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Reconstructing the ecological history of the extinct harp seal population of the Baltic Sea

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ABSTRACT

The harp seal (*Pagophilus groenlandicus*), today a subarctic species with breeding populations in the White Sea, around the Jan Mayen Islands and Newfoundland, was a common pinniped species in the Baltic Sea during the mid- and late Holocene. It is puzzling how an ice dependent species could breed in the Baltic Sea during the Holocene Thermal Maximum (HTM), and it remains unclear for how long harp seals bred in the Baltic Sea and when the population became extirpated. We combined radiocarbon dating of harp seal bones with zooarchaeological, palaeoenvironmental and stable isotope data to reconstruct the harp seal occurrence in the Baltic Sea. Our study revealed two phases of harp seal presence and verifies that the first colonization and establishment of a local breeding population occurred within the HTM. We suggest that periods with very warm summers but cold winters allowed harp seals to breed on the ice. Human pressure, salinity fluctuations with consequent changes in prey availability and competition for food resources, mainly cod, resulted in physiological stress that ultimately led to a population decline and local extirpation during the first phase. The population reappeared after a long hiatus. Final extinction of the Baltic Sea harp seal coincided with the Medieval Warm Period. Our data provide insights for the first time on the combined effects of past climatic and environmental change and human pressure on seal populations and can contribute with new knowledge on ongoing discussions concerning the impacts of such effects on current arctic seal populations.

1. Introduction

Ice breeding seal populations are seriously impacted by climate change and suffer from global warming, ecosystem change and habitat loss. One such species is the harp seal, in which reduced ice coverage and thickness in warm years are associated with high rates of pup mortality during the breeding and post-weaning period (Johnston et al., 2012; Stenson and Hammill, 2014). Furthermore, harp seal populations are subjected to commercial and subsistence harvesting (Hammill et al., 2015). Climate change over the last millennia, as well as changes in sea salinity and seal hunting had a large impact on seal populations. This is obvious in the Baltic Sea, where the seal populations have fluctuated and one species, the harp seal, was extirpated. Historical changes and the combined effects of climatic/environmental change and hunting pressure on seal populations can be investigated using palaeoenvironmental data (Anderson et al., 2006).

The harp seal (*Pagophilus groenlandicus*, Erxleben 1777), today a subarctic species with breeding populations in the White Sea, the Jan Mayen Islands and around Newfoundland, was a common pinniped species in the Baltic Sea during prehistory and is now extinct. The species is the most common seal in refuse faunas from coastal hunter-gatherer sites dating from the late Atlantic to the early Subboreal climatic period (Fig. 1; c. 4000-2000 cal BC) (Glykou, 2014, 2016; Lõugas, 1997a, 1997b; Schmölcke, 2008; Storå, 2001a; Storå and Lõugas, 2005; Ukkonen et al., 2014). However, their presence in the Baltic Sea during the late Atlantic climatic period has been long debated, as it coincides with a warm phase of the Holocene, the so called Holocene Thermal Maximum (HTM) (Ekman, 1922; Lepiksaar, 1964; Lõugas, 1998; Møhl, 1971). The HTM

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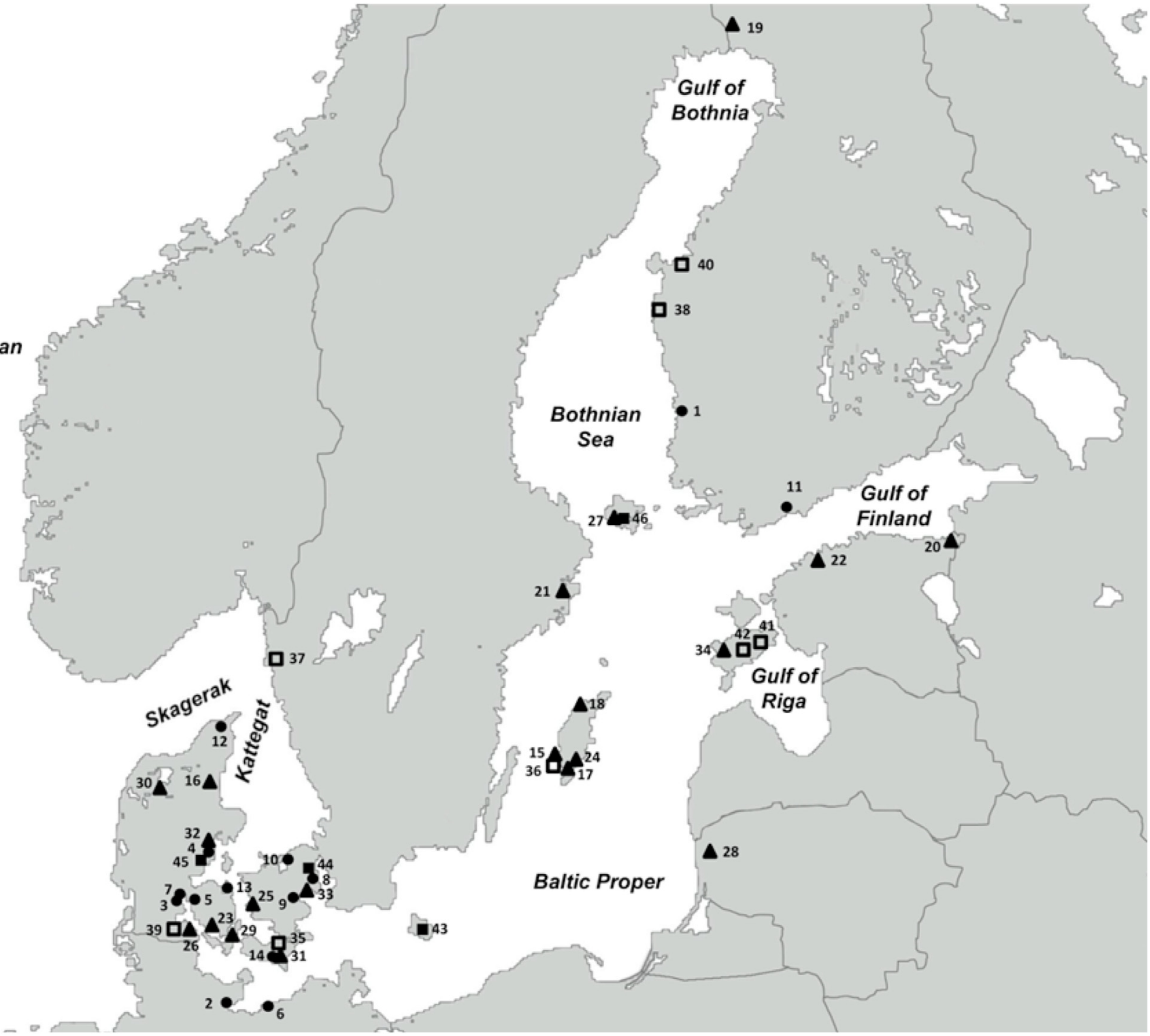

Fig. 1. Map of the Baltic Sea region showing the location where the radiocarbon dated harp seal bones come from. The numbers refer to the site numbers and are presented in Table A.1. Legends: Circle: Late Mesolithic/Early Neolithic sites. Triangle: Neolithic sites. Open square: Bronze Age sites. Filled square: Iron Age sites.

lasted approximately between 6050 and 2850 cal BC, according to continental and marine records from the Baltic Sea (Hammarlund et al., 2003; Seppä et al., 2005, Seppä et al., 2009; Zillén et al., 2008). In the eastern Baltic Sea region, for instance, the annual mean temperature was c. 2.5 °C higher than today (Seppä and Poska, 2004). The coincidence of harp seals and HTM is puzzling, since modern harp seal populations are strongly dependent on pack ice for breeding and moulting (King, 1983; Sergeant, 1991). Ice is vital for the survival of pups as they spend six to eight weeks on the ice after weaning, until moult is completed, and have developed the ability to swim and feed (Sergeant, 1991). Today, facing the challenges of global warming, in years with poor ice conditions with subsequent decline in ice extent, coverage and thickness, harp seals give birth either on the existing thin ice in their normal breeding areas, resulting in high pup death rates, or in cases of absence of ice, they move northwards in search of pack ice to give birth (Stenson and Hammill, 2014). This strong reliance of harp seals on ice for breeding and moulting has raised discussions on whether or not appropriate climatic conditions for their breeding existed in the Baltic Sea during the middle and late Holocene, and if the lack of ice led to the extinction of the population.

According to archaeological finds, the oldest harp seal bones in the Baltic Sea derive from Danish Mesolithic sites that date approximately to 5000 cal BC (Andersen, 1995; Forstén and Alhonen, 1975; Lepiksaar, 1986; Møhl, 1970, Møhl, 1971; Ukkonen, 2002). However, harp seals appear in those assemblages in extremely low numbers, and there is no evidence of pups younger than 3 months which would indicate local breeding. The earliest evidence for a breeding ground of harp seals in the Baltic Sea derive from the faunal assemblage of Neustadt LA 156, a Late Mesolithic-Early Neolithic site in Germany at the Southwestern Baltic Sea which dates between 4400 and 3800 cal BC (Glykou, 2013, 2014, 2016). It is puzzling that this coincides in time with the warmest phase of the HTM, and it is therefore crucial to radiocarbon date the harp seal bones to clarify the exact dating of the oldest breeding colony.

Harp seals appear frequently in the archaeological record after 3800 cal BC, during the Early Subboreal climatic period, when the temperature gradually decreased (Fig. 2) (Aaris-Sørensen, 2009; Fredén, 1975; Seppä et al., 2005, Seppä et al., 2009; Storå, 2001a;

Ukkonen, 2002). A pupping area is assumed to have existed between the archipelago of Åland and the island of Gotland, based on the age structure and the presence of pups in the archaeological assemblages (Storå, 2001a; Storå and Ericson, 2004; Storå and Lõugas, 2005). The frequencies of harp seal bones in the archaeological record decreased during the Bronze Age to become scarce during the Iron Age (Boessneck and von den Driesch, 1979; Møhl, 1957; 1970; Sellstedt, 1966; Storå and Lõugas, 2005; Ukkonen, 2002).

Overall, the Baltic harp seal had a smaller body size compared to modern harp seals from the Atlantic Ocean (Ekman, 1922; Forstén and Alhonen, 1975; Lepiksaar, 1964, 1986; Lõugas, 1997a) and a decrease in body size of the Baltic Sea harp seal population has been observed towards the Middle/Late Neolithic (Table A.4) (Glykou, 2016; Storå, 2001; Storå and Ericson, 2004). However, the decrease in adult body size is observed only in the Baltic harp seal population. Harp seals from Neolithic archaeological sites from Varangerfjord in Norway had the same adult body size as the extant White Sea population (Hodgetts, 1999). Osteometric analysis of harp seal bones from the Bronze and Iron Age showed a smaller mean adult body size compared to the modern ones, suggesting a continuing local breeding population in the Baltic Sea during the Iron Age (Storå and Lõugas, 2005).

In a study by Bennike et al. (2008), where 24 harp seal bones from Danish archaeological sites were radiocarbon dated, two chronologically distinct groups of harp seals were identified. The first group dated to 4100-3800 cal BC (Late Mesolithic-Early Neolithic) and the second group to 3000-2400 cal BC (Middle Neolithic). However, this study was regionally restricted to harp seal bones from Danish archaeological sites and there is no information on the biological age of the sampled individuals. Therefore, it remains uncertain if these individuals belonged to a local Baltic Sea breeding population or were just occasional visitors from the Atlantic breeding populations. Even if the exact distribution of the harp seal populations in prehistory is not known, we assume a source population from the subarctic, most probably the White Sea population. Harp seals from the White Sea population appear along the Norwegian north coast during the spring-summer migration and occasionally, in years with unusually cold temperatures in the Barents Sea, they migrate further south than their normal range, reaching down to Skagerakk (Ekman 1922; Lepiksaar 1964; Forstén and Alhonen 1975). Such invasions have been recorded in e.g. 1902-03 and 1987-88, when many thousands of harp seals reached as far as Skagerakk in search of food (Nilssen et al., 1998; Haug and Nilssen 1995;Siversten, 1980). In prehistory, harp seal was the most common hunted seal in the Varangerfjord (Hodgetts, 2010; 1999).

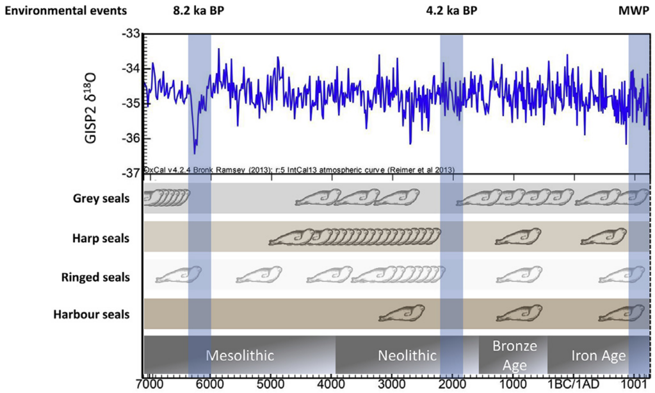

Fig. 2. Relative frequencies of grey, harp, ringed and harbour seals as represented by NISP. The x-axis represents calendar years and the archaeological periods. The blue bands represent three major environmental/climatic events: the 8.2 ka cold event, the 4.2 ka aridification event and the Medieval Warm Period. For exact representation of data, see Table A.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

To explore the factors that led to the final extirpation of harp seal in the Baltic Sea, we use zooarchaeological, isotopic, chronological and palaeoenvironmental data to reveal their ecological history. We are aware that the composition of faunal assemblages from archaeological excavations might not necessarily reflect the natural abundances of species as they can be biased by human subsistence choices towards a preferred prey, or by taphonomical processes. However, archaeological faunal assemblages are recognized to offer valuable insights not only into past human culture and biological history, but also into the distribution and ecology of extirpated species, as in the case of the Baltic harp seal (Lyman 2017, 326). We base our analysis and interpretations on three assumptions: 1. The extirpated Baltic Sea harp seal had the same ecological tolerances as the modern living harp seal populations. 2. The presence of harp seals in the Baltic Sea indicates that the specific environmental conditions required for its successful reproduction existed, while absence of harp seals does not necessarily mean that environmental conditions were unfavourable. 3. The faunal composition of the archaeological assemblages can be used as proxies for the natural abundances of species.

We perform radiocarbon dating of 24 bones from harp seals from different regions of the Baltic Sea area. The bones cover all individual age groups (newborn, subadults, adults). We combine these data with stable isotope data and previously directly dated harp seal bones together with environmental data. We investigate the presence/absence of harp seals, focusing on when they first immigrated into the Baltic Sea, when the oldest breeding population was established there and for how long the species bred in the Baltic Sea. Finally, we investigate when the Baltic Sea harp seal population disappeared or went extinct and how this all correlates with climatic fluctuations. We investigate the combined effects of past climatic and environmental change and human pressure on harp seal populations. We provide insights into past processes and contribute to discussions concerning the impacts of such effects on current arctic seal populations.

2. Materials and methods

2.1. Archaeological context and samples

In total 24 harp seal bones were radiocarbon dated. The bones chosen for analysis cover the entire range of the temporal and spatial distribution of harp seals in the Baltic Sea (Fig. 1). Sampling selection was based on the relative chronology of the archaeological context, bone identification to species level, and the age structure of harp seals in each archaeological assemblage. For the purpose of this study, we ensured that all faunal assemblages with presence of harp seal pups (age cluster 0–3 months old) were radiocarbon dated (Table A.1).

Bones from the following archaeological sites were collected for radiocarbon dating: The Late Mesolithic/Early Neolithic site Neustadt LA 156 (Fig. 1, site nr. 2), situated at the Southwestern Baltic Sea in Northern Germany. The site represents the oldest evidence of an extensive exploitation of harp seals in the Baltic Sea and is linked to the presence of a harp seal breeding population close to the site (Glykou, 2013, 2014, 2016). According to a series of radiocarbon dates the site was used from 4400 to 3800 cal BC, i.e. during the Late Mesolithic Ertebølle culture and the Earliest Neolithic Funnel Beaker culture (Glykou, 2016). Marine mammals comprise 37% of the mammals (NISP, Number of identified specimens) (Glykou, 2013, 2016). Aquatic resources, fish and marine mammals, were of immense importance for the inhabitants of the site (Glykou, 2014). The marine mammal assemblage is dominated by harp seals (Table A.2). Four bones from this site were radiocarbon dated (Table A.1).

The Middle Neolithic site Brunn (Fig. 1, site nr. 21), situated in the parish of Ösmo in Södermanland, dates to the Middle Neolithic (MN A) and is assigned to the Pitted Ware Culture. At the time of occupation the site was situated in the outer archipelago, on the eastern coast of Sweden. A preliminary analysis of the faunal remains shows that seal bones predominate in the mammal faunal remains (Table A.2) (Storå, 2001a). Four bones from this site were radiocarbon dated (Table A.1).

Jettböle I and Jettböle II (Fig. 1, site nr. 27), situated in Jettböle, Jomala, on Åland, are assigned to the Middle Neolithic and Middle/Late Neolithic Pitted Ware Culture (MN A and MN/LN) respectively. Harp seal hunting was very extensive at this site (Table A.1) (Storå, 2001a). Large amounts of bones were recovered at this site including harp seal (Storå, 2001a). One bone from this site Jettböle I was radiocarbon dated (Table A.1).

The site Hemmor (Fig. 1, site nr. 24), located on the island of Gotland, dates to the Middle Neolithic Pitted Ware Culture (MN A). According to the faunal remains of the site, the economy of the inhabitants was based mainly on domesticated pigs, but wild resources were also exploited, mainly represented by seals (Table A.2). Harp seal is the most common seal species at this site (Storå, 2001a). Three bones from this site were radiocarbon dated (Table A.1).

The site Ajvide (Fig. 1, site nr. 17) located on the western coast of the island of Gotland, dates to the Pitted Ware Culture and consists of three areas with slightly different chronology. The Ajvide D-upper dates to the MN A (3100-2700 cal BC), Ajvide-D lower and Ajvide C date in the late MN B/LN (Burenhult, 1997). For this study harp seal bones from the faunal assemblage of Ajvide D-upper were analyzed. The faunal assemblage consists mainly of fish and seals while pig is the only domesticated animal (Lindquist, 1997; Lindquist and Possnert, 1997). The dominant seal species is the harp seal followed by ringed seal (Rowley-Conwy and Storå, 1997; Storå, 1997). A decrease of the relative frequencies of harp seals has been observed towards the younger layers of the Ajvide D-upper (Storå, 1997). Two bones from this site were radiocarbon dated (Table A.1).

The Šventoji archaeological complex (Fig. 1, site nr. 28), situated on the Lithuanian coast, consists of more than 60 sites as well as many stray finds (e.g. stone and bronze axes) dating from the Late Mesolithic to the tLate Bronze Age. The sites were interpreted as habitation areas, refuse layers and fishing stations. The subsistence of all Šventoji sites was based on freshwater fishing and hunting. The seal bones comprise c. 40% of all mammal bones. Harp seal prevails in all sites, followed by ringed, harbour and grey seals (Piličiauskas, 2016a;Piličiauskas, 2016b; Piličiauskas et al., 2017). One bone from Šventoji 4 was radiocarbon dated.

Stora Förvar (Fig. 1, site nr. 15), a cave site situated on the northern part of the island of Stora Karlsö, to the west of the island of Gotland, dates from the early Mesolithic up to Iron Age (Lindquist and Possnert, 1999). It is assumed that the site was mainly used because of the abundant presence of harp, grey and ringed seals (Apel and Storå, 2017; Clark, 1946, 1976; Ericson and Knape, 1990; Lindquist and Possnert, 1997, 1999; Pira, 1926). Three bones from this site were radiocarbon dated (Table A.1).

The site Asva (Fig. 1, site nr. 41), situated on the south-eastern part of the island Saaremaa in Estonia, mainly dates to the late Bronze Age (Lang, 2007), but the upper layer of the settlement area yielded finds of the Iron Age. Seal bones are mainly associated with the Bronze Age layer (Storå and Lõugas, 2005). According to the osteological material, the economy of the Asva settlers was based equally on farming and seal hunting. The harp seal is the most common seal, followed by grey seal, harbour seal and ringed seal (Lõugas, 1997a, Lõugas, 1997b, Lõugas, 1998). Two bones from this site were radiocarbon dated (Table A.1).

The site Brömsängsbacken (Fig. 1, site nr. 46), situated in the parish of Jomala, Åland Islands, dates to the Late Iron Age. The faunal remains have not been published yet but the seal bones have been included in a study from Storå and Lõugas (Storå and Lõugas, 2005; Storå et al., 2012). Three bones from this site were radiocarbon dated (Table A.1).

2.2. Species determination

We restricted our sample selection only to the temporal bone, humerus and femur, since pinniped bones display such pronounced morphological similarities. Species identification cannot be obtained with accuracy for skeletal elements such as axial bones, vertebrae, ribs and lower limb bones (Hodgetts, 1999). Cranial bones and specific postcranial elements, however, allow a secure identification at a species level (Heinrich, 1991; Hodgetts, 1999; Storå, 2001b; Ukkonen, 2002).

2.3. Ageing of seal bones

Osteometric analysis allows age determination of yearlings into two age clusters: newborns (yearlings 0–3 months) and older yearlings (3–11 months). According to modern data, newborns do not have the physiological maturity to swim long distances (Sergeant, 1991). Thus, presence of newborns in archaeological assemblages suggests that breeding grounds existed in the Baltic Sea during the late Mesolithic and during the Middle Neolithic (Glykou, 2013, 2016; Storå 2001a). In order to ensure that all postulated breeding populations are taken into consideration for radiocarbon dating, we included all faunal assemblages with harp seal pups of the age cluster of newborns (Table A.1; Table A.3).

2.4. Radiocarbon dating

Collagen from 24 harp seal bones has been radiocarbon dated at the Tandem laboratory at Uppsala University. In addition, dates from two harp seal bones dated at Aarhus University (AAR-25996 and AAR-27414) and two dated at Helsinki Accelerator Laboratory (Hela-1328 and Hela-1329) were included in this study. Another 45 previously published radiocarbon data were integrated in this study (Table A.1).

2.4.1. Reservoir age

The harp seal, as it is a migratory species and moves between waters with different salinity, could potentially represent an average of reservoir ages of different marine regions (Lougheed et al., 2013). Strontium isotope ratios indicate that seals were feeding close to riverine discharge areas in the Southwestern Baltic Sea region (Glykou et al., 2018). Thus, a mixture of marine and freshwater reservoir effects is possible for the seals of the Baltic Sea. However, due to the lack of available data/studies on that, we apply a Baltic Sea marine reservoir correction.

The oceanic reservoir effect is estimated to range between 400 and 500 years, even though significant variations within one region can be detected (Taylor et al., 1996). Marine reservoir effects correlate with salinity and in the Baltic there are major freshwater inputs that might have affected the reservoir age regionally (Lougheed et al., 2013). Thus, we considered regional variations in the marine reservoir and estimated the reservoir effect value for each region separately:

2.4.2. Reservoir offsets R(t)

2.4.2.1. SW Baltic Sea. For the site Neustadt LA 156 in Southwestern Baltic Sea the regional reservoir offset R(t) was determined by calculating the reservoir offset in three paired marine/terrestrial samples (Table A.4): Two paired samples originate from two ceramic pots and the offset was determined between the dated charred food crust and the charcoal from the ceramic matrix. The charcoal dated originated from a short-lived plant that was unintentionally mixed into pottery clay during manufacturing; therefore the dating should not be affected from an old-wood effect. The first paired sample yielded an offset of 174 ± 60 ^{14}C years. The second paired sample yielded an offset of 302 ± 71^{14}C years (Glykou, 2016). The third paired sample includes a date from a harp seal femur and charcoal from the tempering of a pointed based pot. Both radiocarbon dated samples were found in close connection and at the same depth, revealing a reservoir offset of 103 ± 65 years. The mean offset of these three paired samples was calculated to 193 ± 116 years.

Our calculations of the reservoir offset for this region are based on two assumptions:

1. The carbon derives from a mixture of marine and terrestrial sources, based on both lipid analysis of ceramics and faunal analysis (Craig et al., 2011; Glykou, 2014, 2016; Saul et al., 2014).
2. It is highly likely that there were no changes in the salinity during the period in which the site was inhabited (4400-3800 cal BC (Glykou, 2016),) and thus by implication we assume that the marine reservoir age remained constant during the period in question.

Our calculated reservoir offset of 193 ± 116 ^{14}C years differs from the marine reservoir offset of 400 years that has been used for correcting the radiocarbon dates of harp seal bones from Danish sites in a previous study (Bennike et al., 2008). These calculations were based on a study of the marine reservoir effect in Denmark (Krog and Tauber, 1974) and the estimation that the reservoir effect is higher close to the Danish fjords, due to a limited water exchange in the fjords (Bennike et al., 2008).

2.4.2.2. Baltic Proper. For the Middle Neolithic sites of the Baltic Proper, a compilation of paired radiocarbon data from Pitted-Ware sites on Gotland, provided a mean offset of 111 ± 34 radiocarbon years (Eriksson unpublished data; Eriksson, 2004). We apply this reservoir offset for all the Pitted-Ware sites: Brunn, Hemmor, Jettböle and Ajvide.

2.4.2.3. SE Baltic Sea. For the Neolithic site Šventoji at the southeastern coast of the Baltic Sea, a marine reservoir offset of 190 ± 43 years was estimated based on offsets between paired dates of terrestrial samples (hazelnut shells) and seal bones (no species determination possible) at the site Šventoji and Nida (Piličiauskas and Heron, 2015).

2.4.2.4. Other sites. Since we lack information on the regional marine reservoir offset R(t) of the Bronze Age and Iron Age sites included in this study, we apply the regional reservoir offset R(t) of the previous chronological stages: for the dates from the Bronze Age site Asva we apply the same marine reservoir offset as for Šventoji (190 ± 43 years) and for the dates from Stora Förvar and Brömsängsbacken we apply the same marine reservoir offset (111 ± 34 years) as for the Middle Neolithic sites from the same region.

2.5. Calibration of data and OxCal model

For the calibration of the dates we used the software OxCal 4.4 (Bronk Ramsey 2009) using the IntCal 20 calibration curve (Reimer et al., 2020). The reservoir offsets R(t) of different regions and time periods in the Baltic Sea (see section 2.4.2) were included in OxCal.

All radiocarbon data were integrated in a model. The model boundary-interval-boundary was chosen to calibrate predefined groups of dates as it calculates the duration of the intervals between the groups. The dates have been organized in groups of events according to a predefined chronological sequence which corresponds to the relative chronology of the archaeological context, i.e. Late Mesolithic/Early Neolithic (LM/EN), Middle Neolithic (MN), Bronze Age (BA) and Iron Age (IA). Thus, we assume for these phases a chronological sequence deduced from the archaeological record.

The first group LM/EN includes dates from the late Mesolithic and earliest Neolithic site Neustadt LA 156. The MN group includes dates from the Middle Neolithic sites Brunn, Hemmor, Jetbölle, Ajvide and Šventoji. The next group BA includes dates which count to the Bronze Age phase of Stora Förvar and the Estonian site Asva. The final group IA includes dates from the site Brömsängsbacken.

2.6. Body size reduction

To investigate body size reduction related to chronology we used measurements from two skeletal elements, the humerus and the temporal bone. We used published data on the diaphyseal height of the humerus (Glykou, 2016; Storå and Ericson, 2004) and for this study, we added new data from the Neolithic from Šventoji and the Bronze Age from Stora Förvar and Asva (Table A.5). No data from the Iron Age sites were available. For the temporal bone, we used published data on the greatest diagonal breadth of the pars mastoideus (Storå and Lõugas, 2005). However, in the published table the mean values for each period include bones of all ages, subadults and adults (Storå and Lõugas, 2005, p. 102 Table 4). This is because the temporal bone is not appropriate for making a detailed age determination, only a rough division between subadults and adults is possible (Storå and Lõugas, 2005). Thus, depending on the frequencies of juvenile harp seals, the mean value can be biased resulting in a slightly smaller mean size than if only the adult population was examined (Table A.5). However, the temporal bone is a very important skeletal element because it is one of a few bones that allow determination to species (see also 2.2). Additionally, because of its high mineral density, it is one of the most commonly found and best-preserved bones in archaeological faunal assemblages. In the current study, there were no measurable humeri available for the Iron Age and therefore the use of temporal bones was deemed necessary. Because of this bias, the interpretation of the results will be based on the measurements of the humerus. However, the measurements of the temporal bone will be assessed to see if any tendencies observed in the humerus are confirmed. For this study, we added measurements on the temporal bone from the Late Mesolithic/Early Neolithic site Neustadt and the Neolithic site Šventoji. Data for modern seals were from Storå and Ericson (2004) (Table 2). According to Storå and Ericson (2004), the majority of modern harp seals used for their study were from the White Sea population while some of the bones were from the Newfoundland population (Storå and Ericson 2004, 120–121; Table 2). To test for significance we used a non-parametric *t*-test (SISA, https://www.quantitativeskills.com/sisa/index.htm).

2.7. Carbon isotope analysis

We performed $\delta^{13}C$ analysis of 170 individuals, covering different biological ages, sites around the Baltic Sea and different time periods (Table A7). The mean $\delta^{13}C$ values were used to correlate with salinity fluctuations in the Baltic and not to discuss foraging and migration patterns. Twelve modern samples are from the collection of Swedish Museum of Natural History. These harp seals originated from the White Sea population and were caught in Norway.

For the isotopic analysis, only species-specific bones were used (see section 2.2). Cortical bone was cleaned with demineralized water and after it was dried, the surface layer was drilled and discarded to prevent contaminations. For the analysis, ~100 mg of bone powder was obtained by using a microdrill. The stable isotope analysis was performed on collagen. Collagen extraction was performed according to the protocol from Brown et al. (1988) and took place at the Archaeological Research Laboratory, Stockholm University. Collagen (~0.5 mg) was weighed into tin capsules and the samples were analyzed using a Carlo-Erba elemental Analyser connected to a continuous flow Isotope Ratio Mass Spectrometer (EA-IRMS) at the Stable Isotope Laboratory, Department of Geological Sciences (SIL), Stockholm University. All 170 samples included in this study yielded atomic C/N ratios that were within the limits of 2.9–3.6 for unaltered collagen (DeNiro 1985). The carbon content was between 22.2 and 50%, the one sample (AJV037) with 50% carbon weight deviated from the accepted for modern collagen (carbon 15–47%, Ambrose 1990). However, because the C/N was within the accepted range and no other visual sign of diagenesis was observed, the sample was regarded as suitable for analysis (Ambrose 1990; van Klinken 1999). For statistical analysis we used the software IBM SPSS 23. For significance testing, we applied a non-parametric Kruskal-Wallis test.

2.8. Strontium isotope analysis

We sampled nine canines from harp seals (Table A.8). Strontium isotope ratios of enamel were measured on the teeth at the Vegacenter facility at the Swedish Museum of Natural History using a NWR193 excimer laser ablation system (ESI) coupled to a Nu Plasma II multi-collector ICP-MS (Nu Instruments Ltd), following the method described in Glykou et al. (2018). Instrument parameters are listed in Table A.10. The teeth were mounted to a sample cell and contaminations were removed by pre-ablating the surface. All canines were sampled in the same way. Tracks perpendicular to the direction of growth of the tooth were ablated. The tracks had a length of 650–900 μm using a 140 μm spot size. The number of ablation lines per tooth ranged from 15 to 26, depending on the tooth size.

3. Results

3.1. Radiocarbon dating

The 24 new radiocarbon dates expand the overall range of the harp seal occurrence in the Baltic Sea from c. 4500 cal BC to 1100 cal AD (Fig. A.1; Table A.1). All available radiocarbon dates ($n = 73$) have been organized in groups of temporal events corresponding to the relative chronology of the archaeological context (see section 2.5). The model used calculates the duration of the four predefined groups (LM/EN, MN, BA and IA; Fig. A.2-A.3) and shows if any hiatus between the groups existed. Our data show one hiatus in the presence of harp seals in the Baltic Sea between the Middle Neolithic and the Bronze Age.

The first group LM/EN dates from 4654-4324 to 4123-3806 cal BC (2σ). The second group MN dates from 3932-3659 to 2771-2486 cal BC (2σ). The interval between the first two groups is calculated to 0–342 years (2σ). According to the model this implies an uninterrupted continuation from the Late Mesolithic to the Middle Neolithic. The Bronze Age group dates from 1744-1345 to 742-454 cal BC (2σ). The model yielded a hiatus of 849–1346 years (2σ) between the Middle Neolithic and Bronze Age groups. Finally, the Iron Age group dates between 630 and 10 cal BC and 876–1626 cal AD (2σ). Here, the model suggests an uninterrupted continuation from the Bronze Age to the Iron Age as the interval between the two groups is calculated to 0–616 years (2σ).

Consequently, for the following discussion, we define two phases of harp seal presence in the Baltic Sea: Phase I, which dates from 4654-4324 cal BC to 2771-2486 cal BC (2σ) and covers the Late Mesolithic/Early Neolithic until the Middle/Late Neolithic. After a hiatus of approximately 1000 years, follows phase II that dates from 1744 to 1345 cal BC to 876–1626 cal AD (2σ). However, there are no harp seal finds from post-Iron Age contexts, meaning that the dates roughly correspond to the Bronze Age and Iron Age (Fig. 5). Thereafter, there is no evidence of harp seal presence in the Baltic Sea.

3.2. Body size

To explore body size changes in harp seals during the mid- and late Holocene we used all available osteometric data (see section 2.6; Table A.5). Based on the measurements of humerus there are four main observations. 1) We confirm a significant body size reduction from the Mesolithic towards the Neolithic. 2) We demonstrate that body size reduction ends with the late Neolithic, i.e. the end of Phase I (Fig. 3). 3) During the Bronze Age harp seals body size is larger than before the hiatus. While the differences in size between Neolithic and Bronze Age harp seals are not statistically significant for the humerus ($p = 0.9$), they are significant for the temporal bone ($p = 0$). Although the measurements of the temporal bone might be biased towards a smaller size as the bones can originate from both subadults and adult seals, we find it highly unlikely that this bias would only act upon the Neolithic sample.

4) The harp seals from the Bronze and the Iron Age display similar body size, according to the measurements of the temporal bone, but they are still smaller compared to modern seals (Fig. 3). The size difference between the modern and the BA and IA harp seals suggests that the Baltic Sea harp seal population was still a separate population during the Late Holocene, as previously suggested (Storå and Lõugas 2005, see discussion below).

3.3. $\delta^{13}C$ data

The differences between the mean $\delta^{13}C$ values of the four archaeological groups are not statistically significant. However, a slight increase is noted from the LM/EN samples ($\delta^{13}C$ −17‰) to the MN ($\delta^{13}C$ −16.7‰), the Bronze Age ($\delta^{13}C$ −16.7‰) and the Iron Age ($\delta^{13}C$ −16.6‰) (Fig. 5; Fig. A.4; Tables A.6-A.7). The mean $\delta^{13}C$ values are higher in the modern samples ($\delta^{13}C$ −16.1‰) and this difference is statistically significant ($p < 0.05$) compared to all archaeological groups. Since the modern samples originate from harp seals from the White Sea population caught off the Norwegian coast, it is not surprising that the $\delta^{13}C$ is significantly different. Furthermore, this indicates that the Baltic Sea harp seals from BA and IA had the same isotopic signature as the MN/LN samples, again suggesting that they were local populations.

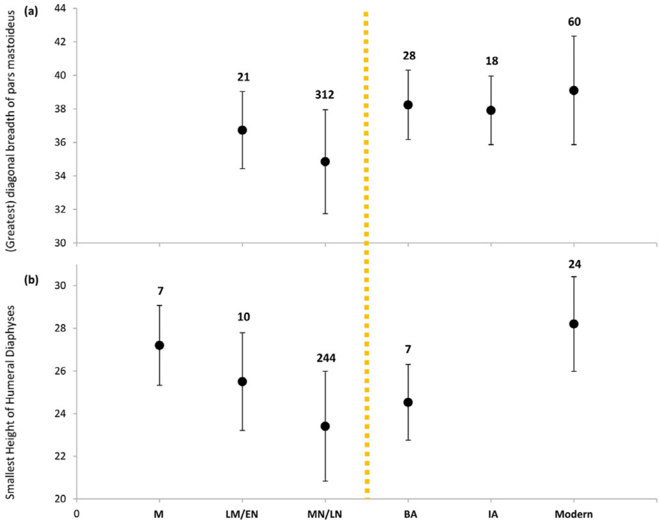

Fig. 3. Osteometric analysis of two different skeletal elements of harp seals. The x-axis represents the archaeological periods M: Mesolithic, LM/EN: Late Mesolithic/Early Neolithic, MN/LN: Middle/Late Neolithic, BA: Bronze Age, IA: Iron Age, Modern: White Sea/Newfoundland population. The yellow line represents the hiatus in the radiocarbon dates. Y-axis: (a) (Greatest) diagonal breadth of pars mastoideus in mm. Data for LM/EN this study, for MN/LN, BA, IA and Modern (White Sea/Newfoundland population) from Storå and Lõugas (2005); (b) Smallest height of humeral diaphysis in mm. Data for M, MN/LN and Modern (White Sea/Newfoundland population) from Storå and Ericson (2004); Data for LM/EN from Glykou (2016). Numbers represent sample sizes. The error bars show 95% confidence interval. See also Table A.5.

3.4. Strontium isotopes

A sequential strontium isotope analysis was performed on nine harp seal canines from the late Mesolithic/Early Neolithic site Neustadt, and the Bronze Age site Asva (Table A.9). All canines yielded $^{87}Sr/^{86}Sr$ ratios between 0.7095 (lowest value by seal 033) and 0.7130 (highest value by seal 039) (Fig. 4; Table A.9). These $^{87}Sr/^{86}Sr$ ratios deviate strongly from the $^{87}Sr/^{86}Sr$ in oceanic seawater, which is globally homogeneous averaging 0.709171 ± 0.000004 (Mokadem et al., 2015). However, in small basins, such as the Baltic Sea, the strontium isotopic composition of the water can vary considerably. Salinity fluctuations and major freshwater inflow result in $^{87}Sr/^{86}Sr$ ratios that range between 0.7092 and 0.7093 in the Baltic Proper and 0.7095–0.7097 in the Gulf of Bothnia (Åberg and Wickman, 1987; Löfvendahl et al., 1990). Close to the riverine discharge areas, the $^{87}Sr/^{86}Sr$ ratios are much higher, depending on the source sediment the rivers drain (Andersson et al., 1992). The $^{87}Sr/^{86}Sr$ values, (0.7095–0.7130) obtained from the seal teeth in this study correspond to the $^{87}Sr/^{86}Sr$ ratios of the Baltic Sea (Glykou et al., 2018; Andersson et al., 1992; Widerlund et al., 2011). Further, because in pinnipeds deciduous teeth are shed in utero and permanent dentition erupts at birth (Beloborodov 1975; Stewart and Stewart 1987), the isotopic composition of permanent teeth reflects to a great extent the mother's diet during the last months of gestation (Glykou et al., 2018). Thus, $^{87}Sr/^{86}Sr$ ratios on tooth enamel from pinnipeds reflect mostly the mother's diet (Glykou et al., 2018). According to that and given that all individuals yielded $^{87}Sr/^{86}Sr$ that correspond to the Baltic Sea, we assume that these harp seals were foraging in the Baltic Sea where they subsequently gave birth to their pups, i.e. they belonged a local breeding population.

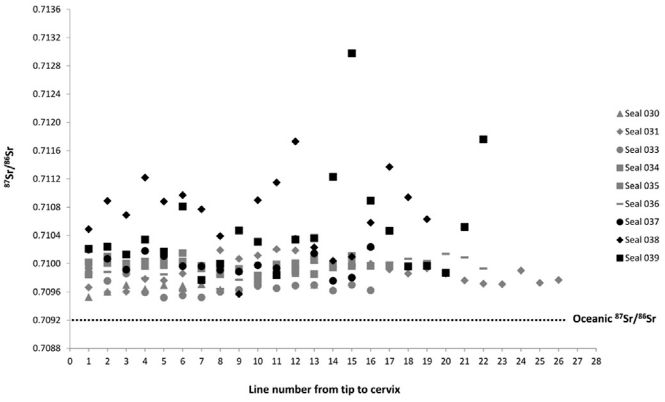

Fig. 4. $^{87}Sr/^{86}Sr$ ratios for harp seal teeth. The x-axis represents the sampling lines from the tip of the canine towards the cervix. The dotted line marks the oceanic $^{87}Sr/^{86}Sr$ ratio. The grey legends represent individuals from the Late Mesolithic/Early Neolithic site Neustadt. The black legends represent individuals from the Bronze Age site Asva.

4. Discussion

Our study shows that harp seal breeding populations were present in the Baltic Sea within two periods: The first period lasted from 4654-4324 to 2771-2486 cal BC (in 2σ, phase I) without interruptions (Fig. 5). Within phase I, two breeding grounds existed successively in the southwestern Baltic Sea during the Late Mesolithic/Earliest Neolithic and in the Baltic Proper during the Middle Neolithic. While the presence of harp seals during these periods was already known from previous analyses (Bennike et al., 2008), our study shows that the harp seal presence was continuous until the mid-3rd millennium BC. After a hiatus of approximately 1000 years, phase II begins in 1744-1345 cal BC and ends 876–1626 cal AD (2σ), covering the Bronze Age and the Iron Age (Fig. 5). During phase II, the harp seal presence in the Baltic Sea occurred without any interruptions and is again linked to a breeding population.

Spatio-temporal temperature changes, salinity fluctuations, environmental events and eventually anthropogenic impact may have played a crucial role to the harp seal presence/absence in the Baltic Sea. This includes initial immigration, population increases, decreases, and the final extirpation of the Baltic Sea harp seal, which are going to be discussed here.

4.1. Phase I of harp seal presence in the Baltic Sea (Late Mesolithic-Middle/Late Neolithic)

One of the most fascinating questions when reconstructing the history of the Baltic Sea harp seal is when this cold adapted species entered the Baltic Sea and started to reproduce there. It has been proposed that harp seals migrated into the Baltic Sea during the 8.2 cold event (Schmölcke, 2008). This event that occurred approximately 6200 cal BC is recorded in the GISP2 ice core as a pronounced decrease in $\delta^{18}O$ (Fig. 5) (Stuiver, 1999; Stuiver et al., 1995) and in other proxy climate indicators from lake sediments in southern and western Sweden (Antonsson and Seppä, 2007; Seppä et al., 2005). However, this cooling had a short duration of approximately 300 years and thus, it did not coincide with the earliest evidence of harp seals in the Baltic which according to the present study is placed c. 2000 years later (Fig. 5). In addition, a cooling period alone did not necessarily attract seals to enter the Baltic Sea, as other conditions would be required. Higher salinity with subsequent organic productivity and increased nutrient levels would attract new fish species in the Baltic Sea and thus create attractive environmental conditions for the harp seal (Lepiksaar 1986; Lõugas, 1997b,Lõugas, 1999·Schmölcke and Ritchie, 2010).

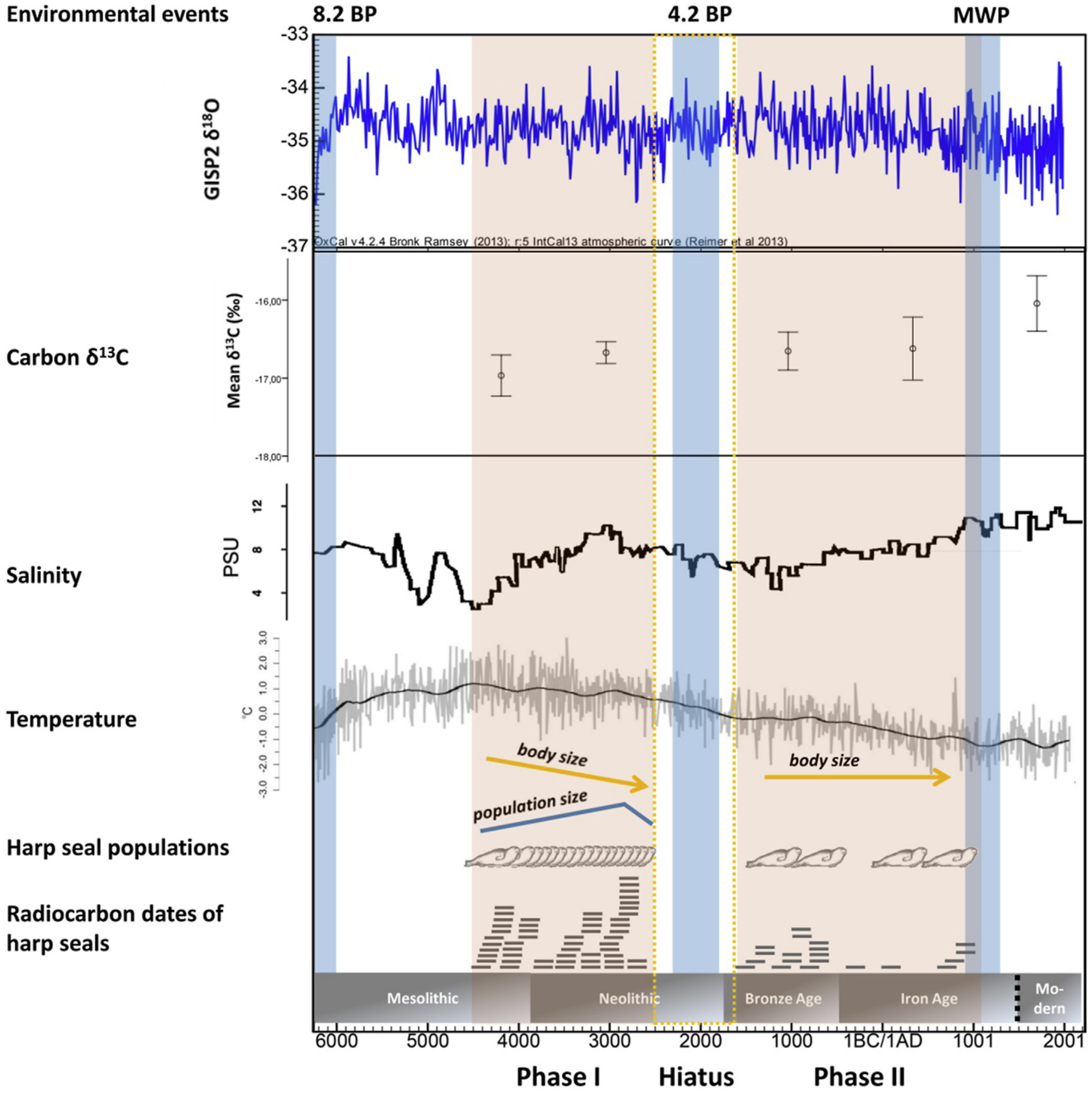

Fig. 5. All radiocarbon dates are presented here in lines showing the range in 1σ. North-European pollen based temperature curve from Seppä et al. (2009) presents the mean annual temperature. Salinity estimates for the Gotland basin from Emeis et al. (2003). Mean $\delta^{13}C$ values for harp seals from this study, n = 170 (see also Table A.6-A.7). The blue bands represent three major environmental/climatic events: the 8.2 cold event, the 4.2 aridification event and the Medieval Warm Period. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Harp seals appear sporadically in the Baltic Sea shortly after 5000 cal BC (Bennike et al., 2008; Ukkonen, 2002) but the oldest evidence of a breeding population comes from the site Neustadt, dated between 4400 and 3800 cal BC (Glykou, 2016) (Fig. A.1, A.2). Two bones from this site yielded dates before 4000 cal BC (Ua-50214 and Ua-50215; Table A.1) and the oldest one (Ua-50214: 4638-4093 cal BC 2σ) comes from a newborn harp seal. We assume that this pup was born in the Baltic Sea because harp seals of that age have not yet completed the physiological maturation that enables them to swim long distances. That the harp seals from this region were breeding locally is also confirmed by the strontium analysis (Fig. 4). All sampled harp seals from this group (LM/EN) yielded $^{87}Sr/^{86}Sr$ values > 0.7095 thus, corresponding to $^{87}Sr/^{86}Sr$ values from the Baltic Sea water and riverine discharge areas in the southwestern Baltic Sea (Andersson et al., 1992; Glykou et al., 2018; Löfvendahl et al., 1990). Two previous radiocarbon dates, one from Kolding Fjord in Denmark, approx. 4600-4100 cal BC (2σ, LuS-6129, Table A.1) and one from Närpiö in Finland, approx. 4800-4450 cal

BC (2σ, Hela-441, Table A.1) confirmed the presence of harp seals in the Baltic Sea during the HTM. Our data, however, provide the first evidence of a local breeding population in the Baltic Sea during the HTM, based on age structure (presence of newborns (Glykou, 2016)), radiocarbon dating and strontium isotope analyses. Thus, initial immigration and establishment of local harp seal breeding populations took place during the HTM. It is difficult to determine the source population for the Baltic harp seals; for that genetic analysis would be required. However, assuming that the distribution of the prehistoric harp seals populations was similar to modern ones, and based on historical migrations we would estimate a possible origin from the White Sea.

How come this ice dependent species was able to breed in the Baltic Sea during the HTM? There are two explanations: 1) They had a different breeding behavior from the modern populations that allowed them to breed on land; 2) The winters during the HTM in northeastern Europe were colder than so far assumed. Based on environmental data we think that the most plausible explanation would be that winters were colder.

Modern harp seals are highly dependent on pack ice as they give birth and nurse their pups on it. After weaning, young harp seals stay on ice for a few weeks until the post-weaning moult is completed (Sergeant, 1991). During this time, the young seals undergo a physiological maturation process, which will enable them to store oxygen so that they can dive (Burns et al., 2007). Therefore, the quality of ice during the post-weaning period is crucial for the survival of young harp seals. Studies on the current harp seal population of the Northwest Atlantic show that climate related environmental changes such as reduced ice coverage and thickness in warm years are associated with high rates of harp seal pup mortality during the breeding and post-weaning period (Johnston et al., 2012; Stenson and Hammill, 2014). Despite the current environmental challenges there is, however, no evidence at all that harp seals are able to land breed or “emergency” land breed in case of poor ice conditions (Stenson and Hammill, 2014). Additionally, climate and environmentally associated declines or changes in the fish stocks preyed upon by harp seals (capelin, Atlantic cod) have negative impacts on their reproduction rates (Stenson et al., 2016). In sum, modern harp seals are highly sensitive to any changes in their habitat that affect breeding and foraging patterns, and such changes have evidently negative impacts on their population dynamics and their general body condition (Stenson et al., 2016). Since modern harp seal breeding populations, so far, do not show any adaptability to environmental and habitat change, we assume that the prehistoric harp seal populations of the Baltic Sea had similar behavior and bred and moulted on pack ice during the HTM.

Climate reconstructions show that after the 8.2 cooling event, the Holocene temperature increased. The HTMHTM lasted approximately until 2850 cal BC with its warmest phase between 6050 and 5050 cal BC. Afterwards the temperatures started to decline steadily towards the present (Antonsson and Seppä, 2007; Seppä et al., 2005, Seppä et al., 2009; Brown et al., 2012). However, there are indications that temperatures fluctuated during the HTM. A detailed observation of the stacked mean annual atmospheric reconstructions in northern Europe published by Seppä et al. (2009) shows pronounced variabilities with colder periods between 5050 and 3350 cal BC. While the authors (Seppä et al., 2009) assume that these temperature fluctuations do not reflect significant climatic events as they are not replicated in the annual summer (July) temperature reconstructions, other climatic proxies verify the existence of cold winters. Climatic reconstructions based on lake sediment proxies in Lake Belau in northern Germany suggest temperature fluctuations with cold winters at this period of the Holocene (Dreibrodt et al., 2012). Such fluctuations are to a lesser extent recorded in the lake sediments from Flarken (Seppä et al., 2005), Gilltjärnen (Antonsson et al., 2006) and Trehörningen (Antonsson and Seppä, 2007) in Sweden.

Sea surface temperature (SST) reconstructions based on sediment cores at the region of Skagerrak show a significant temperature drop of ~5–6 °C between 4350 and 3450 cal BC (Krossa et al., 2017). This cooling is explained as a result of enhanced outflow of cold Baltic Sea water that followed the oceanographic changes during and after the Littorina transgression in the Baltic Sea. The authors of this study (Krossa et al., 2017) associate such an outflow of Baltic Sea water with severe winters that would produce a colder annual mean sea surface temperature during the mid-Holocene. This event, together with a continental atmospheric circulation pattern (Antonsson et al., 2009) resulted in a drop in annual temperatures and pronounced seasonal contrasts, with cool winters and warm summers (Antonsson et al., 2006; Krossa et al., 2017; Seppä and Poska, 2004). To maintain a viable population of harp seals, a sufficiently cold winter with formation of appropriate sea ice conditions every other year would be enough.

The magnitude of these cold events is differently recorded in the various environmental proxy records and their impact is not fully understood yet, especially considering the fauna that was present in the Baltic Sea at this phase of the Holocene. However, it is not only the presence of the harp seal breeding populations that contradicts the notion of a steady warm mid-Holocene climate. Even more intriguing, and supporting for a seasonal temperature contrast, is the coexistence in the Baltic Sea area of temperature-sensitive species with different ecological requirements as it is recorded in various archaeological faunal assemblages: besides the harp seal, the arctic ringed seal (*Phoca hispida;* (Ukkonen et al., 2014)), and the European pond turtle (*Emys orbicularis;* (Sommer et al., 2007)) occurred quite frequently. In some cases, bones from all species are found in the same archaeological context suggesting that they were seasonally available for exploitation by humans (Enghoff, 2011; Glykou, 2016; Richter and Noe-Nygaard, 2003). In addition, the Dalmatian pelican (*Pelecanus crispus)* is recorded in the Danish archipelago during the HTM (Nikulina and Schmölcke, 2015).

Both the harp and the ringed seal need a genuine winter with ice cover for several weeks as they depend on pack ice and snow for their breeding. The ringed seal is known from several regions of the Baltic Sea during the HTM (Ukkonen et al., 2014) Gulf of Bothnia (Ukkonen, 2002), Gulf of Riga (Lõugas, 1999), Öland, Gotland (Storå, 2001a) and the southwestern Baltic Sea (Glykou, 2016). The European pond turtle, which was distributed in southern Scandinavia during this period (Sommer et al., 2009), requires a warm summer with minimum summer temperature of 18 °C for the incubation of its clutches (Schneeweiβ, 2004). However, the pond turtle can tolerate cold winter temperatures during hibernation (Fritz, 2003). The extinction of the pond turtle from Southern Scandinavia around 3550 cal BC is associated to declines in summer temperatures (Sommer et al., 2009). Between 4700 and 3900 cal BC the Dalmatian pelican had breeding colonies in the Danish archipelago far beyond their present range in the southeastern Mediterranean, and its presence and later disappearance is linked to climate changes (Nikulina and Schmölcke, 2015).

4.1.1. Salinity and $\delta^{13}C$

The stable carbon isotope composition in seal bones is based on a mixture of diet, physiological processes and environmental impacts. The diet in seals might differ between adults and subadults, which can have impact on the $\delta^{13}C$ values (Haug et al., 2000, 2017). Further, it is well established, that salinity correlates with $\delta^{13}C$ because carbon is less enriched in ^{13}C in freshwater environments than in marine environments (Angerbjörn et al., 2006; Lougheed et al., 2013). Therefore, the $\delta^{13}C$ from seals is expected to reflect the salinity of ambient water. Because the salinity in the Baltic Sea differs both spatially and temporally (Emeis et al., 2003), it is expected that seals which are highly mobile would be affected by different $\delta^{13}C$ values. Even though it is unknown whether the extinct harp seal population of the Baltic Sea had an annual migration route like modern ones, we assume for this study, that their isotopic composition reflects an average of the annual mobility or migration in different regions in the Baltic Sea, as it has been established for harbour porpoises from the same area (Angerbjörn et al., 2006). That their isotopic composition reflects mobility only within the Baltic Sea is indicated from the $^{87}Sr/^{86}Sr$ values (Fig. 4). For this study, we use the mean $\delta^{13}C$ values of collagen from seals from different chronological groups to correlate with salinity fluctuations and not to discuss foraging and migration patterns.

The $\delta^{13}C$ values of the oldest samples (group LM/EN) yielded a mean $\delta^{13}C$ value of −17.0‰ (Fig. 5; Fig. A.4; Tables A.6-A.7). This value is depleted, reflecting the low salinity of the Baltic Sea. A sudden increase in salinity is recorded between 4450 and 4050 cal BC according to Sea Surface Salinity reconstructions based on $^{87}Sr/^{86}Sr$ of mollusk shells (Emeis et al., 2003; Ning et al., 2017). This salinity increase coincides temporally with the first group (LM/EN) of radiocarbon dates of Phase I and especially the dating of the oldest breeding population in southwestern Baltic Sea (Fig. 5; Fig. A.1-A.3). Salinity continues to increase during the Neolithic and it remains more or less high and stable until approximately 1950 cal BC (Emeis et al., 2003), creating gradually more marine conditions in the Baltic Sea (Fig. 5). Despite the increase in salinity during the Middle Neolithic the mean $\delta^{13}C$ values stay more or less stable at −16.7‰ (group MN) (Fig. 5; Fig. A.4). A change from brackish to more marine-affiliated fish species is recorded during this period in several archaeological fish assemblages and fish diversity increased with more species, reflecting the environmental changes and increase in salinity after the Littorina transgression (Eriksson, 2004; Glykou, 2016; Lepiksaar, 1986). This change in fish species might have attracted the harp seal to inhabit the Baltic Sea (Lindquist and Possnert, 1997; Forstén and Alhonen, 1975; Lõugas, 1997a, Lõugas, 1998).

As salinity increased gradually within Phase I, the harp seal population in the Baltic Sea increased as well (Figs. 2 and 5). Within the next centuries, in the Middle Neolithic, the harp seal became the most common seal species in the Baltic Sea as reflected in the archaeological faunal assemblages, and the breeding area was now located further north, in the Baltic Proper (Storå, 2001a; Storå and Ericson, 2004). Bones from harp seal pups from Åland and Gotland show that prehistoric hunters of the Pitted Ware Culture intensively exploited the harp seal breeding grounds (Storå, 2001a; Storå and Ericson, 2004). On Gotland, the subsistence of the coastal communities of the Pitted Ware Culture relied heavily on the exploitation of harp seals and the inhabitants evidently consumed almost exclusively seals (Eriksson, 2004). Also, in the eastern and southern Baltic Sea, bones from harp seals are commonly found in Middle Neolithic archaeological assemblages (Lõugas, 1997a, 1997b, 1998; Storå, 2006). The increase in harp seal population size coincided with salinity increases towards the Middle Neolithic and a large regional cooling recorded in the North Atlantic and central Europe between 3850 and 3150 cal BC (Hammarlund et al., 2003; Seppä et al., 2009) that might have created more favourable environmental conditions for harp seal breeding. No cultural change or shifts in subsistence are observed during this time at the coastal sites of the Pitted Ware Culture that could result in an increased frequency of harp seal bones in archaeological faunal assemblages (Storå, 2000; 2001). Despite the population size increase and the more favourable foraging conditions, the body size of harp seals decreased steadily from the Late Mesolithic towards the Middle/Late Neolithic (Glykou, 2016; Storå and Ericson, 2004).

4.1.2. Body size decrease and population decrease during the Neolithic

During the approximately 1700 years that phase I lasted, the harp seal population of the Baltic Sea underwent a significant and gradual body size reduction (Figs. 3 and 5) (Glykou, 2016; Storå 2001; Storå and Ericson, 2004). In this study, we showed that when harp seals re-appeared after a hiatus (Phase II), they had a larger body size (Figs. 3 and 5). Intriguingly, during Phase I body size reduction occurred while the harp seal population increased in the Baltic Sea. After 3000 cal BC, still in Phase I and while the body size continued to decrease, a decline in the frequencies of harp seal bones (NISP) in archaeological assemblages is recorded (Fig. 5; Table A2). Since this change does not coincide with other significant changes in human subsistence, we assume that the hunting assemblage reflects the available natural resources, suggesting a decrease in population size.

The significant body size reduction of the harp seal during the Neolithic (Storå and Ericson 2004) has been previously discussed and many authors suggested that the harp seal in the Baltic was an isolated population living in suboptimal environmental conditions trapped in the brackish Baltic Sea (i.e. Forstén and Alhonen, 1975). A contribution of several factors such as ecosystem productivity, interspecific competition, Bergmann's rule and reduced predation have been named as possible reasons (Schmölcke, 2008; Storå and Ericson, 2004; Ukkonen, 2014). The body size reduction could also be a result of inbreeding (Fredrickson and Hedrick, 2002). Human pressure as an additional aspect will be discussed below.

After 3000 cal BC, salinity starts to decrease in the Baltic Sea (Fig. 5). This is associated with changes on the phytoplankton distribution and density, affecting benthic invertebrates and subsequently fish abundances and distribution (Emeis et al., 2003). Such changes can evidently affect the physiological stage of higher trophic levels consumers (big fish, grey seal) in the Baltic Sea (Karlson et al., 2019). Also, the harp seals of the Barents Sea have experienced physiological stress due to ecological fluctuations that affected their main prey, with implications for their breeding success and population dynamics (Øigård et al., 2013).

Therefore, we assume that the decrease in salinity after 3000 cal BC changed the abundances of benthic invertebrates and fish species that ultimately affected the physiological status of harp seals and resulted in general poor body condition. The Atlantic cod (*Gadus morhua*) appears to be widely distributed during this period in the Baltic Sea (Olson, 2008) and the salinity decrease did not have obvious negative impacts on it since it requires high salinity only for the fertilization of its eggs (Nissling and Westin, 1997). In the Barents Sea, cod is assumed to be one of the most important competitors to the harp seal for shared food resources such as benthic invertebrates (Bogstad et al., 2000, Bogstad et al., 2015). In the Baltic Sea, the predator-prey systems can be more complex and variable. Today, the grey seal is the top predator feeding mainly upon sprat, herring and cod, while cod is the predominant piscivorous fish feeding mainly on sprat and herring (Elmgren, 1984; Lundström et al., 2010). Interspecific competition among marine mammals for shared food resources in the Baltic has been previously suggested as a reason for the harp seal body size reduction (Schmölcke, 2008; Storå and Ericson, 2004). However, the grey seal frequencies in the Baltic Sea increase later, during the Bronze Age, and do not coincide with the decline in harp seal population during the Middle/Late Neolithic. Ringed seal could be a potential competitor, as it seems to appear quite frequently towards the Late Neolithic (Fig. 2). However, the littoral ringed seal is not considered a significant competitor to the pelagic harp seal for shared food resources (Ukkonen et al., 2014; Wathne et al., 2000).

Zooarchaeological analyses of the faunal assemblages of the Middle Neolithic Pitted Ware Culture show systematic exploitation of all ages of harp seals during the breeding seasons (Storå and Ericson, 2004). Based on the age structure of the faunal assemblages of the Pitted Ware Culture sites on Gotland a prolonged hunting season has been suggested including all ages of seals, even newborns, indicating access to breeding grounds (Storå 2001). During the Late Neolithic the relative abundances in seals changed and the ringed seal became the main hunted prey, followed by the harp seal. While the age distribution during this period indicated a long hunting season for ringed seals, this became significantly shorter for harp seals compared to the Middle Neolithic. Further, the frequency of bones from harp seal pups decreased during the late Neolithic to such a degree that in some sites bones from this age cohort are either absent (Västerbjers, Ajvide-D lower) or very few (Hau on Gotland, Ålandic sites; Storå 2001). The change in relative seal frequencies, together with a shorter period of hunting, has been interpreted as reflecting a decreased availability of harp seals (Storå, 2000).

Human pressure, in combination with the above-mentioned environmental changes and competition with other species (ringed seals and mainly cod) for shared food resources, contributed ultimately to a combined body size reduction and population decline. As anthropogenic disturbances and environmental variables can have an impact on predator-prey relationships and cause trophic cascades in marine environments (Casini et al., 2008;Casini et al., 2009; Easterbrook, 2016), one explanation would be that these led to the extirpation of the Baltic Sea harp seal population. Another, less severe, consequence would be a significant population decline of the Baltic Sea harp seals. However, from now on and for the coming 1000 years there is no physical evidence of harp seals in the Baltic Sea, causing the hiatus in the radiocarbon record (Fig. 5).

4.2. Phase II of harp seal presence in the Baltic Sea (Bronze Age and Iron Age)

After the hiatus, harp seals appear again sporadically in Bronze and Iron Age archaeological contexts in Finland (Åland islands), Estonia (Saaremaa Island), Sweden (Gotland) and Denmark (Bornholm), but both the total numbers and the relative frequencies remain very low until their final extirpation from the Baltic Sea (Storå and Lõugas, 2005). During the Bronze and Iron Age, human subsistence mainly relies on animal husbandry and farming. However, the importance of seal exploitation remains high in coastal regions (Storå and Lõugas, 2005). In the areas where harp seal used to be the most common seal, grey seal now becomes the most frequent seal species (Figs. 2 and 5). Thus, the low relative frequencies of harp seals suggest a smaller population size than during the Neolithic and cannot be explained by a change in human subsistence. Interspecies competition, caused by environmental changes, may also have favored the expansion of grey seals at the cost of harp seal (Storå and Lõugas, 2005).

There are two possible explanations for the reappearance of harp seals in the archaeological record after the hiatus. 1) A recolonization of the Baltic Sea with harp seals from the Atlantic Ocean breeding stocks occurred, which could explain the bigger body size of the Bronze Age harp seals. However, if there was a recolonization, then we would expect the seals to have the same body size as the Neolithic harp seals from the Varangerfjord (Hodgetts 1999). Such a recolonization would require mobility of the harp seals between the Atlantic and the Baltic Sea, which has been proven possible by previous strontium isotope analysis (Glykou et al., 2018). Although our $^{87}Sr/^{86}Sr$ ratios from the sampled Bronze Age population display values corresponding to the Baltic Sea, this does not rule out immigration from the Atlantic to the Baltic, as only the individuals that entered the Baltic Sea would carry Atlantic isotopic values.

2) A local breeding population recovered and increased in size, as has been observed for the ringed seal population of the Baltic Sea (Härkonen et al., 1998). This could have been possible by a shift in the economy which gradually started during the late Neolithic and was established during the Bronze Age. The subsistence no longer relied exclusively on the exploitation of wild resources, mainly seals, but increasingly on domesticated animals and agriculture, resulting in a decreased hunting pressure.

Phase II shows an uninterrupted presence of harp seals for approximately 2500 years. Even though the relative frequencies of harp seals are low, there is evidence for a local breeding population in the Baltic Sea during the Bronze Age. This is provided by the presence of harp seal pups and $^{87}Sr/^{86}Sr$ ratios from the individuals from the Bronze Age site of Asva (Fig. 4; Table A.3). However, we still lack information on breeding populations dated to the Iron Age. Nevertheless, since the adult harps seals of the Iron Age display a body size comparable to the Bronze Age harp seals, that bred in the Baltic we assume that the Iron Age harp seals also bred in the Baltic (Storå and Lõugas 2005).

The Baltic Sea salinity decreases gradually up to 850 cal BC and then increases gradually until modern times (Ning et al., 2017). However, the mean $\delta^{13}C$ values for both the Bronze Age and Iron Age samples (group BA $\delta^{13}C$ −16.7‰ and IA $\delta^{13}C$ −16.6‰) are identical to the Neolithic samples, confirming a Baltic origin. The modern samples display less negative values with a mean $\delta^{13}C$ −16.1‰ as expected considering that they originate from the Atlantic stock. Various terrestrial and palaeoclimatic records show a cooler period with decreasing temperatures and increasing humidity from approx. 2000 cal BC to 1000 cal BC (Zillén et al., 2008; Hammarlund et al., 2003; Seppä et al. 2005, 2009). This cooling coincides with the re-appearance of harp seals in the archaeological record after the hiatus.

According to our model, Phase II ends at 876–1626 cal AD, but if we consider each single date no one extends beyond 1105 cal AD (2σ). This final date coincides with the beginning of the Medieval Climatic Anomaly or Medieval Warm Period (MWP), (Easterbrook, 2016), which lasted approximately between 900 and 1300 cal AD and was followed by a cold period known as the Little Ice Age (Lamb 1982). In the Baltic Sea region, the MWP started at c. 950 cal AD and was abruptly terminated at 1100 cal AD based on various palaeoclimatic proxies and temperature reconstructions (Andrén et al., 2000, ; Zillén et al., 2008; Briffa et al., 1992).

Thus, the last evidence of harp seals in the Baltic Sea coincides with the onset of the MWP in the Baltic Sea region. From now on, no harp seals are recorded in the Baltic Sea. This indicates that the population was extirpated. It still remains puzzling why this short warm period led to the final extirpation of harp seals while they managed to survive during the HTM.

A combination of parameters has to be considered here. During phase II, the grey seal becomes the dominant species and the frequency of harp seals is lower compared to Phase I. This might have caused substantial competition for shared food resources and ecological niches (Storå and Lõugas, 2005). However, considering the long time span, several millennia, it is unlikely that this competition was the single cause for the extirpation of harp seals. We think that the decisive factor to consider here is the absence of suitable ice conditions for harp seal pupping. During the MWP mean annual temperatures were approximately 1 °C higher that today (Lamb 1982). Most proxy records refer to warm and moist summers during this period (Büntgen et al., 2011; Sicre et al., 2008; Patterson et al., 2010) but some indicate higher seasonality with cold winters and warm summers. The coldest winter temperatures in the Orkney islands, however, are reconstructed to be 6.0 ± 0.6 °C (Surge and Barrett 2012), thus not cold enough for the formation of appropriate ice conditions for harp seal pupping. Historical records and temperature reconstructions of the last two centuries from the Baltic Sea, show that ice formation can strongly fluctuate between years, depending on temperature, winds, currents and solar activity, shifting from mild years with less ice coverage (−4 °C), to medium severe, or severe winters with extensive ice coverage (−5.5 °C) (Palosuo, 1953). Thus, we assume that the warmth during the 11th century with a lack of proper ice conditions for pupping during several decades led to the final extirpation of the already vulnerable Baltic harp seal population.

5. Conclusion

Surprisingly, the first harp seal colonization in the Baltic Sea falls within the HTM and coincides with increased salinity. Temperature fluctuations with seasonal contrast (very cold winters and warm summers) probably allowed harp seals to breed on ice during the winters. Already from the first colonization, there is a continuous body size reduction. In the late Neolithic, human pressure, salinity fluctuations with consequent changes in prey availability and competition for shared food resources, mainly with cod, resulted in physiological stress of the harp seals that ultimately led to a population decline and even local extirpation. After a hiatus with no harp seal finds of approximately 1000 years, harp seals reappear in the archaeological records. Based on our data we cannot solve whether this is due to recolonization from the Atlantic breeding population or an increase in local surviving populations. However, this could be addressed by genetics. Our data support that the late Holocene harp seal population is a continuous local population from the Bronze Age until the final extirpation during the Medieval Warm Period.

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Credit author statement

Aikaterini Glykou: Conceptualization; Methodology; Validation; Formal analysis; Investigation; Writing-Original Draft; Visualization; Supervision; Project administration; Funding acquisition. Lembi Lõugas: Resources; Writing-Review & Editing. Giedrė Piličiauskienė: Resources; Writing-Review & Editing. Ulrich Schmölcke: Resources; Writing-Review & Editing. Gunilla Eriksson: Conceptualization; Investigation; Supervision; Writing-Review & Editing. Kerstin Lidén: Conceptualization; Investigation; Supervision; Writing-Review & Editing.

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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Appendix A. Supplementary data

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