



Ecological globalisation, serial depletion and the medieval trade of walrus rostra

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ABSTRACT

The impacts of early ecological globalisation may have had profound economic and environmental consequences for human settlements and animal populations. Here, we review the extent of such historical impacts by investigating the medieval trade of walrus (*Odobenus rosmarus rosmarus*) ivory. We use an interdisciplinary approach including *chaîne opératoire*, ancient DNA (aDNA), stable isotope and zooarchaeological analysis of walrus rostra (skull sections) to identify their biological source and subsequent trade through Indigenous and urban networks. This approach complements and improves the spatial resolution of earlier aDNA observations, and we conclude that almost all medieval European finds of walrus rostra likely derived from Greenland. We further find that shifting urban nodes redistributed the traded ivory and that the latest medieval rostra finds were from smaller, often female, walruses of a distinctive DNA clade, which is especially prevalent in northern Greenland. Our results suggest that more and smaller animals were targeted at increasingly untenable distances, which reflects a classic pattern of resource depletion. We consider how the trade of walrus and elephant ivory intersected, and evaluate the extent to which emergent globalisation and the “resource curse” contributed to the abandonment of Norse Greenland.

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1. Introduction

Ecological globalisation, the spatial displacement of our interface with nature, creates interdependencies between rural or hunter/gatherer communities and distant centres of consumption. It can impact flora and fauna through the serial depletion of wildlife and the search for new hunting or fishing grounds (Richards, 2003; Pitcher and Lam, 2015) which may further lead to expanding colonisation (Barbier, 2011). Combined with other exacerbating factors, it can threaten the socio-economic resilience of

communities dependent on hunting and fishing (Campbell and Butler, 2010; Dugmore et al., 2012; Pitcher and Lam, 2015). Here, we consider the impacts of ecological globalisation by investigating the medieval trade in walrus ivory through a unique combination of interdisciplinary methods – using *chaîne opératoire* (manufacturing sequence), ancient DNA (aDNA), stable isotope and zooarchaeological (osteometric) analysis – of modified walrus skulls (rostra) in which tusks were often traded as pairs. The ivory was valued in medieval Europe as raw material for a variety of art objects (Williamson, 2010; Dectot, 2018), most famously the Lewis Chessmen (Caldwell and Hall, 2014).

It is often difficult to constrain pre-modern human impacts on the environment, even when the ecological and historical implications are potentially major (e.g. Barrett, 2016, 2019; Koch et al., 2019). Atlantic walruses (*Odobenus rosmarus rosmarus*) are an important focus of study in this regard. They are particularly susceptible to over-exploitation (Kovacs et al., 2014; McLeod et al.,

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2014) given their propensity to return to the same feeding grounds and to haul out in large groups (Lydersen, 2018). It has thus been proposed that the trade of walrus ivory was at least partly responsible for the Norse colonisation of Greenland in the 980s CE, after Iceland's walrus population became overexploited (Frei et al., 2015; Smiarowski et al., 2017; Keighley et al., 2019). In this study we focus on subsequent walrus exploitation during medieval times, considering possible serial depletions, their causes and their consequences, by studying walrus rostra from between the 11th and 15th centuries CE. We build on recent aDNA evidence for a temporal shift between two distinct mitochondrial genetic clades among traded, medieval European finds of walrus rostra (Star et al., 2018). These clades have specific geographic distributions, whereby a western clade is only present in populations from western Greenland and Arctic Canada. Thus medieval European finds of this clade must have arrived via Norse Greenland. An eastern clade is more widely distributed: it is the only clade from Arctic Europe to eastern Greenland, yet co-occurs with western clade walruses in western Greenland and Canada (Star et al., 2018). The observed temporal shift from eastern to western mitochondrial clade may thus imply a change of source population during walrus hunting. Our interdisciplinary approach tests this hypothesis and explores its possible archaeological and ecological implications. The relationship between archaeological and genomic approaches is often contentious (Kershaw and Røyrvik, 2016; Vander Linden, 2016; Knipper et al., 2017; Callaway, 2018). We employ an integrated research design, in which the disciplines together yield discoveries that would not be achievable using a single method in isolation. The methods associated with each aspect of the study are provided at the start of the relevant subsections.

2. Current and past distribution of the atlantic walrus

Narrowing the potential sources of medieval finds of walrus rostra begins with a consideration of the distribution of the taxon and the accessibility of different populations to medieval hunters. The Atlantic walrus is found from the Kara Sea north of Siberia to the Canadian Arctic, although it has retracted through time due to over-exploitation (Kovacs et al., 2014; Stewart et al., 2014; Higdon and Stewart, 2018; Keighley et al., 2019). For a study of medieval trade, the key known changes were the probable Viking-age extirpation of an Icelandic population and the 19th-century disappearance of walruses from Bear Island in the central Barents Sea. Icelandic zooarchaeological, historical and literary sources indicate that walruses were rare visitors to the island after the initial Viking-age settlement (Einarsson, 2011:48; Frei et al., 2015; Smiarowski et al., 2017; Murray-Bergquist, 2017; Keighley et al., 2019). For example, of 34 radiocarbon dates on Icelandic walrus finds published by Keighley et al. (2019), only three postdate the 9th century CE. Iceland is thus likely to have been a net consumer rather than exporter of walrus ivory during the predominantly 11th-to 14th/15th-century chronology of the rostra under study (cf. Brown, 2015; Keighley et al., 2019). The existence of a past walrus population on Bear Island in the Barents Sea (Lønø, 1972:199–201) may explain 17th-to early 19th-century incidental records of walruses in Finnmark, northern Norway (Munthe-Kuas Lund, 1954), during a period also characterized by the cold conditions of the Little Ice Age (Grove, 2004). On this evidence, small-scale walrus hunting may have been possible in northern Norway during the Middle Ages. Atlantic walruses would also have been accessible further east in the Barents Sea, along the northern coast of the Kola Peninsula, and from the Kanin Peninsula to the Kara Sea (Boltunov et al., 2010; Mäkinen and Vanhatalo, 2018). The Barents Sea region was noted as a source of walrus ivory, acquired by a Norse chieftain through trade with Sámi hunters, in the famous Ohthere account of

the late 9th century (Bately and Englert, 2007). Subsequently, the continued relevance of a Barents Sea source throughout the Middle Ages could be implied by finds of walrus ivory and rostra from Novgorod (Smirnova, 2001, 2005) and Kiev (Сагайдак et al., 2008; Khamaiko, 2018), which had strong trading links with northern Russia and Norway (Hansen and Olsen, 2014:146–152).

Conversely, there is no accepted evidence for walrus hunting or other human activity in the Svalbard archipelago prior to its post-medieval discovery in the sixteenth century (Arlov, 1996:50–51; 2005; Hultgreen, 2000:305–307). The medieval 'Svalbard' of Icelandic sources is more plausibly Jan Mayen (Hofstra and Samplonius, 1995). Moreover, contrary to general belief (e.g. Frei et al., 2015; Dectot, 2018), it is also unlikely that walruses were hunted in the White Sea proper (beyond the Gorlo Strait) during the Middle Ages. Today, and in the past, walruses have been present very rarely in the White Sea, and then mainly in winter on sea ice where hunting would have been problematic (Ognev, 1962:285; Chernook et al., 2010).

Greenland was accessible to trade with medieval Europe from the foundation of a Norse settlement c.985 until its disappearance in the 15th century (Arneborg, 2003; Keller, 2010; Nedkvitne, 2019). Here walruses occur at high latitudes on both the east and west coasts (Born et al., 1994, 1997). Difficult sea-ice conditions mean that the eastern Greenland population was unlikely to have been targeted by medieval hunters (Ljungqvist, 2005) as walruses seldom occurred south of Scoresby Sund (Kangertittivaq) along the east coast, even in the past (Born et al., 1997:9) (see Fig. 1). The western option was far more accessible to medieval Norse hunters, especially given the short summer navigation season. Small numbers of walruses could have been hunted locally from Greenland's Western Settlement (Born et al., 1994:6–8; McGovern et al., 1996), but based on historical records and some archaeological evidence the main hunting grounds for the Greenland Norse are thought to have been around Disko Bay (Qeqertarsuup Tunua) or even further north (Roedahl, 1995, 1998; Arneborg, 2003:171; Gulløv, 2016; Nedkvitne, 2019:174–176). Longer trips to High Arctic Greenland and Canada (e.g. around Smith Sound), including trade with Thule Inuit (and possibly their Dorset predecessors), are also plausible (Schledermann and McCullough, 2003; Appelt and Gulløv, 2009; Gulløv, 2016).

Throughout the range of Atlantic walrus, climate change can also influence its distribution. However, this variable intersects with human disturbance and accessibility to hunters in complex ways. In Svalbard, for example, walruses are increasing in number due to legal protection from hunting, despite decreases in sea ice (Kovacs et al., 2014). In western Greenland, a paucity of sea ice during warm years leads to fewer walruses near the coast, but to greater accessibility to hunting boats and an increased harvest (Born et al., 2017:89–92). Predicting the impact of medieval climate change on potential sources of walruses is thus not yet practicable, but may become so as our understanding of past hunting pressure improves. What can be observed is that, in the absence of firearms and aircraft, walruses would always have been most accessible to pre-modern hunters in the summer months when they frequent shallow feeding areas to which they return annually (Freitas et al., 2009). In such locations they could be taken either from boats in navigable coastal waters or (perhaps most pertinent in antiquity) when vulnerable at terrestrial haul outs (e.g. Born et al., 2017). In winter, walruses disperse to broken offshore pack ice where hunting would have been difficult and even modern scientific observation proves challenging (Freitas et al., 2009).

In sum, knowledge regarding current and historical walrus distributions establishes a framework for attempting to determine where medieval archaeological finds of rostra were originally procured. The most pertinent options for initial consideration are

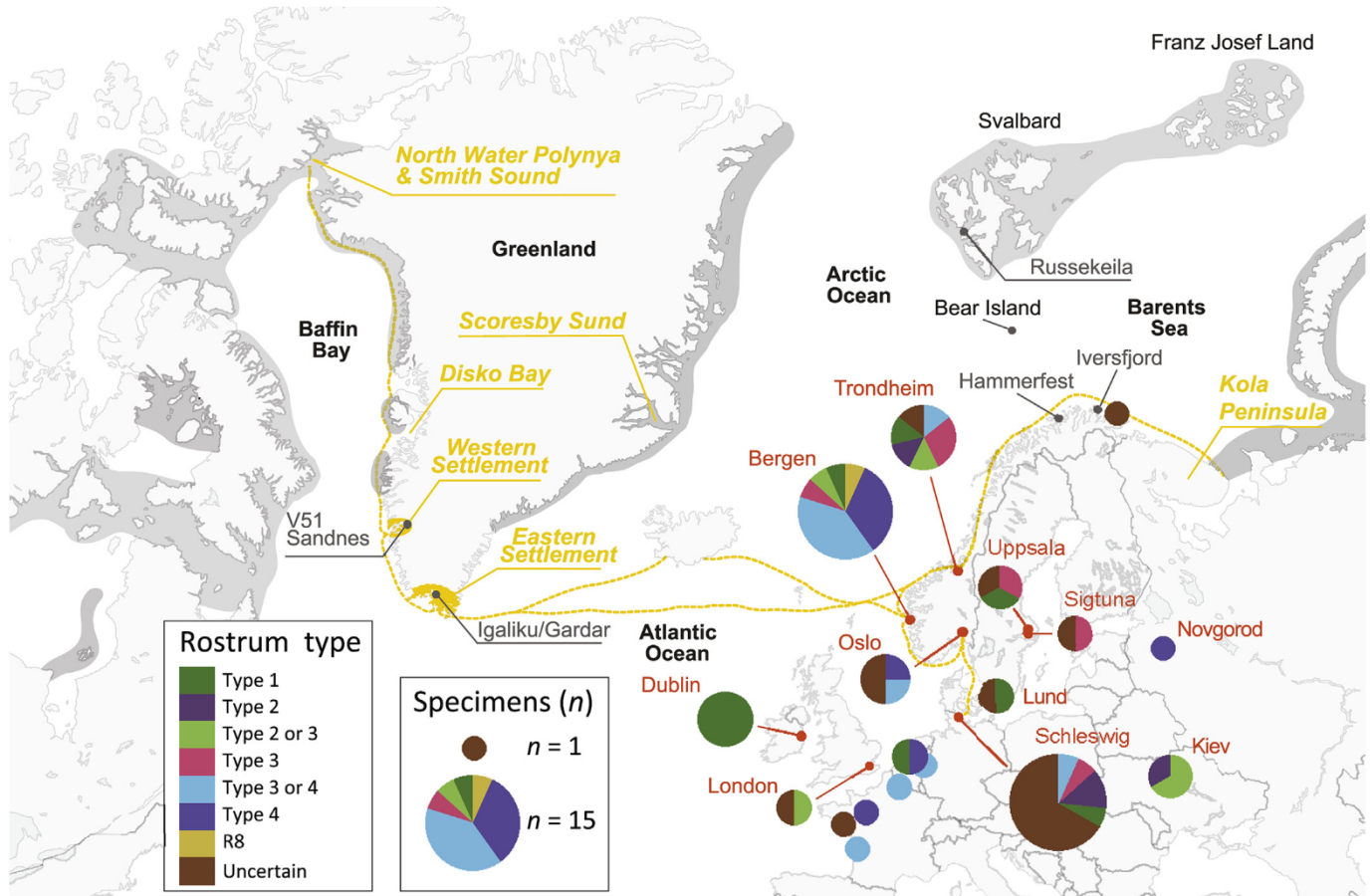


Fig. 1. Distribution of the 67 European finds of walrus rostra considered in this paper, divided by type based on the *chaîne opératoire* of manufacture (see text). Most are from excavated medieval settlements. The three specimens from France (lower left) are unprovenanced examples in museum collections. The locations of control samples from Igaliku/Gardar in Greenland, Iversfjord in northern Norway and Russekeila in Svalbard are also shown, as are potential trade routes for medieval walrus rostra. The modern distribution of the Atlantic walrus is shaded grey. In previous times, some walrus also occurred around Iceland (until extirpated during the Viking Age), as far west as the Hammerfest area in northern Norway and as far south as the former Western Settlement in western Greenland. In eastern Greenland, they have probably always been uncommon south of Kangerittivaq/Scoresby Sund. Basemap after Star et al. (2018) and references therein.

likely to be the Barents Sea coast (in northern Russia and Norway) and western Greenland, given the rarity of walrus in Iceland during the centuries of present concern and the inaccessibility of populations in Svalbard and north-eastern Greenland during the Middle Ages.

3. Modified walrus rostra: a *chaîne opératoire*

Although medieval finds of walrus rostra were once thought unusual hunting trophies (Roesdahl, 1998:21; Stoklund and Roesdahl, 2005; Roesdahl and Stoklund, 2006), our literature review and museum research has now discovered 67 examples (Fig. 1, Supplementary Data 1). Most datable specimens were broken during the Middle Ages, with the tusks removed for ivory working or onward trade (see Supplementary Data 1). Using a *chaîne opératoire* approach (*sensu* Bergsvik and David, 2015), in which the steps of artefact production are established by systematic recording of superimposed manufacturing traces as observed under low-magnification (10x–50x), we have identified specific modifications to these rostra that show they served as “packages”, intended for the initial transport of tusks (Supplementary Data 1). We further identified a series of modifications with no such practical purpose, but that instead may have been applied as folk art and to increase intrinsic value.

When killed, some walrus were processed by removing the anterior portion of the head – the snout or rostrum, following a

surprisingly consistent *chaîne opératoire* (Fig. 2; Supplementary Data 1), although not all rostra received every sequential treatment. We identify four classes (Types 1–4) according to the number of steps and the fineness of their execution. These four types all share a specific set of modifications and order of production, which links them as the outputs of a community of practice (cf. Stahl, 2013; Jarvis, 2017). Excluding rostra with missing data due to high fragmentation or inaccessibility (19 specimens), only a single modified example (R8) clearly differed from the typical *chaîne opératoire*.

In all four types the rostrum was removed using a blade (probably an axe) with chopping blows delivered from the lower right (or occasionally left) side of the walrus’s head, just behind the tusks, working (anatomically) upward until severed (Fig. 3a). The blows were skilful, leaving parallel marks that, although sometimes smoothed by later carving, do not overlie rougher primary butchery (Fig. 3b). Based on chop-mark orientation, the hunter presumably stood over a walrus laying on its left (or sometimes right) side and chopped with gravity (Fig. 2). Further finishing would have been difficult on specimens covered in soft tissue. Thus rostra must next have been defleshed, initially by knife (a step leaving occasional shallow randomly-oriented cut marks) and subsequently perhaps by flyblowing. Initial rostrum removal regularly fractured the thin upper (dorsal) margin and the resulting edge was often neatly chamfered to disguise this damage. Rostra of **Type 1** (n = 11) were otherwise unmodified (Fig. 3c), except insofar as secondary breakage and/or cutting may be present from tusk removal.

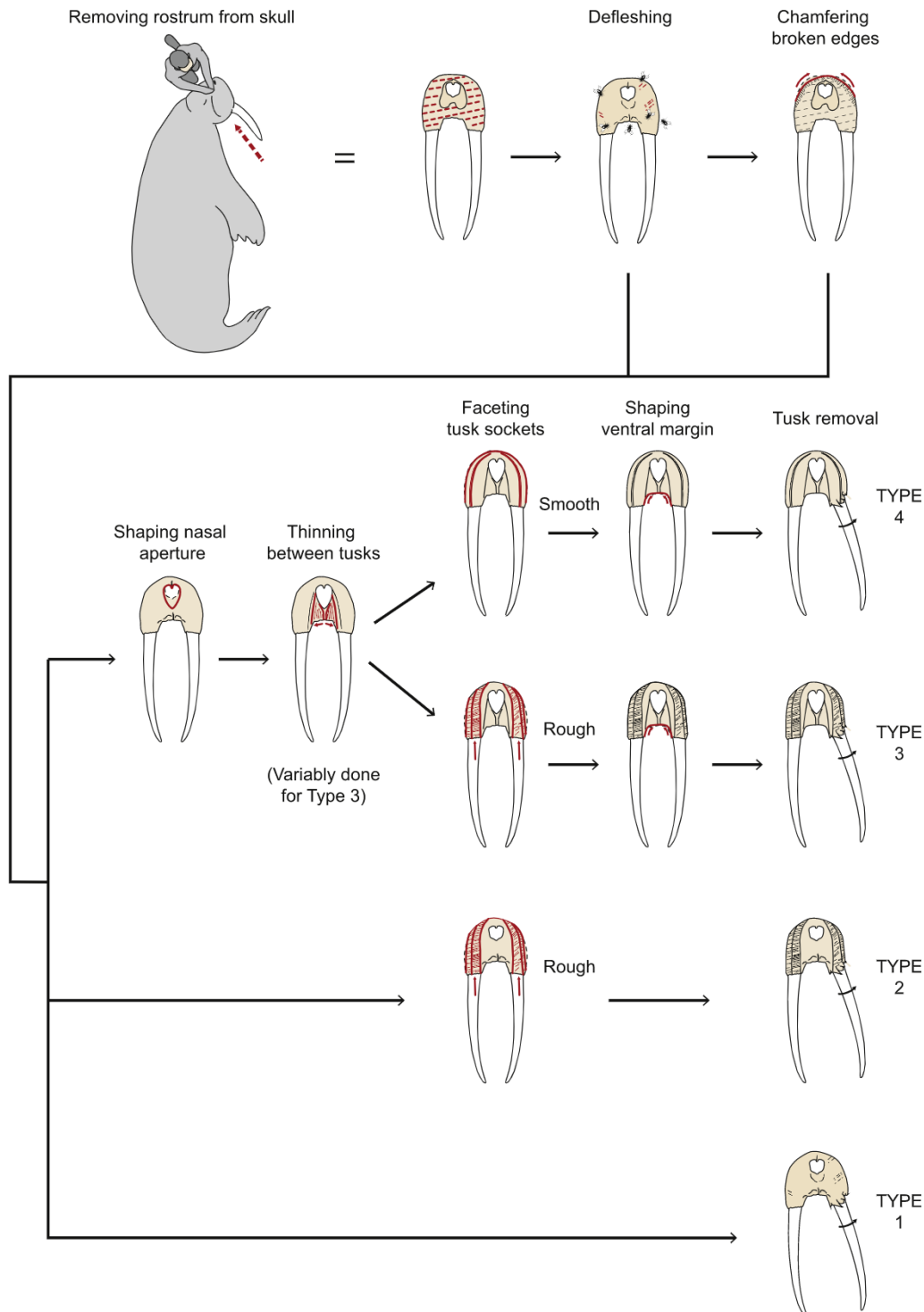


Fig. 2. A chaîne opératoire (manufacturing sequence) of rostrum removal and modification. The rostra can be grouped into four main types based on the number of steps employed and the fineness with which they were executed.

In **Type 2** ($n = 4$), each tusk socket was thinned on the anterior and lateral sides by careful parallel chops delivered from (anatomical) below. The blows created flat facets running along each tusk socket, resembling an incomplete octagon (Fig. 3d). The individual chop marks were not smoothed, leaving *roughly* faceted surfaces. Subsequent tusk removal was eased by this thinning of the dense alveolar bone. In **Type 3** ($n = 6$) and **Type 4** ($n = 9$) the natural heart shape of the nasal aperture was enhanced – sometimes

dramatically (Fig. 3f–k). Carving the aperture demarcated the upper edge of the next operation: thinning and shaping the anterior surface between the tusk sockets. In Type 3, this step was sometimes omitted or haphazardly employed. In Type 4 it was carefully executed. It usually entailed cutting into the bone from anterior, using a blade held almost vertically, and trimming away the surface. The result was a central peak, executed with varying care. In one instance from Oslo (Grieg, 1933) this peak was carved into a

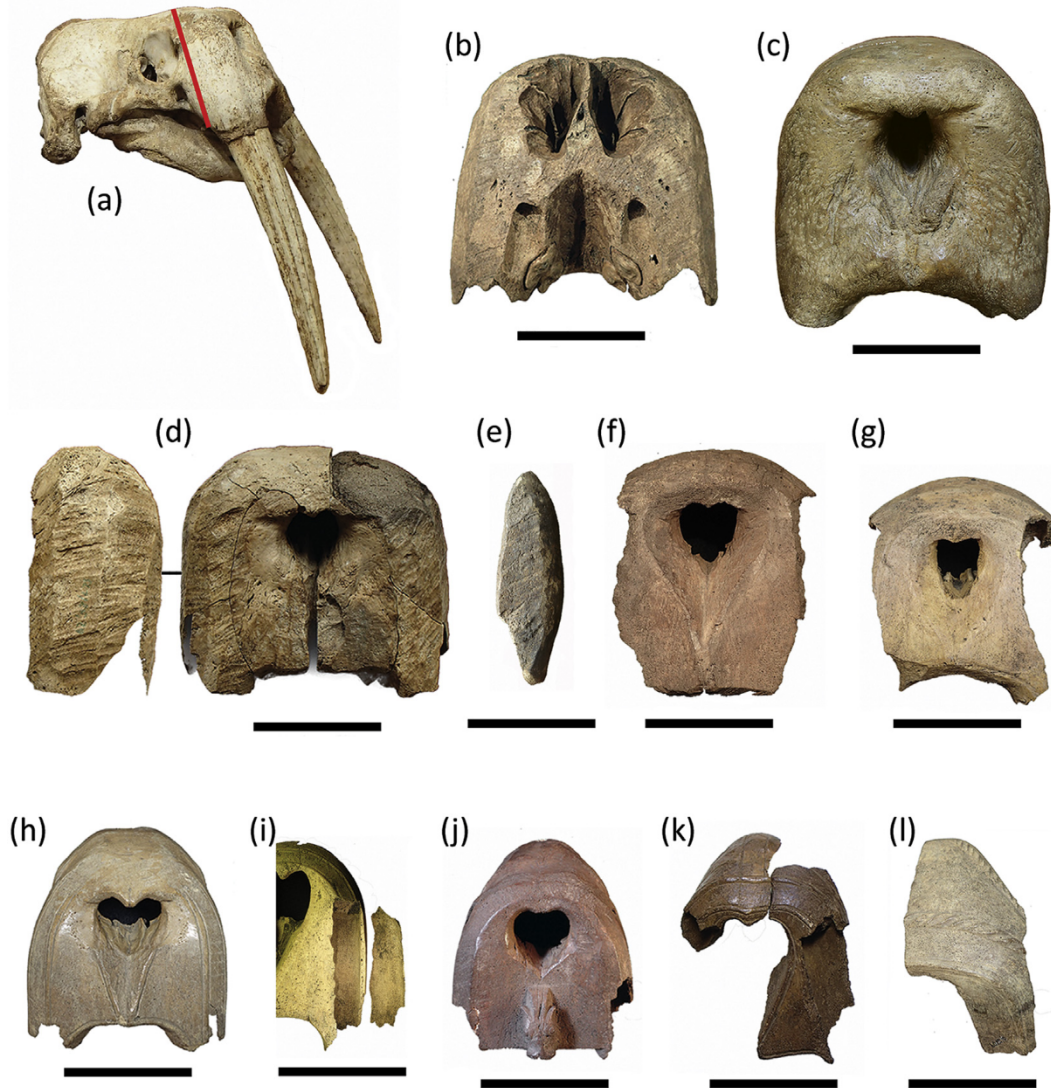


Fig. 3. Modified walrus rostra: (a) modern skull for comparison, with red line indicating plane of rostrum removal; (b) posterior view of R4 showing parallel chop marks (Trondheim); (c) R28 of Type 1 (Dublin); (d) R49 of Type 2 (Schleswig); (e) tusk-socket fragment with parallel chop marks from V51 Sandnes, Greenland; (f) control sample of Type 3 from Igaliku/Gardar, Greenland; (g) R12 of Type 4 (Bergen); (h) R9 of Type 4 (Bergen); (i) R13 of Type 4 showing thinned tusk socket (Bergen); (j) R27, a variant of Type 4 (Oslo); (k) R50 of Type 4 (Novgorod); (l) R8 of atypical manufacture (Bergen). Scale bars c.10 cm. Photographs by J.H. Barrett. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

three-dimensional animal head (Fig. 3j).

In Type 3, the bone of the tusk sockets remained roughly faceted as in Type 2 (Fig. 3f). In Type 4, the tusk sockets have a knife-smoothed finish (Fig. 3g–k). In Types 3 and 4 the ventral margin of the rostrum between the tusks might then also be shaped. Unfinished examples suggest that this was a concluding step. The method involved parallel cuts into the bone, followed by trimming away the resulting ridges. The result ranged from rough straightening to the creation of careful arches. In a few cases rostra were subsequently decorated with incised geometric and foliate designs (Roesdahl and Stoklund, 2006; Supplementary Data 1). In Types 3 and 4 (as in Types 1 and 2), the tusk sockets were usually broken or cut during ivory removal. All the decorative modifications made this easy by thinning the bone. In some specimens the normally thick bone over the canines was reduced to as little as c.1 mm (Fig. 3i).

Many fragmentary rostra exhibit certain elements of the sequence just described, and can be attributed to types 2/3 ($n = 5$)

or 3/4 ($n = 12$) only. Other examples must be left entirely unclassified due to insufficient data ($n = 19$), a result of high fragmentation or inaccessibility for study. As noted above, only a single specimen (R8) clearly follows a different *chaîne opératoire* (Fig. 3l). The anterior surface was cut completely flat and the perimeter, although shaped and decorated with raised bands, was not faceted as in Types 2–4.

4. The trade of rostra through time and space

4.1. Dating and the chronology of the *chaîne opératoire*

The walrus rostra cannot be dated using ^{14}C with sufficient precision for present purposes due to a lack of appropriate ΔR values for walrus bone *per se* (Dyke et al., 2019) and uncertainty in ΔR location. Instead we must rely on the contextual dating of excavated examples, on the runological dating of an inscription on an unprovenanced find now in Le Mans (Imer, 2017) and on the art

historical dating of decorative features (see Supplementary Data 1).

Dates are available for 29 of the 47 rostra that can be attributed to Types 1–4 (Supplementary Data 1). The date range of many is broad, and a few outliers are probably residual or curated objects (e.g. R1, R4 and possible R19). Nonetheless, we find that the typology based on an increasingly elaborate *chaîne opératoire* is also a roughly chronological sequence (Fig. 4). Types 1 and 2 start in the eleventh century, Type 3 in the twelfth century and Type 4 appears in the twelfth or early thirteenth century. Type 4 may persist into the fifteenth century, but most rostra (even those for which type is unknown) probably date no later than the 1300s (Fig. 5). Rostrum R8, the single example with a different *chaîne opératoire*, dates between 1248 and 1332 (Gitte Hansen pers comm.). A rostrum from Løkvik in northernmost Norway, for which type is not known, is late in date (mid-fifteenth to mid-seventeenth century). This specific rostrum may not be comparable with the rest of the specimens under consideration (see below).

4.2. Geographic distribution of the *chaîne opératoire* through time

Treating the typology as a rough chronological sequence, and augmenting its information with the evidence of dated examples, the towns of Dublin, Trondheim and Schleswig appear among the first nodes for rostrum imports into Europe (Fig. 1; Figs. 4 and 5). Trondheim and Schleswig may have continued in this role after Dublin dropped out. Dublin has only Type 1 rostra, the latest example of which (R63) shows an aborted and unskilled attempt to turn it into a Type 3 or Type 4 (Supplementary Data 1). Trondheim and Schleswig have a mix of Type 1, Type 2 and Type 3 rostra, with no definite Type 4s. A predominance of Type 3/4 and Type 4 finds suggests that Bergen subsequently took on the dominant role of rostrum trade.

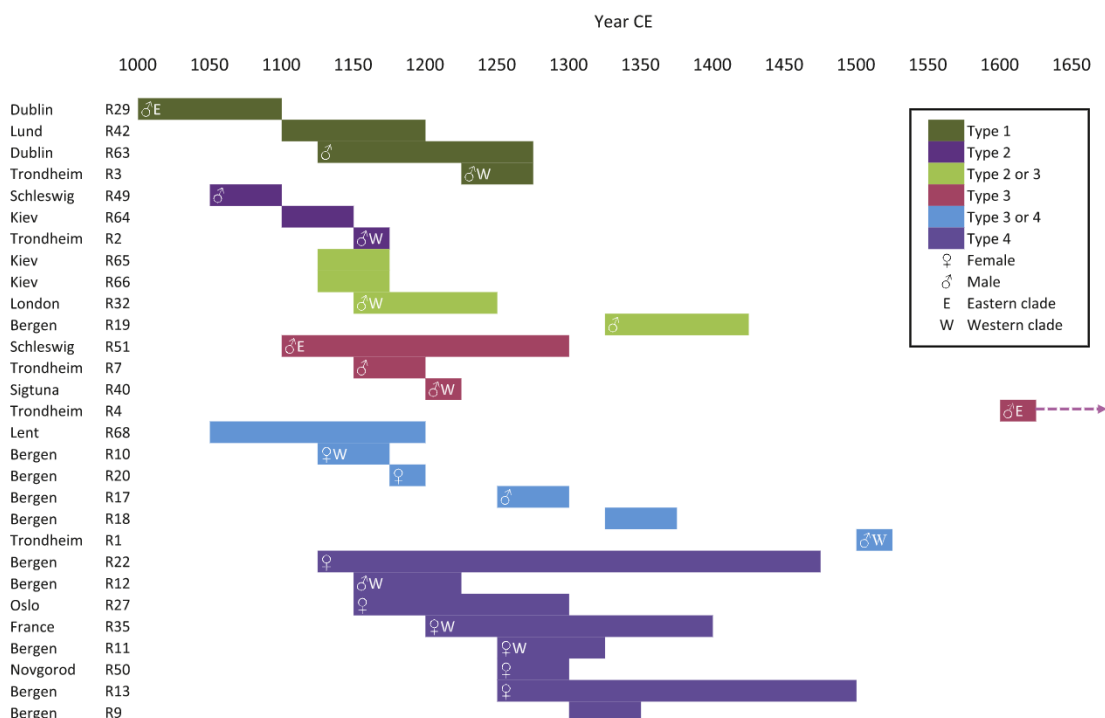
Other settlements have few rostra, be they occasional destinations of traded walrus ivory such as London (Bowsher et al., 2007: 343) and Kiev (Сагайдак et al., 2008:143–144; Khamaiko, 2018), or

major manufacturing centres such as Sigtuna (Karlsson, 2016) and Novgorod (Smirnova, 2001, 2005). Moreover, some towns with known walrus ivory workshops, such as Köln (Berke, 1997; Williamson, 2010:265–305), have produced no rostra at all. Thus nodes like Dublin, Trondheim, Schleswig and (later) Bergen must have redistributed tusks. Only occasionally were whole rostrum packages sent on to ultimate consumers – the most far-travelled examples being Type 2 and Type 2/3 specimens from Kiev (Сагайдак et al., 2008:143–144; Natalia Khamaiko, pers comm.) and a single Type 4 find from Novgorod (Smirnova, 2001) (Fig. 3k). In other instances rostra must have been broken up in the main distribution nodes and only tusks traded onwards. It is a question for future research whether some centres of ivory working, Novgorod for example, also received tusks from entirely different networks of supply, which did not entail initial association with rostra.

5. Determining rostra origins

5.1. Typology

We explored whether rostra modified as discussed above are known from specific hunting grounds. None were found in Arctic Russia or Iceland (Einarsson, 2011; Frei et al., 2015; Smiarowski et al., 2017; Boeskorov et al., 2018; Pálsdóttir et al., 2018). A single rostrum, poorly dated and of uncertain type, does exist from Arctic Norway, excavated at Løkvik in Finnmark (Olsen et al., 2011:69–70). If post-medieval, as is possible with the mid-fifteenth to mid-seventeenth century date (Henriksen, 2011:231; Myrvoll et al., 2011:154), it could relate to hunting in Svalbard rather than the medieval activity of present concern (see Section 2 above). Conversely, the medieval farms of Greenland's Eastern and Western Settlements have produced numerous severed rostra brought back from more northern hunting grounds. These were often broken up on site to remove the tusks (McGovern, 1985a, 1985b; McGovern et al., 1996; Smiarowski et al., 2017). Research on



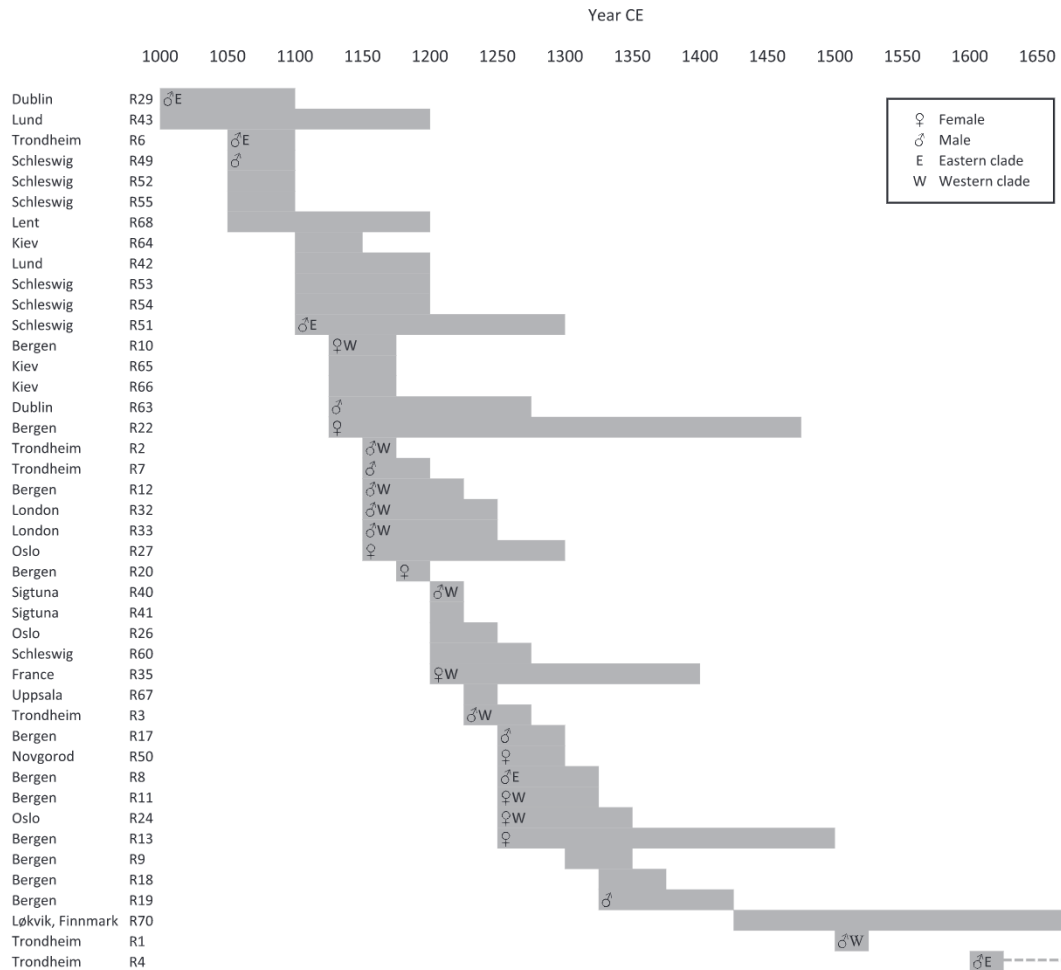


Fig. 5. Chronology (rounded to quarter century) of datable rostra. Find location, sex and genetic clade are indicated where known.

this material is ongoing (Konrad Smiarowski pers comm.), but for present purposes we examined 10 specimens from past excavations at the medieval bishop's settlement of Igaliku (Gardar) in the former Eastern Settlement (Degerbøl, 1929) and seven from the high status site of V51 Sandnes in the former Western Settlement (Degerbøl, 1936; McGovern et al., 1996) – held by the Natural History Museum of Denmark and the National Museum of Denmark. One example attributed to the 1926 excavations at Igaliku (Gardar) is of Type 3 (Fig. 3f), and others from both sites preserve elements of the *chaîne opératoire* discussed above, such as closely spaced parallel chop marks on tusk sockets (Fig. 3e). Thus Norse Greenlanders appear to have been part of the community of practice defined by the rostra found in Europe. Fully modified skulls are, however, the exception among Greenlandic finds. It is possible that only examples destined for trade were finished, or that the final decorative steps were usually applied after export (see also Section 7 below).

5.2. Ancient DNA clade determination and the *chaîne opératoire*

Through ancient DNA analyses we have previously determined the phylogenetic clade of 25 of the archaeological walrus specimens that are included in the present study, including 20 European finds of rostra, four control samples from Greenland and one control sample from Svalbard (two further control samples, from Finnmark in northern Norway, did not have sufficient DNA

preservation for clade determination) (Star et al., 2018; Supplementary Data 2). Briefly, DNA was extracted from bone powder in the University of Oslo ancient DNA laboratory following strict aDNA precautions (Poinar and Cooper, 2000; Gilbert et al., 2005). Genomic libraries were built and sequenced on an Illumina HiSeq 2500. The obtained reads were aligned to the Pacific walrus nuclear genome (Foote et al., 2015) to determine the overall endogenous DNA content (which varied between 0.01 and 71%), and aligned to the Atlantic walrus mitogenome (Arnason et al., 2002). Ancient DNA damage was investigated, genotypes called and phylogenetic analyses performed (see Star et al., 2018 for details).

Two distinct phylogenetic clades are observed within Atlantic walrus (Star et al., 2018) with specific geographical distributions; one clade is restricted to the Canadian Arctic and western Greenland, whereas the other clade is found over the entire range of the Atlantic walrus (Andersen et al., 1998, 2017; Born et al., 2001; Lindqvist et al., 2016; Star et al., 2018). Based on this geographical distribution, the clade that is restricted to the Canadian Arctic and western Greenland is defined as western whereas the other clade is defined as eastern (Star et al., 2018; Supplementary Fig. 1). Of the 20 European rostrum finds for which we identified these clades, thirteen were of the western clade, and thus from Norse Greenland, while seven were of the eastern clade, which could in theory come from any number of potential sources (Star et al., 2018; Supplementary Data 2). The western clade specimens occur across Types 1 to 4 of the *chaîne opératoire*. If these types all represent a related

origin, as suggested above, this would imply a consistently Greenlandic source. However, what of eastern clade specimens, which are represented among Types 1 and 3 (Fig. 4)? Moreover, the one anomalously modified rostrum (R8) is also of eastern clade. Were these specimens harvested in Greenland or elsewhere? If elsewhere, where might this be? Although early finds of walrus ivory in Europe may have come from an Icelandic population before its extermination (Keighley et al., 2019), we might speculate that the Barents Sea (Arctic Fennoscandia/Russia) provides the most probable alternative to Greenland given that the rostra of present concern date to the eleventh century and later (see Section 2 above).

5.3. Genetic and osteometric sexing

Walrus are sexually dimorphic and walrus behaviour differs between males and females, in terms of diet and mobility (e.g. Wiig et al., 2007) which can influence stable isotope values (cf. Clark et al., 2019). Thus before employing isotope analysis to infer possible rostrum origins it is pertinent to ascertain sex for each specimen. We successfully determined genetic sex for 22 European rostra finds and six control samples (Supplementary Data 2) by calculating the relative coverage of reads aligning to the X chromosome relative to autosomal chromosomes (X:A, coverage, following Schubert et al., 2017; Nistelberger et al., 2019). These analyses used the genomic data of Star et al. (2018) and six additional specimens for which sequence data was generated. All these data have been deposited in the European Nucleotide Archive (ENA, www.ebi.ac.uk/ena) and are available under study accession numbers PRJEB25536 and PRJEB35165. The sole available reference genome for walrus (the Pacific walrus reference genome (Foote et al., 2015)) is not resolved to the level of individual chromosomes and cannot directly be used for genetic sexing. We therefore aligned all walrus sequencing data to the dog genome (CanFam 3.1 assembly), as recommended by Bro-Jørgensen et al. (2019), using PALEOMIX (Schubert et al., 2014), collapsing sequencing reads (AdapterRemoval v1.5 (Lindgreen, 2012)) before alignment.

We investigated the reliable determination of sex when limited numbers of aligned reads (i.e. less than 20 000) were obtained. For this, subsets of reads were randomly down-sampled from those archaeological specimens (Supplementary Data 2) with more than 20 000 endogenous reads (and for which genetic sex could be reliably determined), from 500 reads up to 20 000 reads, in increments of 500 reads. For each increment and individual, the random resampling procedure was iterated 20 times to obtain a bootstrapped confidence interval of the ratio of the calculated autosomal to X-chromosome coverage (Nistelberger et al., 2019). We observe a clear separation between the sexes with females obtaining a ratio of ~1 and males ~0.5, following theoretical expectation (Fig. 6). The sex-coverage ratios of those samples with less than 20 000 reads were compared to the randomly obtained probability distributions of the sex ratios of the other specimens. The genetic sex of those samples with more than 4000 endogenous reads could be reliably determined (Fig. 6), resulting in sex determination of 27 of the 31 specimens having stable isotope data (see below), plus one additional specimen (a medieval rostrum from Le Mans) without isotope data (Supplementary Data 2).

The aDNA sex determination showed that male and female groups can also be differentiated by tusk socket size. Measurements of the internal maximum and minimum cross section of each tusk socket were taken by callipers where practicable, and rounded to the nearest mm. Broken archaeological specimens were usually measurable near the base of the alveolus (where open canine root meets bone), but there was some variation in precisely what portion of each tusk socket was intact, and thus where the cross

section measurements could be taken. This variability is not a major source of bias because it is independent of sex, and walrus tusk sockets are approximately parallel sided. For example, based on seven tusk sockets from five walrus skulls of varying size, the maximum internal cross section exhibited a mean difference between socket base and socket lip of 1.6 mm (base measurements ranged from 38 mm to 72mm and lip measurements from 40 mm to 72mm). Based on six tusk sockets from four walrus skulls the minimum internal cross section exhibited a mean difference between socket base and socket lip of 1.2 mm (base measurements ranged from 23 mm to 57mm and lip measurements from 25 mm to 57mm). To estimate tusk socket maximum internal cross section in mm (Max) in two cases where only minimum internal cross section in mm (Min) could be measured, a linear equation was derived by least squares regression analysis in R (R Core Team, 2017) ($r^2 = 0.90$, $p < 0.001$) of data from 48 intact tusk sockets from 34 individual walrus (Supplementary Data 3): $\text{Max} = 1.27 (\text{Min}) + 7.95$.

Comparing the tusk socket measurements and the genetic sexing showed that the maximum internal cross section measurements ≤ 44 mm are exclusively female whereas values ≥ 54 mm are exclusively male. Osteometric sexing is simplified in this context because the rostra are not from juvenile animals based on the state of bone and tooth development. Combining genetic and osteometric data, we identified sex for 30 of the 31 isotopically analysed samples (Supplementary Data 2). These combined results are key to interpreting the stable isotope data below. As discussed further in Section 6, the osteometric data are also fundamental to assessing temporal changes in the sizes of walrus harvested.

5.4. Stable isotope analysis

We conducted stable isotope analysis on 24 European rostrum finds (19 with known aDNA clade) and seven control samples (five with known aDNA clade) (Supplementary Data 2). We employed methods developed for tracing the trade of dried fish, wool textiles and elephant ivory – using carbon, nitrogen, sulphur and hydrogen isotope analyses (Barrett et al., 2008, 2011; von Holstein et al., 2016; Coutu et al., 2016). Although animals or animal products are often traced with strontium, oxygen or lead isotopes (e.g. Frei et al., 2015; Coutu et al., 2016; Makarewicz et al., 2018), to be reliable measures, these isotopes ideally require tooth enamel which is resistant to diagenesis (e.g. Montgomery et al., 2014). Walrus rostra are of bone or, when cheek teeth remain in place, also of cementum and dentine (enamel caps wear away early in the life of this species). Thus we measured $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$ and non-exchangeable $\delta^2\text{H}$ (hereafter $\delta^2\text{H}$) ratios on defatted and purified bone collagen (Supplementary Data 2). These isotope ratios reflect diet and baseline ecosystem values, which vary across space and thus place of origin (e.g. Trueman and St John Glew, 2019). For instance: $\delta^{13}\text{C}$ is influenced by variables such as sea-ice cover, benthic versus pelagic feeding and inshore versus offshore location (Clark et al., 2019; Szpak et al., 2019); $\delta^{15}\text{N}$ reflects both baseline values and trophic level (Kelly, 2000); $\delta^{34}\text{S}$ is an indirect proxy for salinity (Nehlich et al., 2013); $\delta^2\text{H}$ is influenced by temperature and trophic level (Reynard and Hedges, 2008; Vander Zanden et al., 2016).

The bone samples for stable isotope analysis were collected as powder using a handheld electric drill or as pieces using a handheld electrical drill or a fine manual saw. Powdered and whole-chunk samples have been shown to yield comparable results (Tsutaya et al., 2017). For samples collected as powder the outer surface was cleaned by abrasion and then c. 0.5–1g drilled out for analysis. For samples collected as whole chunks, subsamples of between 0.5 and 1.0g were taken using a handheld electrical drill that was cleaned between specimens. The outer surface of the bone was

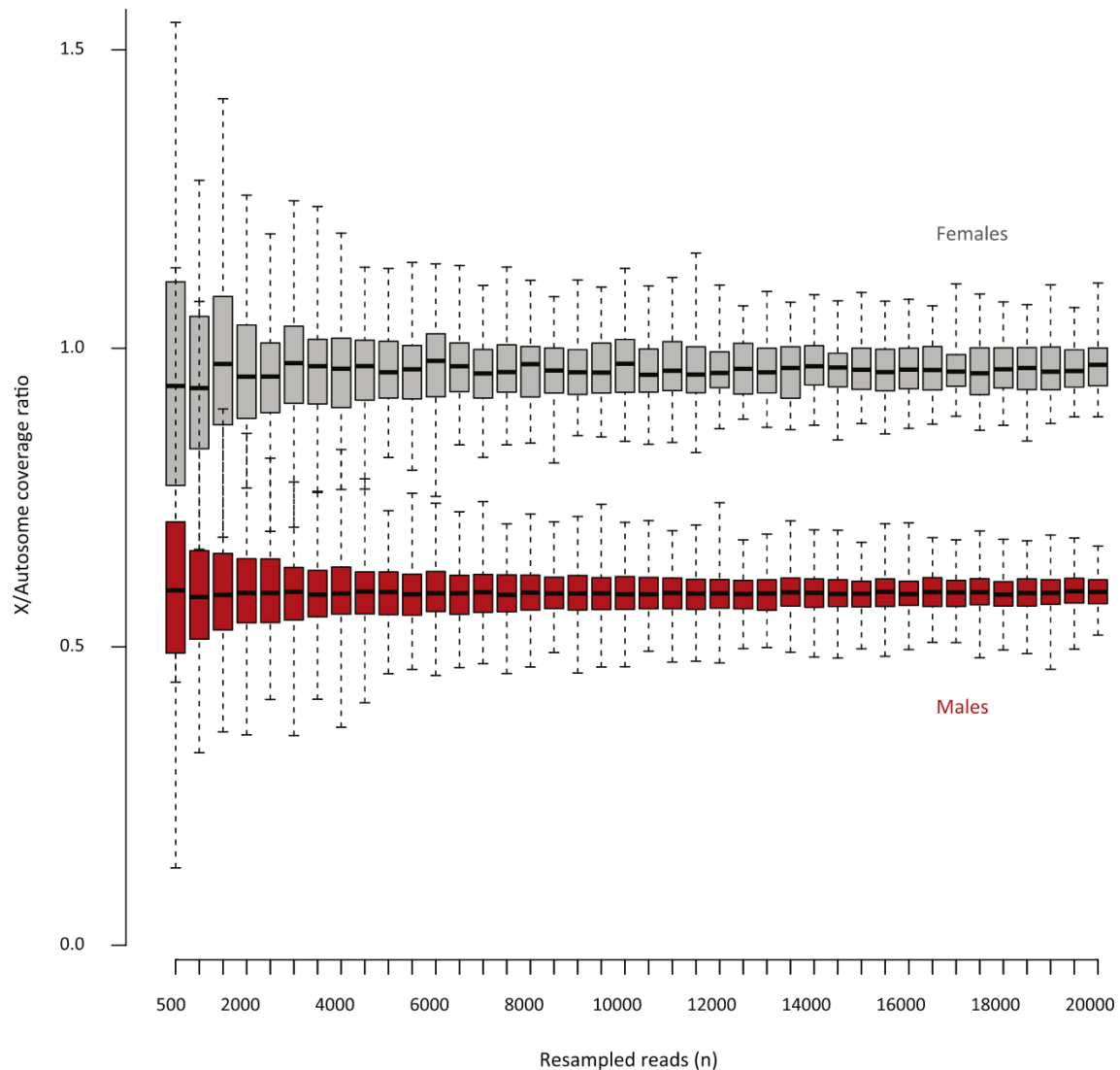


Fig. 6. Genetic sexing of walrus remains. The genetic sex of walruses can be obtained by calculating the ratio of X chromosome to mean autosome coverage (X:A). Samples for which only a low number (<20 000) of reads is obtained can be compared to confidence intervals for the sexing estimates (obtained by down-sampling BAMfiles from 20 000 to 500 reads in 500 read increments for all ancient walrus specimens with more than 20 000 aligned sequence reads). At each interval, and for each individual, the down-sampling is iterated 20 times to generate a confidence distribution. Boxplots represent the median (solid line), the 25th and 75th percentiles (box) and the entire ratio range (dotted lines) at each read interval bin. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

abraded using a sandblaster and each piece pulverised by percussion mortar. Lipids were removed by solvent extraction: first soaking in 8 ml of 2:1 chloroform:methanol mixture whilst in an ultrasonic bath, changing the solvent every 15 min until it remained clear (up to 15 rinses), then repeating with 8 ml of 2:1 methanol:chloroform mixture. Samples were then demineralised with 0.5M aq. hydrochloric acid at 4 °C following the [Privat et al. \(2002\)](#) protocol with some modifications. The samples were gelatinised in a pH3 aqueous solution for 48 h at 75 °C and then filtered (Ezee filters). The filtrate was lyophilised to produce 'collagen'.

Carbon and nitrogen isotope analyses were performed in the Godwin Laboratory, Department of Earth Sciences, University of Cambridge, using an automated elemental analyser coupled in continuous-flow mode to an isotope-ratio-monitoring mass spectrometer (Costech elemental analyser coupled to a ThermoFinnigan Delta V mass spectrometer). Samples were analysed in triplicate ($0.8 \text{ mg} \pm 0.1 \text{ mg}$ weighed into tin capsules). Based on replicate analyses of international and laboratory standards, measurement

errors are less than $\pm 0.2\%$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Subsamples of collagen were sent to Iso-Analytical Limited for sulphur and hydrogen isotope analysis, using an automated elemental analyser coupled in continuous-flow mode to an isotope-ratio-monitoring mass spectrometer (Ian Begley pers comm.). For sulphur, samples were combusted in tin capsules at 1080 °C with oxygen and converted to SO_2 . Analysis entailed monitoring m/z 48, 49 and 50 of SO^+ from SO_2 in the ion source. For hydrogen, $1.0 \pm 0.1 \text{ mg}$ collagen samples were weighed into open silver capsules. For 10 days the samples were simultaneously equilibrated with laboratory air moisture, before being sealed, dropped into a furnace at 1080 °C and decomposed to H_2 and CO over glassy carbon. Mean $\delta^2\text{H}$ values for measured reference standards (see Supplementary Data 2) facilitated a 3-point linear calibration to correct for exchangeable hydrogen. All isotope data in this paper are reported as δ values using international scales: VPDB for carbon, AIR for nitrogen ([Hoefs, 1997](#)), VCDT for sulphur, and VSMOW for hydrogen ([Hoefs, 1997](#); [Coplen, 2011](#)).

Carbon and nitrogen have the most established criteria for identifying well preserved collagen (Roberts et al., 2018). All samples passed appropriate quality-control thresholds. A number of criteria were used: collagen yield, %C, %N, and atomic C/N ratio. All samples had atomic C/N ratios well within the range 2.9–3.6 (all were 3.1–3.3) (DeNiro, 1985). All collagen samples analysed had %C greater than 13 and %N greater than 5.

The measurement of collagen sulphur isotope ratios is increasingly routine in archaeology. However, robust sulphur quality control criteria exist only for fish and terrestrial mammals at present (Nehlich and Richards, 2009). In particular, it is not fully established what appropriate ranges of atomic C/S and N/S ratios should be for sea mammals. Nehlich and Richards (2009) suggested that carbon to sulphur and nitrogen to sulphur atomic ratios can also be used to assess the quality of collagen and gave the expected ranges of atomic C/S as 600 (± 300) for terrestrial mammals and 175 (± 50) for fish and atomic N/S as 200 (± 100) for land mammals and 60 (± 20) for fish. The walrus values ranged between 580 and 170 (C/S) and 184 and 54 (N/S) but as walrus are marine mammals it is unclear what range of values should be expected and so these figures were not used to exclude any individuals. The sulphur data reported here are instead accepted on the basis of the carbon and nitrogen quality thresholds noted above.

The online measurement of collagen hydrogen isotope ratios is developmental, with varying published laboratory protocols and methods of controlling for exchangeable hydrogen (e.g. Reynard and Tuross, 2016). Nevertheless, we consider the data – generated by a consistent laboratory protocol – a valuable additional indicator of walrus environment and diet (cf. Vander Zanden et al., 2016). The isotope results can be evaluated with and without this fourth variable. Collagen quality control indicators do not yet exist for hydrogen isotope data in isolation. As with sulphur, the $\delta^2\text{H}$ data reported here are accepted on the basis of satisfactory carbon and nitrogen variables.

Fig. 7 provides biplots of the three most informative isotope data pairs, with symbol indicating sex and genetic clade. Control samples and selected rostra are individually labelled. In Fig. 8, variability across the isotopes is summarised using Principal Component Analysis (PCA), conducted using R (R Core Team, 2017). Principal Component (PC) 1 and PC3 (together accounting for 71% of the variance) are plotted because PC2 is strongly influenced by a single outlier having a very low $\delta^{34}\text{S}$ value.

The stable isotope data cannot indicate a definitive provenance, not least because of environmental change through time (cf. Clark et al., 2019) and the fact that comparanda do not yet exist for all conceivable sources. Nevertheless, by comparing the values of unknown eastern clade specimens with known western clade specimens, and with additional control samples, it is possible to observe indicative matches and mismatches (see Section 5.5). The additional control samples include four medieval walrus rostra from Igaliku in Greenland (which must have been transported from more northerly hunting grounds) and three archaeological walrus bones from the Barents Sea region (two third-millennium BC specimens from Iversfjord in Finnmark (Helskog, 1983) and one eighteenth- to nineteenth-century CE specimen from Russekeila, Isfjorden, Svalbard (Anne Karin Hufthammer pers comm.). The two Finnmark specimens (one skull fragment and one phalanx) actually represent all definitively identified pre-reformation archaeological walrus bones known from this northernmost county of mainland Norway. They are thus the best available control samples for this region, despite being from two different parts of the skeleton, which may introduce additional variability in isotope values (Clark et al., 2017). One further possible fragment proved to be a seal on aDNA analysis (Star and Boessenkool, unpublished data) and the rostrum from Løkvik discussed above, which was not available for study, may be

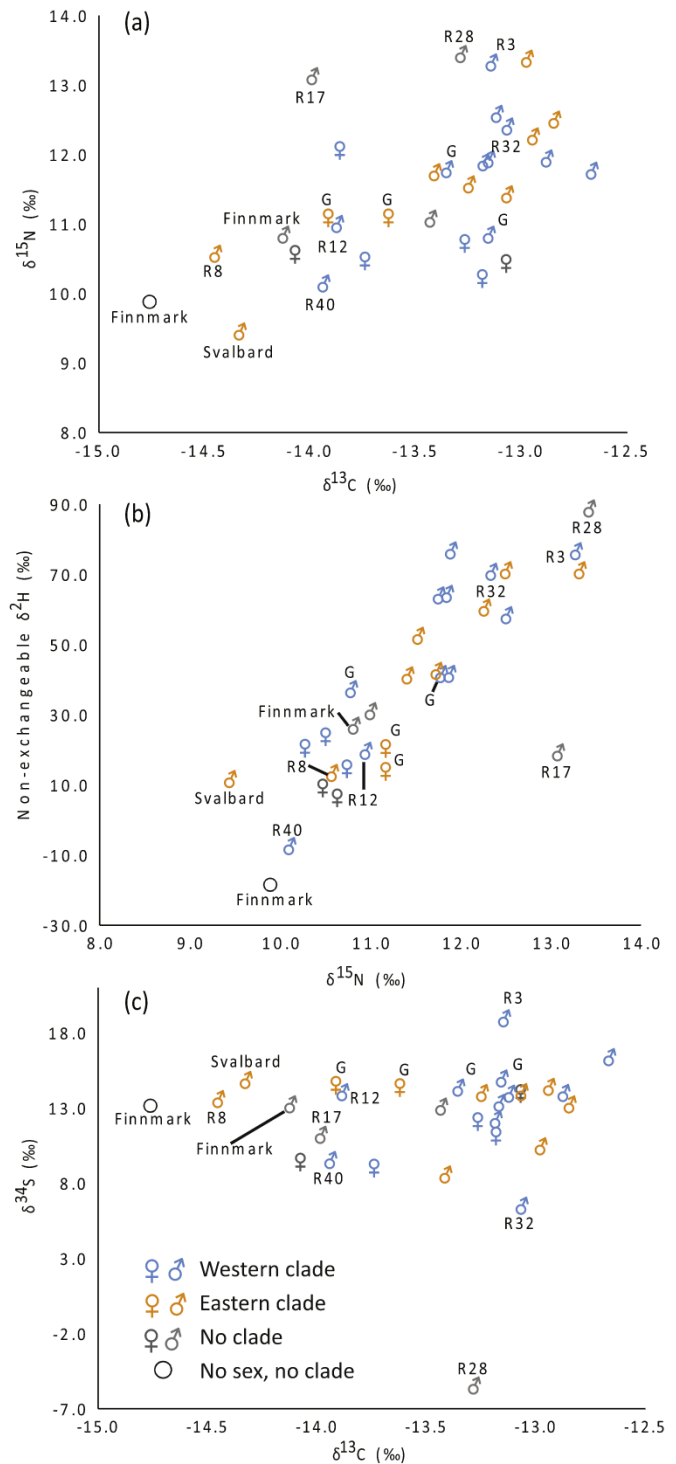


Fig. 7. Stable isotope values for archaeological walrus rostra and control samples. Symbols indicate sex and genetic clade where known. Labels indicate the origin of control samples (G being Igaliku/Gardar in Greenland) or the rostrum number for specimens discussed individually in the text. (a) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; (b) $\delta^{15}\text{N}$ and non-exchangeable $\delta^2\text{H}$; (c) $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$.

of post-medieval date.

5.5. Integrating the stable isotope and aDNA results

Integrating the stable isotope, mitochondrial clade and sexing

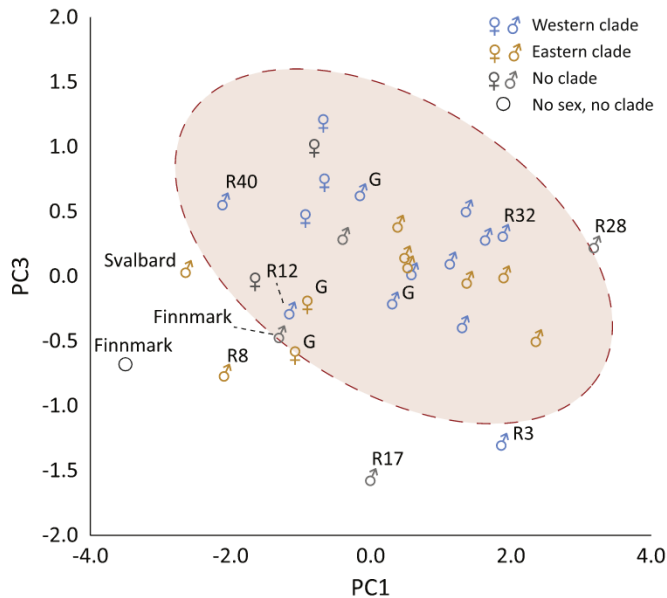


Fig. 8. Plot of PC1 and PC3 of a Principal Component Analysis including $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, non-exchangeable $\delta^2\text{H}$ and $\delta^{34}\text{S}$ values for archaeological walrus rostra and control samples. PC1 and PC3 (accounting for 71% of the variance) are plotted because PC2 is strongly influenced by an extreme $\delta^{34}\text{S}$ outlier. Symbols indicate sex and genetic clade where known. Labels indicate the origin of control samples (G being Igaliku/Gardar in Greenland) or the rostrum number for specimens discussed individually in the text. Shaded area is the 95% confidence interval for all specimens of the western genetic clade.

analyses yields several observations. First, most male walrus have higher $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$ values than female walrus of the same genetic clade (Fig. 7). One can thus infer that they fed differently, with males presumably feeding at a higher trophic level; some walrus consume marine birds and seals in addition to shellfish (Lydersen, 2018). Second, the three control specimens from Finnmark and Svalbard have among the lowest $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$ values in the dataset – despite the fact that two were from male animals and the third is of unknown sex. They may thus derive from an environmental and/or dietary niche that differs from that represented by almost all of the other rostra, insofar as this can be judged from three specimens (Fig. 7). Third, summarizing the isotope data using Principal Component Analysis (PCA, R Core Team, 2017), with a single exception, the medieval eastern clade rostra are isotopically consistent with the western clade examples (Fig. 8). The former fall within the 95% confidence interval of the latter based on PC1 and PC3 using ggplot2 in R (Wickham, 2016) (Fig. 8). The single outlier, rostrum R8 from Bergen and a genetic male of the eastern clade, is most consistent with the isotope values of the three Barents Sea control samples. It is the single example modified using a different *chaîne opératoire*. We infer that this walrus was not from Greenland. Perhaps it was caught along the coast of the Barents Sea, but more control data are needed for comparison.

Other outliers may indicate walrus with atypical feeding or migration patterns, or occasional hunts in distinctive environmental contexts. Two males of the western clade (R12, R40) have isotope values more consistent with females of this genetic group. Two other walrus have low $\delta^{34}\text{S}$ values (R28, R32), more consistent with brackish conditions or even freshwater than fully marine conditions (e.g. Nehlich et al., 2013). One is of the western clade and one is of uncertain clade. The western clade example (R32) is presumably from a location in Greenland or Arctic Canada. The specimen of unknown clade (R28) could be from elsewhere.

Specimen R3 of the western clade conversely has a high $\delta^{34}\text{S}$ value. It may also have fed in a distinctive location within Greenland/Arctic Canada. R17 (of unknown clade) has an unusual $\delta^{15}\text{N}$ value given its other parameters.

Based on the isotope data, almost all of the European rostra of both western and eastern clades (including the majority of the outliers) were probably traded from Norse Greenland. One stable isotope outlier (R8) is likely to be from another source, perhaps the Barents Sea and two isotope outliers (R17, R28) are of uncertain clade and cannot yet be attributed to a known source.

6. Serial depletion of walrus

We observe distinct chronological patterns in the size and sex of walrus targeted for rostra (Fig. 9, European finds only). Measurements from Types 2 ($n = 2$), 2/3 ($n = 1$) and 3 ($n = 5$) are grouped for clarity given small numbers. A statistically significant change in size is evident through typological time (Kruskal-Wallis chi-squared = 15.07, $df = 3$, $p = 0.002$), with a clear decrease concurrent with the introduction of Type 4 (see Fig. 4 for chronological change in typology). Given that tusk-socket size is associated with walrus sex, this decrease in size is also indicative of a shift from the harvest of male animals to a mixture of sexes. The genetic sexing evidence corroborates this observation. Types 1 to 3 combined include ten male and no female specimens; Types 3/4 and 4 include four female and three male rostra (Supplementary Data 2).

An increasing reliance on smaller female walrus is suggestive of greater hunting pressure. Large males, with the largest tusks, may have proven insufficient to supply the demand for ivory. We must ask whether there was thus also need to seek out increasingly distant populations. Mass hunting can end the use of traditional haul outs by walrus (Lønø, 1972), which otherwise show great site fidelity (Freitas et al., 2009) and thus offer a reliable resource for repeated exploitation. In this context it may be relevant that the hunting of female walrus was characteristic of pre-modern Inuit practices in north-western Greenland (Gotfredsen et al., 2018). Moreover, concentrations of unambiguously Norse artefacts of thirteenth to fourteenth century date have been found around the North Water (the polynya between Ellesmere Island and north-western Greenland) and Smith Sound, mainly in Thule Inuit contexts of the Ruin Island phase (Holtved, 1944:298–302; Schledermann and McCullough, 2003; Gulløv, 2016). These have been interpreted convincingly as trade goods (Schledermann and McCullough, 2003; Gulløv, 2016). It is plausible that the medieval

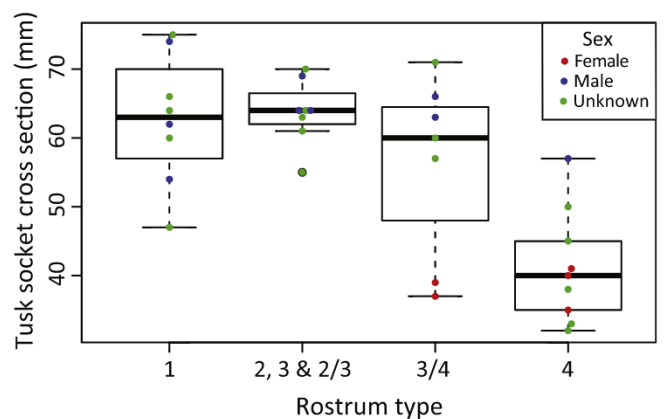


Fig. 9. Boxplot and bee-swarm plot of maximum tusk socket internal cross section by rostrum type. Sex is indicated where known based on aDNA analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Norse Greenlanders ultimately travelled to the northernmost limits of human habitation on Earth to secure sufficient animals to meet European demand. Inuit and Norse hunters may both have supplied the workshops of very distant artisans.

A northward move to hunting and/or trading in the Smith Sound area, or an analogous shift in harvesting location within Greenland, could explain the statistically significant transition from eastern to predominantly western clade walrus through time that is observable in the aDNA data (Star et al., 2018, Fig. 5). Before the mid-twelfth century, the three dated rostra with genetic data are all of the eastern clade. Conversely, between the mid-twelfth and fourteenth/fifteenth century, 10 of 11 dated rostra with aDNA results are of the western clade, with only one being eastern clade. This shift from eastern to western clade specimens over time is statistically significant (Fishers exact test p-value = 0.011). The two very late and presumably residual outliers, R1 and R4, are of the western and eastern clades respectively. Today, walrus from the area of Smith Sound are almost exclusively of the western clade, whereas the populations found further south in Greenland are of mixed eastern and western clade (Star et al., 2018).

7. Discussion and conclusions

Combining inferences from typology, aDNA and isotopes, three key observations are merited. First, almost all medieval European finds of walrus rostra most likely derived from the activities of the Norse settlement in Greenland. This was not a forgone conclusion given the possibility of a major Barents Sea source, as noted in the Ohthere account and implied by finds of walrus ivory and rostra in Novgorod and Kiev. The combination of *chaîne opératoire* study and stable isotope analysis suggests that even rostra that are genetically of the eastern clade (widely distributed from Arctic Russia to Arctic Canada) are consistent with trade from Norse Greenland. Given this discovery, it is relevant that the only known medieval textual reference to a decorated walrus skull with tusks (in the fictional *Króka-Refs saga*) relates to a gift sent from Greenland to Norway (Halldórsson, 1959:142). Based on our results, only a single rostrum (R8) clearly appears to be from somewhere other than Greenland – in this case perhaps the Barents Sea.

Second, specific urban nodes redistributed the walrus ivory originally transported with rostra. The earliest of these would appear to have been Dublin, Trondheim and Schleswig. Later Bergen took on the dominant role and Dublin may have ceased to participate. Other towns, including Oslo, Lund, Sigtuna and Uppsala, may have served as secondary hubs. Rostra were broken up for local ivory working at all of these centres. Some rostra and extracted tusks were also traded on, both near (e.g. London and Utrecht) and far (e.g. Novgorod and Kiev).

Third, the latest rostra were from smaller walruses, often female, and mostly of the western aDNA clade. Together, these findings suggest serial depletion as animals with smaller tusks, from sources further north along the western Greenlandic coast, had to be harvested to maintain the medieval trade in walrus ivory. These trends may have begun by the mid twelfth century, but are clear in the thirteenth and fourteenth centuries – the floruit of Type 4 rostra.

These discoveries provide important new evidence regarding the medieval trade of walrus ivory, supporting arguments in favour of a predominantly Greenlandic trade (Star et al., 2018; Nedkvitne, 2019:170–172) while also revealing the shifting sequence of urban nodes through which the trade flowed. Most significant is the observation that there was a transition in the kind and size of walrus harvested. The chronology of this important change is counterintuitive *vis-à-vis* existing narratives regarding the history and art history of walrus ivory use in medieval Europe. It is well-established that elephant ivory became more available during the

thirteenth century, probably due to changing trade patterns in the Mediterranean and sub-Saharan Africa (Guérin, 2010, 2017). This new availability was concurrent with a shift from Romanesque ivory carving (dominated by walrus) to the new Gothic style (typically in elephant) (Williamson, 2010; Williamson and Davies, 2014). Demand for walrus ivory should thus have declined. This reasonable assumption has sometimes been implicated in the demise of Norse Greenland (cf. Roesdahl, 1998; Seaver, 2009). Intriguingly, there are hints in historical sources that the value of walrus ivory declined, evident by the late thirteenth century. Most relevant is a famous (if slightly ambiguous) letter from Pope Martin IV to the Archbishop of Nidaros (Trondheim) in 1282 (DN, 2011:1 no. 71). It requests that a tithe payment including walrus tusks from Greenland, for which a fair price was apparently hard to secure, be converted to silver or gold for the Holy See. In 1327, documentation of another papal tithe makes it possible to establish that, in Bergen, two walrus tusks (i.e. the content of one rostrum) were equivalent in value to one Norwegian Mark, three English shillings, or approximately 100 dried cod (Nedkvitne, 2019:125–126; 178; see also Keller, 2010). We lack an earlier quantitative comparison, but by the early fourteenth century walrus ivory, although still valuable, was apparently not a precious commodity. Yet the rostra evidence implies that the exploitation of walrus probably continued unabated or even increased in the thirteenth to fourteenth centuries, when the demand for, and value of, walrus ivory may have been in decline. How can this evidence be reconciled? With decreasing value per tusk, more rather than fewer animals may have been harvested. Norse Greenlanders sought trade with Europe – for iron, timber and luxuries – and had mainly walrus products to export in exchange (Arneborg, 2003; Keller, 2010; Nedkvitne, 2019). Overexploitation of the walrus (and the need to travel to increasingly distant hunting and/or trading grounds, perhaps as far north as Smith Sound) may thus have undermined the resilience of the colony – especially in the Western Settlement, for which hunting was particularly important (McGovern, 1985a; Enghoff, 2003). Like earlier Norse expeditions to Newfoundland, abandoned after experimentation around 1000 CE (Wallace, 2003), lengthening northern voyages may not have been sustainable. No Greenlandic exports of walrus tusks are historically recorded after 1327 and the Western Settlement is generally thought to have been abandoned in the fourteenth century (Arneborg et al., 2012:4; Nedkvitne, 2019:172, 350–355). The Eastern Settlement continued to function into the fifteenth century (Jackson et al., 2018). Its demise probably entailed additional factors beyond the scope of the present paper, not least climate change (Lasher and Axford, 2019), but the loss of income as an intermediary in the ivory trade is likely to have been one relevant variable.

The walrus harvests of Greenland's medieval Norse colonists were sustainable for over a century. By the thirteenth century, however, this resilience may have been undermined by changes in value driven by increasingly global trade. The main hunting grounds around Disko Bay (Qeqertarsuup Tunua) may have been overexploited. Perhaps some harvesting moved further north, and it is possible that there was also trade with Indigenous hunting experts. These solutions required extended voyages, as far north as Smith Sound in some cases, with high opportunity costs and high risks. One collection of Norse artefacts from Ellesmere Island included numerous rivets from ship planks, implying that the crew did not make the return journey (Schledermann and McCullough, 2003). Ultimately, Greenland's Eastern and Western Settlements were abandoned or died out.

The existence of boom and bust economics is not unique to Norse Greenland. A “resource curse” has been characteristic of many economies dependent on raw materials in past and present (Innis, 1930; Badeeb et al., 2017). Sometimes it is driven by price

volatility in global or globalising systems. It can also be driven by resource depletion. Here we may see the interplay of both. Fortunately for the walrus, the end of trade with medieval Europe, and a return to harvesting guided by traditional ecological knowledge, contributed to its survival in western Greenland. Despite medieval and post-medieval episodes of heavy exploitation, it remains an important part of the Arctic ecosystem and of traditional hunting culture (Born et al., 2017).

Declaration of competing interest

None.

CRediT authorship contribution statement

James H. Barrett: Conceptualization, Funding acquisition, Investigation, Methodology, Visualization, Writing - original draft, Writing - review & editing. **Sanne Boessenkool:** Funding acquisition, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Catherine J. Kneale:** Investigation, Methodology, Writing - original draft. **Tamsin C. O'Connell:** Methodology, Writing - original draft. **Bastiaan Star:** Funding acquisition, Investigation, Methodology, Visualization, Writing - original draft, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2019.106122>.

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