their presence in archaeological contexts associated with past human settlements is evidence of the transport of skin and its underlying blubber, and potentially also meat, for human use (Kandel and Conard, 2003). Furthermore, as certain barnacle species are quite specific to particular whales (Hayashi, 2013; McMillan, 2015), they can be used to understand which whale species was likely used. For Tubicinella major and Cetopirus example, complanatus are barnacle species found today almost exclusively in association with right whales (Hayashi, 2013), so their finding in a Magdalenian site in Spain is strong evidence that right whales were exploited by contemporary maritime-oriented forager human groups (Álvarez-Fernández et al., 2014). Similarly for the finding of C. complanatus in the late Middle Pleistocene human settlement of Pinnacle Point in South Africa (Collareta et al., 2017). Findings of Coronula diadema in Later Stone Age sites in southern Africa point instead to the likely use of humpback whales (Megaptera novaeangliae; Kandel and Conard 2003). Coronula reginae, associated to humpback whales, were discovered in the Nuu-chahnulth sites (northern coast of Vancouver Island, Canada), together with Cryptolepas rachianecto, specific to gray whales (Wessen, 1994 cited by McMillan, 2015).

3.3. Lipid and protein residues

Surfaces that came into contact with whale meat, blubber or oil may still hold residues that reveal their previous uses. For example, characterization of organic residues in fragments of large ceramic containers, taken from a 16th-17th century warehouse in Lekeitio (Basque Country, northern Spain), indicate that these were whale oil containers (Blanco-Zubiaguirre et al., 2018).

In another study, chemical analyses of fatty acids in cemented organic residues and charcoal samples of Late Iron Age slab-lined pits in Arctic Norway revealed that they were used for rendering oil from the blubber of marine mammals (Heron et al. 2010). These pits - elliptical or rectangular depressions (2-4 m in length, and 1-2 m in width, up to 1 m in depth), often lined with stone slabs - were initially interpreted as graves or as turf houses. Signs of thermal influence in the slabs, as well as abundant finds of charcoal and fire-cracked rocks are consistent with an oil rendering method involving alternate layers of blubber and heated stones. More than 700 pits are known, usually in groups up to 5, indicative of a widespread use of marine mammal oil, yet the only known faunal remain is a single vertebra of a small whale (Heron et al. 2010).

Besides containers, other promising artefacts to study are those associated with illumination. For example, analyses of Mesolithic shallow oval bowls in the Baltic region (a combination of lipid biomarker and bulk and single-compound carbon isotope analyses) demonstrated their past used as oil lamps fueled with marine animal fat (Heron et al. 2013; Nilsen 2016). However, the degradation of fats and oils within archaeological pottery vessels, particularly if burnt, makes it difficult to specify the species or group of species concerned. For example, the very few chemical analyses of Antique oil lamps in the Mediterranean region have sometimes revealed the presence of animal fat but without being able to distinguish between bovine, ovine, fish or marine mammal origins (Copley et al., 2005; Kimpe et al., 2001). Accordingly, the chemical analysis of burnt fat and other organic residues remains particularly challenging and requires more developed methods to reveal their precise origin (Heron et al. 2010; Lucquin 2016). Analysis of entrapped proteins on ceramic vessels may potentially provide greater taxonomic insights as proteins are often more species-/genus-/family-specific while lipids and isotope composition

are dependent on dietary and environmental factors. For example, proteomic analysis of Iñupiat potsherd fragments from Alaska revealed seal myoglobin (muscle) and hemoglobin (blood) proteins (Solazzo et al. 2008). As specific proteins are frequently expressed only in particular tissues (e.g., blood, skin, muscle), this approach may provide greater insights into particular parts of whales processed or stored in ceramic vessels.

3.4. Environmental DNA

High-value portions of whales like meat and blubber tend to degrade rapidly, but may leave biomolecular traces within archaeological sediments. For example, Seersholm et al. (2016) analyzed sedimentary DNA (sedaDNA) within midden deposits from Greenland, detecting the exploitation of bowhead whales dating back 4,000 years. Indeed, they found that in some Paleo-Indian contexts, marine mammals, and bowhead particularly whale, dominated the recovered DNA profiles, suggesting that the importance of whale products was far greater than would be presumed based on zooarchaeological remains alone.

3.5. Baleen

The degradability of baleen means that archaeological specimens are rare, being mostly found in association with Arctic whaling cultures (e.g. Sinding et al., 2012; Solazzo et al., 2017), although there are exceptions (e.g. 12th century fragments found in waterlogged organic midden layers in Scotland, Moffat et al., 2008). More recent baleen artefacts can be found in museum collections (e.g., 18th-19th century corset busks; an early 20th century Kinguktuk basket, Lauffenburger, 1993).

The analysis of baleen can uncover valuable information regarding the identity of the species as well as of contemporary environmental conditions. For example, Sinding et al. (2012) successfully extracted and amplified DNA from small fragments of baleen dated back more than 4,000 years ago, highlighting its potential value as a source of ancient DNA for studies on whale population genetics. More recently, application of a keratin peptide mass fingerprinting technique to 29 fragments of unidentified and partially degraded samples of baleen excavated from prehistoric archaeological sites in Labrador (Canada), demonstrated a dominance of bowhead whale in the archaeological assemblage (Solazzo et al. 2017). Baleen can also provide a valuable archive of the individual's lifetime, given that it forms continuously over the years and becomes metabolically inert after synthesis. Indeed, stable isotope analyses (of carbon, nitrogen, oxygen and hydrogen) can reveal dietary changes across time, shedding light on environmental changes experienced by the individuals (Bentaleb et al., 2011; Schell, 2000). For example, sequential carbon and nitrogen stable isotope analysis on baleen revealed there was limited exchange in foraging grounds between two subpopulations of fin whale in the Atlantic and Mediterranean (Giménez et al., 2013), while oxygen and hydrogen stable isotope analyses of baleen plates have been used to investigate the migratory routes of bowhead whales, also highlighting the value of baleen as a record of historical sea ice concentration and Arctic climate (deHart and Picco, 2015). Depending on the state of preservation, even certain hormones can be retrieved from whale baleen, which can show insights into the individuals' stress levels (Rolland et al., 2019). Baleen preserved in museum collections can thus provide a rich isotopic and genetic archive for whales living within the last few centuries.

3.6. Isotope analyses of human bones

If whales were an important part of human diet, this will have left a signature in human bones. Indeed, the nitrogen stable isotope values of human bone collagen reflects the trophic level of diets (Kelly, 2000), which combined with carbon stable isotope values can be used to distinguish marine from terrestrial consumption (Chisholm et al., 1982). For example, stable isotope analyses of Eastern Arctic foragers from the Thule period indicates that they relied on bowhead whales for circa 12% of their dietary intake (Coltrain et al., 2004).

4. How the whale might have been obtained

Given a whale bone in an archaeological context, it is inevitable to wonder: was it obtained from a whale found naturally stranded on a beach? Or was it the product of ancient whaling? This section provides context for helping researchers to answer this question. Firstly, we draw on ethnographic and historical sources to overview the diversity of methods humans have developed for exploiting whales. Secondly, we discuss the different types of evidence that whaling can leave, including written sources, graphical representations, archaeological records of whaling implements, and evidence of transformation and use of whale products. Finally, we highlight the need to identify whale bones to the species level to discuss a possible active capture of whales.

Naturally stranded or drift whales can be found along all coastlines, although they are more frequent in some regions ('stranding hotspots'; Brabyn & McLean 1992) and in particular seasons (Evans et al., 2005). Most stranding events correspond to single individuals, but mass stranding of multiple individuals (of the same or different species) can also occur. These events are unpredictable, but they are sufficiently frequent for coastal communities to have developed techniques to take advantage of the abundant resources they bring (e.g., well-developed regulations in Medieval Norse societies regarding rights over beached whales; Lindquist 1997). Freshly deceased whales provide vast amounts of edible meat, blubber as well as other useful materials (veins, tendons, intestines...). Dead whales decompose very rapidly, and so stop being edible (Huelsbeck, 1988), but bones can remained available for exploitation for years or decades (although they progressively lose their oil, and hence their value as fuel).

The active killing of whales requires preparedness and cooperation, but not necessarily sophisticated technologies. Maritime cultures around the world have developed a wide variety of whaling methods, in regions as diverse as the Arctic, both coasts of the North Pacific, Atlantic, South Pacific, Indonesia, the Lesser Antilles, and Equatorial Guinea (Reeves, 2002; Reeves and Smith, 2007).

The first step in whaling is detecting the whale. Before the 16th century (when the navigation technology necessary for offshore whaling developed), only those whales that naturally came very close to the shore were accessible to early whalers.

Once a whale is detected, a much more substantial challenge is to kill it and to retrieve it, particularly for larger whales. One approach involves forcing the whale to strand, which some whalers did by surrounding it with small boats and using nets and/or making much noise to direct it to shore (e.g., gray whale hunting in early 20th Century, Korea Andrews 1916; and in 18th Century Kamchatka, D'Auteroche 1768; ancient and modern pilot whale hunting in the Faeroes, Lindquist 1997). Other options involve the use of traps, natural or artificial. For example,

medieval Norse whalers took advantage of natural traps like closed bays or rivers: of a whale entered it, they would then prevent it from leaving (Lindquist 1997). In estuary of the Saint Laurence River, 18th-20th century whalers installed wooden weirs that allowed whales in during the high tide, while becoming barriers in the low tide (Reeves 1985), a similar mechanism to that of Medieval whaling stone dams in Norway (Lindquist 1997). The whaling scenes in the magnificent Bangudae petroglyphs in southeastern Korea (date undetermined) seem to represent the use of nets and wooden weirs to capture large baleen whales (Lee, 2011). In the Arctic, natural traps also occur as gaps in the sea ice, with whales that surface to breathe being vulnerable to attack (with harpoons) from above.

More active forms of killing whales necessarily involved the use of piercing instruments. Lances or arrows hurled with sufficient energy to pierce deeply across the blubber would cause the whale to die in a few days (Lindquist, 1997), a process sometimes accelerated through the use of poison (e.g., among Medieval Norse and the North Pacific whalers; Reeves & Smith 2007). However, this method does not necessarily guarantee recovery of the whale, as the dead animal could sink in the high seas, or strand far away. To increase the likelihood of recovery, medieval Norse (Lindquist, 1997) and Alaskan Inuit (Reynolds, 1989) whalers marked their lances individually as a means of claiming rights over whales subsequently found by others.

Harpoons - i.e., barbed projectiles with an attached rope - are a technological solution to improve the odds of recovering the whale. In the case of the Makah in the northeastern Pacific (Scammon, 1874) as well as in the Arctic (Reeves and Smith, 2007), whalers approached whales in small boats, and handthrew harpoons attached to inflated sealskin floats (Figure 3). The floats created drag on the harpooned whale's escape and signaled its presence as it resurfaced, allowing whalers to approach it again, throw additional harpoon-line-float arrays, until the whale was sufficiently weakened to be killed with hand lances (Figure 3). The first reliably dated whaling scene, carved in a walrus ivory piece dated to 3,000 BP from the Bering region (Pringle, 2008), may illustrate this method, showing the use of sealskin floats in the capture of a (likely) gray whale. It represents the boat fastened to the whale by a rope, which may indicate that it too was being used to create drag, apparently supported by a drogue (a

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device trailing behind to provide additional resistance). Dragging behind a large whale would however have been a very dangerous endeavor (as a diving whale can easily sink a small boat), and so this scene may have represented the final stages of whaling (the boat fastened to the whale only after the animal became tired). Medieval Basque whalers developed a method that explicitly required them to remain fastened to the whale. They used lines so long that the harpooned whale could sprint away or even dive without endangering the boat, while allowing the whalers not to lose track of it. By following the line, the whalers could then re-approach to attach more harpoons and lines. Once the whale was very tired, the whalers approached it and killed it with long lances (Duhamel du Monceau, 1782). This very efficient method became the foundation of European (and subsequently American) industrial whaling (Reeves and Smith, 2007).



Figure 3: Whaling scenes: (a) English whalers in the North Atlantic, 19th century (Cheever, 1853) and (b) Makah Indians, Washington State, USA (Elliott, 1886)

4.1. The evidence left by whaling

Written records can provide an exceptional level of detail about past whaling activities, including the methods used by past whalers and of the use of whale products. Some examples of particularly rich accounts include the above-mentioned report by D'Auteroche of Kamchatka Indians (witnessed in 1761; D'Auteroche, 1768), the account by Vazquez de

Espinosa regarding Changos in today's Northern Chile (1752-53; Vazquez de Espinosa, 1862), and Scammon's description of Makah whaling in today's Oregon (USA) and Canadian coasts (Scammon, 1874). However, written reports are only available for whaling cultures that persisted into relatively recent times. Furthermore, earlier whaling accounts may be deemed unreliable; for example, a late 16th Century description of whaling by Florida Indians (Acosta et

al., 1880) has been generally discounted and even ridiculed (Braginton-Smith and Oliver, 2008).

Another highly valuable line of evidence comes from graphical representations of whaling, particularly when they realistically illustrate the quintessential scene of a whaling boat linked to a harpooned whale by a line. This is the case with the above-mentioned carved walrus ivory pieve from the Bering region (Pringle, 2008), whaling scenes represented in the Pegtymel petroglyphs in Chukotka, Russia (Dikov, 1999), and in the El Medaño rock art from Northern Chile (Ballester, 2018). Less typical (and thus more ambiguous) are the realistic representations of whales superposed by nets and wood weirs in the Bangudae petroglyphs of South Korea, which have also been considered as evidence of past whaling (Lee 2011). Graphical representations do not necessarily exist, or they may have existed but not have survived, or they may not appear as obvious representations of whaling to a modern observer.

Large harpoons can be strong evidence of past whaling, and have been found in several archaeological contexts associated with whaling cultures (e.g., Monks et al. 2001; Ballester 2018). However, harpoons were also used for the capture of other large marine animals (e.g., seals, turtles, sharks, manta rays) and so their presence is not by itself irrefutable evidence of whaling (Losey and Yang, 2007). Conversely, harpoons may also be rare even in deposits from areas where whaling is definitely confirmed; as prized possessions, they were not often discarded, but reused (Monks et al., 2001). Furthermore, as discussed in the previous section, harpoons were not used in all whaling methods. Their absence from the archaeological record is thus not a proof that whaling did not take place. More broadly, many of the above-mentioned methods for killing whales involve implements (such as small boats, nets, ropes, stone or wood weirs) that are not necessarily specific to whaling and could have been employed in the context of other fisheries (Bekker-Nielsen and Bernal-Casasola, 2010). With ancient whaling being a coastal activity, the boats involved were not necessarily seaworthy, and may appear unremarkable in the archaeological record, or not at all. For example, the Changos in Northern Chile used inflatable rafts made of sea-lion skins (Vazquez de Espinosa 1862; Ballester 2018).

Given the huge size of whales, it is rare to find direct marks on the whale bones that can indisputably

prove that humans captured the live animal. Rare examples include findings of bone points embedded in whale bones, such as in a phalange of a humpback whale found in Oregon (Losey & Yang 2007), or in two bones from the Neolithic site Hwangseong-dong in South Korea (Yoo, 2017), providing strong evidence that the animals were actively attacked. More commonly, though, the harpoons merely pierce the blubber without touching any bone. Other methods of whaling (e.g. using traps) would be even less likely to leave such marks on the bones.

Whaling produces very large quantities of whale bone, so in theory it should result in conspicuous archaeological evidence. In practice, though, shore erosion or sea level rise mean that much of it is currently underwater (McLeod et al., 2008). Conversely, given that a substantial amount of bone can be obtained from a single stranded whale, a relatively high abundance or frequency of bone artefacts (e.g., evidence of a Magdalenian whale bone industry; Lefebvre et al., 2021; Pétillon, 2013) does not by itself demonstrate past whaling. Nonetheless, an increase in the use of whale bone may indicate an increase in its availability. For example, archaeological records show that nonwhaler Pre-Inuit groups manufactured some utensils from whale bones, such as shovels from scapulae in Ipiutak settlements (Larsen and Rainey, 1948), architectural elements in a Late Dorset semisubterranean structure (Ryan, 2003), or sled shoes from ribs in Dorset campsites (Houmard, 2011). However, the quantity and diversity of whale bone implements increased markedly after the 7th century A.D. (in the Old Bering Sea and the subsequent Birnirk and Thule culture) to include the manufacture of tools, weapons, and amulets (Mason and Friesen, 2018; Mason and Rasic, 2019; Mathiassen, 1927), indicating that whale hunting became more intensive then.

Whaling would also have produced large amounts of meat and blubber. These products are even less likely than bones to have been preserved in the archaeological record (but see the above-mentioned analysis of environmental DNA by Seersholm et al., 2016), but other types of archaeological evidence can come from the structures used to process these products. Such structures are unlikely to have existed if whale use was opportunistic (and thus unpredictable in space and time), but may have been built by communities able to bring whales regularly and predictably to designated coastal points. This is the case of tryworks, brick furnaces built by 16th-19th century European and American whalers to render blubber into oil (Paterson, 2006). It may also be the case of the hundreds of Iron Age slab-lined pits found in Arctic Norway, for which residue analysis indicates a prior use for rendering oil of marine mammals. However, their presence alone is not evidence of whaling, as they may also have been used for processing other marine animals such as seals. Conversely, the hundreds of large tanks (cetariae) found in coastal Roman archaeological contexts and known from historical records to have been used for processing tuna (Trakadas, 2005) might have also been used to process whales (Rodrigues et al., 2018). Look-out towers for detecting the whales are another type of physical structure associated with whaling (e.g. Basque atalayas; Aguilar 1986) but again they could have served other purposes too (e.g., detecting enemies).

Overall, in the absence of reliable ethnographic records, realistic graphical representations or very large harpoons (ideally all three), it is very difficult to demonstrate that active whaling took place. Accordingly, the tendency among archaeologists is to fall back on the default assumption that whale remains correspond to scavenged animals (Losey and Yang, 2007). However, a lack of whaling evidence should not be mistaken for evidence that whaling did not occur.

4.2. Species matters

Until quite recently, only those whales that naturally came close to shore (or, in the Arctic regions, close to the edge of the sea-ice) were available to whalers. For this reason, pre-industrial whaling focused mostly on a narrow range of whale species (Reeves, 2002). These include smaller odontocetes, such as beluga (Delphinapterus leucas), narwhal (Monodon monoceros), pilot whales (Globicephala sp.), and killer whales, that are either coastal or approach the coast at predictable seasons. Among the larger whales, the focus was on those that are coastal year round (gray whale) or that come close to shore for calving and during migration (right, bowhead, and humpback whales), with the calves being particularly targeted (Aguilar, 1986; Krupnik, 1993; Savelle and McCartney, 1991). In a few coastal areas adjacent to deep seas, high-seas species that came very close to shore were taken too (e.g. sperm and Bryde's whales off Lamalera, Indonesia; Barnes 1996), but otherwise the technologies for killing and retrieving non-coastal whale species were only developed recently, particularly for *Balaenoptera* species that are quite fast and sink once killed (which only started being exploited systematically in the late 19th century; Reeves & Smith 2007).

For this reason, knowing the identity of whale species (and thus its ecology) is key to contextualizing whale bones found in archaeological contexts, and specifically for talking the question of how the bones might have been obtained. Indeed, whereas all whale species could have been found stranded, only a subset could have plausibly been actively taken with pre-industrial technology (Rodrigues et al., 2016). Accordingly, archaeological species profiles with an abundance of large, off-shore, fast-swimming species (e.g., fin or blue whale) point towards an opportunistic exploitation of beached animals, whereas a species profile dominated by smaller odontocetes, or slower moving, near-shore baleen whales (e.g., right, gray or humpback whales) provides more support for active acquisition strategies (Rodrigues et al. 2016). For example, ZooMS and genetic analyses of bones found in Roman and pre-Roman archaeological sites revealed the past presence of two coastal whales species (North Atlantic right whales E. glacialis; gray whales Eschrichtius robustus) in the Gibraltar region, opening the possibility of their exploitation during the Roman period (Rodrigues et al., 2018). Similarly, genetic analyses of bone fragments from archaeological and paleontological sites in New Zealand revealed a diversity of whales species used by precontact New Zealand Māori, including three small toothed whale species (killer whale Orcinus orca; Cuvier's beaked whale Ziphius cavirostris, unspecified Delphinidae) that could have been plausibly actively whaled (Seersholm et al. 2018). On the Northwest Coast of North America, genetic analyses of pre-contact archeological cetacean bones, associated with the traditional whaling culture, the Nuu-chah-nulth, have revealed a persistent focus on gray and humpback whales dating back 4,000 years (Arndt, 2011; Béland et al., 2020) — the same species identified in oral histories and documented in ethnographic whaling accounts (Drucker, 1951; Monks et al., 2001).

Biomolecular analyses may also confirm or refute hypotheses regarding the dominant target species within historic time frames. For example, right whales were believed to be the dominant species taken by Basque whalers in the Western Cantabrian Sea in the 13th-18th centuries, and this has been confirmed by analyses of cetacean remains from whaling harbours (Rey-Iglesia et al. 2018). In contrast, whereas right whales were also believed to have been the focus of 16th-17th century Basque whaling, in the Strait of Belle Isle and Gulf of St. Lawrence, biomolecular analyses of bones revealed instead a strong focus on bowhead whales (McLeod et al., 2008; Rastogi et al., 2004).

5. Conclusions

The general invisibility of whales in the archaeological record makes the finding of isolated whale bone artefacts difficult to interpret: are they the outcome of an opportunistic use of beached animals, or the last vestiges of an ancient close connection between humans and whales? Here we argue that while the latter is difficult to prove, it is a possibility that archaeologists should keep in mind. Indeed, the high value of whale products has prompted a wide diversity of societies across the world to develop approaches for actively accessing them, many of which involving relatively simple technologies (Reeves, 2002; Reeves and Smith, 2007). It seems likely that a good number of such societies disappeared without leaving undisputable evidence of their whaling activities, such as credible ethnographic records or realistic rock art. Coastal dynamics and sea level rise may have also eliminated much of the possible archaeological evidence (Szabo, 2008). Furthermore, in some cases the coastal whales themselves disappeared (Rodrigues et al., 2018), putting the possibility of whaling even further beyond the radar of archaeologists.

We thus recommend keeping an open mind and taking a broad perspective when analyzing evidence of ancient whale utilization. This involves placing archaeological records in an ecological context, keeping in mind the diversity of uses as well as whaling approaches known from ethnographic records, and taking advantage of modern molecular analytical techniques that are now revealing the presence of whales at the bottom of a container, in an oil lamp, as the tip of a weapon, or even in a dusty archive. The nature of pre-industrial human-whale interactions is still very poorly understood and its prevalence is certainly underestimated. Molecular and isotopic techniques, be it ancient DNA, ZooMS, radiocarbon dating and stable isotope analysis, residue analyses (or better yet the combination of several of these), are gradually helping us to draw the outline of these interactions, rendering visible previously unnoticed giants.

Author contributions

Anne Charpentier: Conceptualization, Writing -Original Draft, Writing - Review & Editing. Ana S.L. Rodrigues: Conceptualization, Writing - Review & Editing. Claire Houmard: Writing - Review & Editing. Alexandre Lefebvre: Writing - Review & Editing. Krista McGrath: Writing - Review & Editing. Camilla Speller: Writing - Review & Editing. Laura van der Sluis: Writing - Review & Editing. Antoine Zazzo: Writing -Review & Editing. Jean-Marc Pétillon: Writing -Review & Editing, Funding acquisition.

Declaration of competing interest

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

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