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## The Holocene occurrence of *Acipenser* spp. in the southern North Sea: the archaeological record

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Archaeological sturgeon remains from the southern North Sea basin used to be automatically attributed to *Acipenser sturio*, since this was the only acipenserid species believed to occur there. These species identifications, however, were in need of revision after a growing number of indications were found for the historical presence of *Acipenser oxyrinchus* in western Europe. In this study, morphological and genetic data on sturgeon remains from archaeological sites along the southern North Sea are revised. A large number of Dutch, Belgian, British and some French archaeological sturgeon remains, dating from the Mesolithic up to Late Modern times, are morphologically examined and fish sizes are reconstructed. This study of >7000 acipenserid bones proves the sympatric occurrence of European sturgeon *A. sturio* and Atlantic sturgeon *A. oxyrinchus* in the southern North Sea at least since the Neolithic (fourth millennium BC onwards), with *A. oxyrinchus* remains always outnumbering those of *A. sturio*. Human influence is documented by the decrease in finds through time, but no clear evidence was found for a diachronic change in fish lengths that could possibly be related to fishing pressure.

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Key words: *Acipenser oxyrinchus*; *Acipenser sturio*; archaeozoology; zoogeography.

### INTRODUCTION

Historically, it has always been assumed that only one sturgeon species, the European sturgeon *Acipenser sturio* L. 1758, occurred in the North Sea and the Baltic. Ludwig *et al.* (2002), however, demonstrated the historical occurrence of the Atlantic sturgeon *Acipenser oxyrinchus* Mitchill 1815 in the Baltic Sea through genetic analysis of museum specimens and later of archaeological samples (Ludwig *et al.*, 2008, 2009a). It was suggested that the Baltic Sea was first colonized by *A. sturio* around 1000 BC, followed by colonization by the North American *A. oxyrinchus* around 800 AD. Later on, during the postmedieval Little Ice Age, a complete species shift from *A. sturio* to *A. oxyrinchus* would have taken place, explained by the fact that *A. oxyrinchus* can spawn at lower temperatures and thus has a selective advantage over *A. sturio* in colder

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climatic conditions (Ludwig *et al.*, 2002, 2008, 2009a; Ludwig & Gessner, 2007). The probable source for the European *A. oxyrinchus* are sturgeon populations from the Canadian St John and St Lawrence Rivers. An alternative scenario for the colonisation of the Baltic Sea was recently proposed by Popović *et al.* (2014). Based on genetic research and the approximate Bayesian computation approach, Popović *et al.* (2014) suggested that *A. sturio* introgressed into *A. oxyrinchus* in western Europe prior to the latter's colonization of the Baltic Sea, which would have happened *c.* 4000–5000 years ago. *Acipenser oxyrinchus* presumably arrived in Europe after the Last Glacial Maximum or the Younger Dryas cold interval *via* the Gulf Stream and the North Atlantic Drift, which brought the fish to the Atlantic coast of Britain and France (Chassaing *et al.*, 2013; Popović *et al.*, 2014). No sustainable population of *A. sturio* would ever have occurred in the Baltic.

The presence of *A. oxyrinchus* has also been demonstrated along the Atlantic coast of France, through morphological and molecular analysis of bone remains found at archaeological sites, dating from the late fourth to the early third millennium BC onwards. In addition, the presence of *A. oxyrinchus* has been attested for the English Channel and the North Sea, based on a limited number of museum and archaeological specimens dating to the last two millennia (Ludwig *et al.*, 2002; Desse-Berset, 2009, 2011a; Desse-Berset & Williot, 2011; Chassaing *et al.*, 2013; Haerter *et al.*, 2014).

*Acipenser sturio* is now critically endangered (Gesner *et al.*, 2010), with relic populations remaining only in the Gironde–Garonne–Dordogne Rivers in France and in the Rioni River in Georgia, although the latter population has an uncertain status and was probably extirpated in the 1990s (Lepage & Rochard, 1995; Williot *et al.*, 1997; Bacalbasa-Dobrovici & Holcik, 2000; Gessner, 2000; Gessner *et al.*, 2006; Kolman, 2011). *Acipenser oxyrinchus* does not occur in Europe anymore, the most recent museum specimens date to the second half of the 20th century (Ludwig *et al.*, 2002) with the youngest one from Grimsby, dated to 1986 (Thieren *et al.*, 2016).

Although currently no breeding populations of *A. oxyrinchus* or *A. sturio* exist in North Sea tributaries, sturgeon used to occur in all major rivers (Hochleithner & Gessner, 1999). This is not only attested by historical fisheries data (Verhey, 1949), but also by archaeological acipenserid finds (for an overview, see Table SI, Supporting information). In the past, such sturgeon remains, as well as museum specimens with a North Sea locality, used to be automatically attributed to *A. sturio*. It is now clear that the possibility that they belong to *A. oxyrinchus* cannot be ignored. In this respect, it is worth mentioning that Kottelat & Freyhof (2009) considered the nominal species of *Acipenser lichtensteini* Bloch & Schneider 1801, described from the North Sea, as a synonym of *A. oxyrinchus*.

The aim of the present study is to verify the temporal distribution of sturgeon species in the southern North Sea basin through the morphological analysis of >7000 archaeological remains from The Netherlands and Belgium and, to a lesser extent, from the U.K. and France. The material includes a number of remains that have also been genetically identified in a previous study (Thieren *et al.*, 2016).

## MATERIALS AND METHODS

*Acipenser* spp. remains from a total of 76 different Dutch, Belgian, British and French archaeological sites, dating from the Mesolithic up to Late Modern times (Fig. 1 and Table SII, Supporting information) were morphologically examined and identified to species. The bones were



FIG. 1. Location of archaeological sites from Belgium, the U.K., France and The Netherlands with examined sturgeon remains. Numbers correspond to those of the localities in Table SII (Supporting information).

collected from refuse deposits and are dated by varying criteria, usually stratigraphic position and association with archaeological objects, or radiocarbon analysis of the remains themselves or associated finds. A morphological distinction between *A. sturio* and *A. oxyrinchus* can be made by differences in the shape of some of the splanchnocranial bones (dentary, palatopterygoid and dermopalatine) (Desse-Berset, 2011b) and by differences in the external surface pattern of the scutes and other dermal bones (Magnin, 1963; Desse-Berset, 2009; Thieren *et al.*, 2016). As the splanchnocranial bones are not often found, the external ornamentation of the scutes and other dermal bones is most frequently used for the species identification of archaeological sturgeon remains.

In the present study, the surface morphology of all dermal bone fragments was evaluated first and described as alveolar, tubercular or unidentified. In a second step, the total lengths ( $L_T$ ) of the fish were reconstructed, as this proved to be an influential factor for the surface pattern of the dermal bones. While the dermal bones of the head and pectoral girdle provide the most accurate fish-length reconstruction, using the Thieren & Van Neer (2014) regression equations, the scutes, although numerically dominant in archaeological samples, have the disadvantage of being less precise for fish-length reconstructions. Despite the wide variation in shape and size among scutes within one row, it remains difficult to establish the exact rank of scutes within a row in the case of isolated finds from archaeological sites. Considering the scutes, it was only estimated whether they belonged to an acipenserid larger or smaller than 1 m, using the criteria described by Thieren & Van Neer (2016).

In a preceding study (Thieren *et al.*, 2016), the validity of the ornamentation pattern as a species-specific characteristic was assessed through a morphological and genetic analysis of museum specimens. Two non-overlapping fragments of cytochrome b (*cytb*) and two nuclear markers, LS68 and D161, were amplified and sequenced. For LS68, sizes of the alleles were determined with capillary electrophoresis. This study on museum specimens shows that dermal bones with an alveolar ornamentation can always be assigned to *A. oxyrinchus*, whatever the fish size. Bones with a tubercular ornamentation can be assigned to *A. sturio*, but only when the reconstructed fish  $L_T$  is  $>1$  m. Bones with a tubercular ornamentation from sturgeons  $L_T < 1$  m cannot be assigned to species, since the tubercular pattern is found in small and large *A. sturio*

TABLE I. Morphological and molecular species identification of archaeological remains of *Acipenser sturio* (Stur) and *Acipenser oxyrinchus* (Oxy), based on scute morphology. Data from Thieren *et al.* (2016). Hybrids and unidentified specimens (Indet.) were not included for the calculation of the percentages of misclassification. The number and proportions of misclassified specimens (Miscl.) are indicated in bold

		Molecular				
		Stur	Oxy	Hybrid	Total	% Miscl.
Morphological	Stur	4	<b>2<sup>a</sup></b>		6	<b>50</b>
	Oxy	<b>2<sup>a</sup></b>	24 <sup>b</sup>	1	27	<b>8</b>
	Indet.			1	1	
	Total	6	26	2	34	
	% Miscl.	<b>33</b>	<b>8</b>			<b>12</b>

<sup>a</sup>Molecular species identification based on mtDNA only.

<sup>b</sup>Molecular species identification from 14 specimens based on mtDNA only.

but also in small *A. oxyrinchus*. It also appears that scutes from the back of the lateral rows and fragments consisting of the edges of bones of *A. oxyrinchus* often display a tubercular pattern and are thus not reliable for morphological identification.

Five of the museum specimens investigated were hybrids, but no clear morphological characteristics could be found to identify them as such. In a next step of the study (Thieren *et al.*, 2016), 34 archaeological *Acipenser* remains that were identified to species by their surface ornamentation were genetically tested (Table I). Of the six remains genetically identified as *A. sturio*, two had been morphologically assigned to *A. oxyrinchus*. Of the 26 remains genetically identified as *A. oxyrinchus*, two had been morphologically assigned to *A. sturio*. It has to be noted that 18 of the 34 samples, including the two misclassified specimens of *A. sturio*, were assigned to species based on mtDNA only (Table I), due to the poor preservation of nucleolar (n)DNA. Two samples were genetically identified as hybrids. In total, there was a disagreement between the morphological and genetic species assignment in 12% of these samples. The high proportion of morphologically misclassified *A. sturio* may be due to chance fluctuations given the low number of samples. Moreover, a hybrid origin of samples identified based on mtDNA only cannot be excluded (Thieren *et al.*, 2016).

## RESULTS

### FREQUENCY OF SKELETAL ELEMENTS AND FISH-LENGTH RECONSTRUCTIONS

Individually, 7382 bones were examined (Table SIII, Supporting information), of which almost one third was too heavily fragmented to allow an identification of the skeletal element. More than half of all identified bones ( $n=4954$ ) are scutes, while pectoral fin spines and bones of the pectoral girdle (cleithrum, supracleithrum and clavicle) are the second most abundant, followed by bones from the skull roof and the circumorbital region (post-temporal, median extrascapular, dermopterotic, parietal, frontal, dermosphenotic, nasal, postorbital, supraorbital and jugal). Other parts of the ossified sturgeon skeleton are less frequently found, *i.e.* bones from the hyoid arch, the opercular series, the caudal, dorsal and anal fins and their associated fin supports.

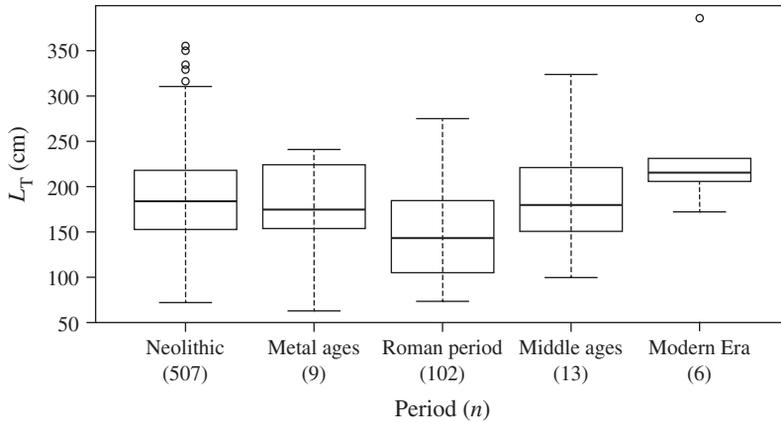


FIG. 2. Reconstructed total lengths ( $L_T$ ) for *Acipenser* spp., compared between different periods. The box delimits the interquartile range, the horizontal black bands are the medians, whiskers equal  $\pm 1.5$  times the interquartile range. The numbers in parentheses indicate the number ( $n$ ) of specimens examined.

Less than 10% of the collection studied consisted of bones from the head or pectoral girdle sufficiently preserved to take the measurements needed for a fish-length reconstruction. These 637 remains derive from 28 excavations, though the number of sturgeon bones per site varies considerably. Vlaardingen, a Dutch Neolithic site, yielded almost 60% of the bones allowing size reconstruction, whereas often only one, or at most a few, of such bones occur per site from more recent periods (see Table SI, Supporting information, for total numbers).

Since several excavations only yielded a limited number of sturgeon remains with reconstructed fish lengths, the finds were grouped in larger time periods as defined by Slechten (2004): Neolithic (507 remains; between about 5300 BC and 2000 BC), Metal Ages (nine remains; between 2000 BC and 57 BC), Roman Period (102 remains; between 57 BC and 402 AD), Middle Ages (13 remains; from the 5th to the 15th century AD) and Modern Era (six remains; from the 16th to the 18th century AD). Boxplots of the reconstructed  $L_T$  for each period are shown in Fig. 2. The Roman *Acipenser* spp. are smaller, while the Modern samples appear to be larger than those in other periods. These differences are statistically significant between Roman and Modern and between Roman and Neolithic fish (Wilcoxon rank sum,  $P < 0.05$  with Bonferroni-adjusted  $P$ -values). Since the Metal Ages, the Middle Ages and the Modern Era, however, are only represented by a small number of remains, these results may not be meaningful.

## SPECIES IDENTIFICATION

Forty-three splanchnocranial bones from 10 excavations were identified to species (Fig. 3), 30 as *A. oxyrinchus* and 13 as *A. sturio*. It is striking that both species were found on all sites yielding two or more identifiable splanchnocranial bones.

The frequency of tubercular and alveolar ornamentation observed in all dermal bones (scutes and bones of the head and pectoral girdle) per time period, disregarding fish size, are shown in Fig. 4(a). In total, 6127 of the 7382 bones (83%) displayed an ornamentation pattern. In general, the tubercular ornamentation type, typical of *A. sturio* but also found in small *A. oxyrinchus*, proved to be less common than the

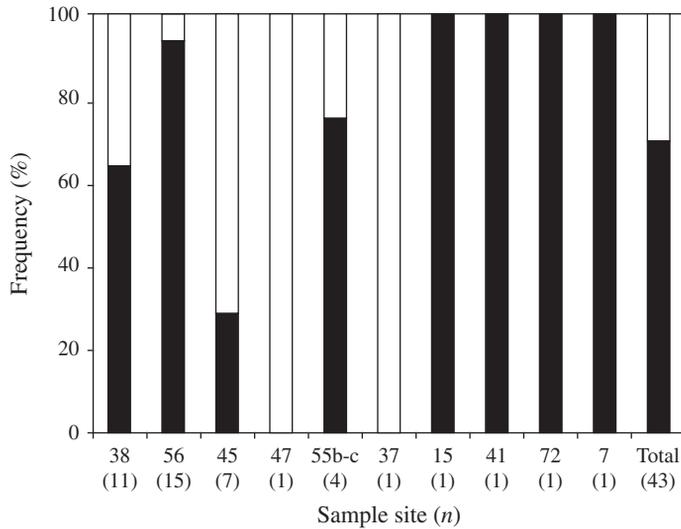


FIG. 3. Species identifications based on splanchnocranial bones: □, *Acipenser sturio*; ■, *Acipenser oxyrinchus*. Code numbers correspond to those shown in Fig. 1 and identified in Table SII (Supporting information). The numbers in parentheses indicate the number ( $n$ ) of samples examined.

alveolar *A. oxyrinchus* pattern. When all periods are combined, about 15% of the remains show a tubercular ornamentation. In the Roman Period, the proportion of the tubercular pattern seems to be greater compared with other periods, which might be related to the smaller fish sizes observed in those sturgeons (Fig. 2). As mentioned, *A. oxyrinchus*, typically displaying an alveolar surface ornamentation, can show a tubercular pattern when  $L_T$  is  $<1$  m (Thieren & Van Neer, 2016). When only the dermal bones are retained indicating a reconstructed  $L_T > 1$  m [Fig. 4(b)], again 15% of the remains have a tubercular ornamentation when all periods are combined. The proportions, however, differ between the periods. In the Modern Era and the Metal Ages, no remains with reconstructed  $L_T > 1$  m with a tubercular pattern are found, an observation most likely due to the small sample size for these periods. In the Roman period, the proportion of bones with a tubercular ornamentation with reconstructed  $L_T > 1$  m is lower compared with the data presented in Fig. 4(a). The alveolar pattern, typical of *A. oxyrinchus*, preponderates in all periods and it is noticed again that where the tubercular (*A. sturio*) type occurs, also the alveolar (*A. oxyrinchus*) pattern is found.

For 34 specimens, the morphological species identification has been validated through genetic analysis (Thieren *et al.*, 2016). The samples date from the Neolithic (3900–3700 BC to 3200 BC) up to Modern Times (1560–1758 AD). The mitochondrial signature of *A. oxyrinchus* is already found in archaeological layers at Ypenburg 4 (Rijswijk, The Netherlands), dated between 3900–3700 BC to 3200 BC. *Acipenser sturio* is also found in this excavation. Together, the samples genetically analysed reveal four sympatric occurrences of *A. sturio* and *A. oxyrinchus* at a total of nine sites from which two or more bones were sampled. In two sites, one dated to the 16th to the 17th century (Antwerpen, Zwartzusterstraat, Belgium) and one to the 6th to the 7th

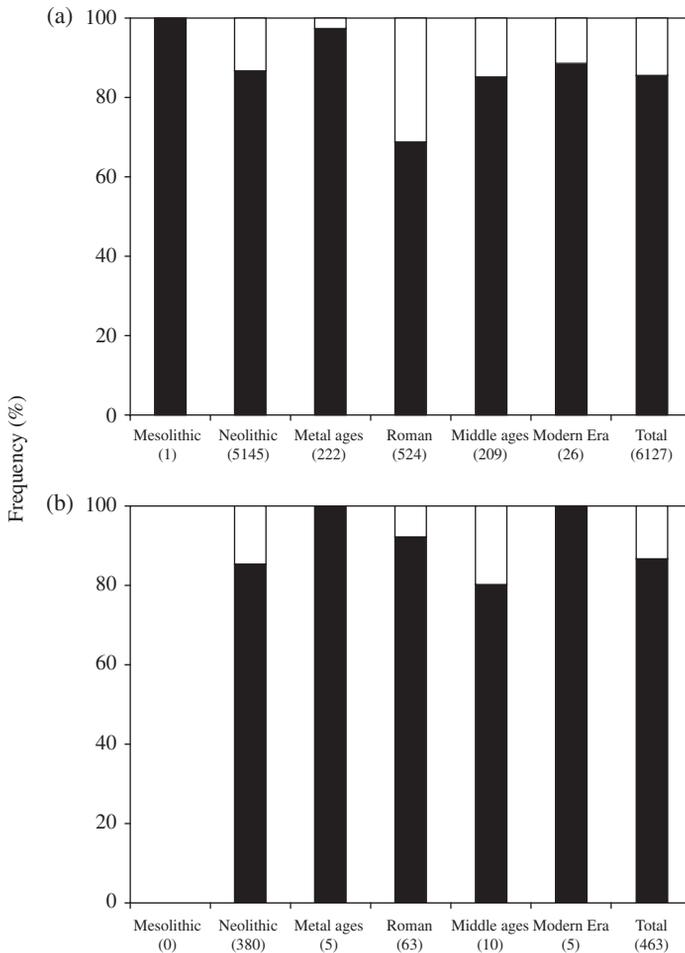


FIG. 4. Frequency of bones with (□) a tubercular or (■) alveolar surface pattern on dermal bones: (a) all archaeological remains and (b) remains with reconstructed total length >1 m. Historic periods are defined as followed: Mesolithic c. 9000 BC – 5300 BC; Neolithic 5300 BC–2000 BC; Bronze Age 2100 BC–800 BC; Iron Age 800 BC – 57 BC; Metal Ages 2100 BC – 57 BC; Roman period 57 BC – 402 AD; Middle Ages 5th century AD – 15th century AD; Modern Era 16th century AD – 18th century AD. The numbers in parentheses indicate the number ( $n$ ) of samples examined.

century (Den Haag, Oldenbarneveltlaan, The Netherlands), *A. oxyrinchus* was found alongside hybrid specimens.

## DISCUSSION

The *Acipenser* spp. remains from the Dutch, Belgian, British and French archaeological excavations examined (Table SII, Supporting information) document the occurrence of sturgeon in the southern North Sea over a time period of c. 6000 years. This discussion starts with a description of the spatial and chronological distribution of

*Acipenser* spp. in the North Sea and elsewhere in western Europe. Subsequently, the diachronic changes observed in the study material is discussed, both in terms of the number of sturgeon finds and of the reconstructed fish lengths.

## SPECIES IDENTIFICATION OF SEA STURGEON IN EUROPE

The oldest find in the southern North Sea material analysed is a single Mesolithic dermal bone fragment from the site of Yangtzehaven (Rotterdam, The Netherlands), roughly dated to 7000–6500 BC. The alveolar ornamentation allows an identification as *A. oxyrinchus*. From the Neolithic onwards, the presence of this species in the southern North Sea is further attested by the morphological and genetic analysis of numerous acipenserid remains (Thieren *et al.*, 2016). It appears from the results presented here that remains with the alveolar ornamentation type of *A. oxyrinchus* are always more frequent than those with the tubercular ornamentation type of *A. sturio* (Fig. 4). Likewise, the number of splanchnocranial bones identified as *A. oxyrinchus* is higher than those identified as *A. sturio* (Fig. 3). Hence, these results suggest that *A. sturio* was outnumbered by *A. oxyrinchus* during the entire Holocene in the southern North Sea.

The oldest remains of *A. oxyrinchus* outside the North Sea basin are found along the French Atlantic coast and are dated to the late fourth to early third millennium BC (Desse-Berset, 2009, 2011a; Chassaing *et al.*, 2013). Since *A. oxyrinchus* probably arrived in Europe *via* the North Atlantic Drift, the colonisation of the French Atlantic coast most probably preceded the North Sea colonisation (Chassaing *et al.*, 2013). An earlier presence, *i.e.* at least before *c.* 7000–6500 BC, of *A. oxyrinchus* at the Atlantic façade of France seems likely, based on the dating of the morphologically identified fragment of *A. oxyrinchus* from Yangtzehaven that is first presented in this article. As mentioned above, the Canadian St Lawrence and St John Rivers have been suggested to be the origin of the European population of *A. oxyrinchus*. The post-glacial colonisation of these rivers by *A. oxyrinchus* is estimated at 9000 years ago for the St John River and 7400 years ago for the St Lawrence River (Popović *et al.*, 2014), which implies that a European colonisation could have happened relatively quickly afterwards.

In several sites along the North Sea, *A. sturio* and *A. oxyrinchus* occurred sympatrically, an observation based on the morphology of the remains (Fig. 3) and confirmed through genetic analysis (Thieren *et al.*, 2016). At Vlaardingen (The Netherlands), for instance, which is one of the most productive sites discussed here, it appears that 14 of the splanchnocranial bones could be identified as *A. oxyrinchus* and that one was from *A. sturio*. Since sturgeons were probably caught there during their spawning run, the sympatric occurrence shows that *A. sturio* and *A. oxyrinchus* used the same rivers for spawning. This behaviour could result in hybridisation between the two species, but at Vlaardingen this could not be proven. Samples from that site yielded mtDNA of both *A. sturio* and *A. oxyrinchus*, but the nDNA was insufficiently preserved to allow further analyses. Hybrid *A. oxyrinchus* × *A. sturio* have been reported from the Baltic Sea and the Atlantic façade in earlier studies and from other North Sea samples studied by the current authors (Tiedemann *et al.*, 2007; Ludwig *et al.*, 2008; Chassaing *et al.*, 2013; Popović *et al.*, 2014; Thieren *et al.*, 2016). As morphological analysis, however, cannot identify hybrid individuals, further genetic analysis will be necessary to determine the extent of the hybridisation. Extensive studies on the matter are thus far lacking for the English Channel, North Sea and north-east Atlantic Ocean, as most of the genetic

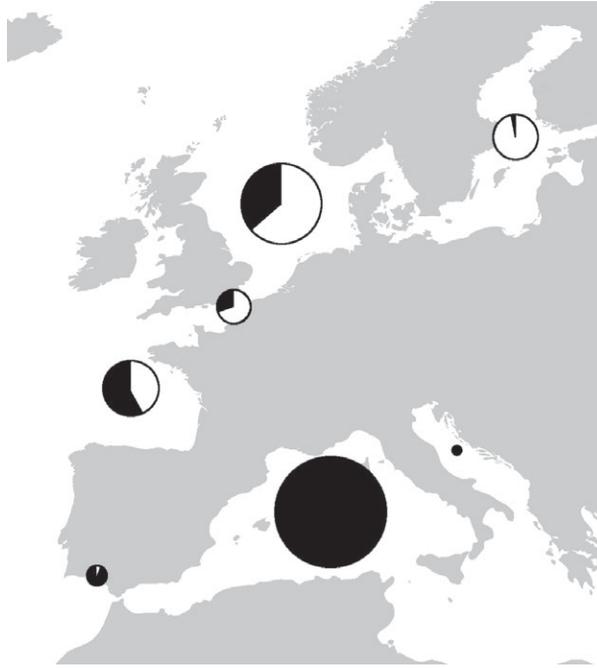


FIG. 5. Proportion of (□) *Acipenser oxyrinchus* and (■) *Acipenser sturio* from literature, based on mtDNA or morphological analysis in Baltic Sea ( $n = 402$ ), the North Sea ( $n = 721$ ), the English Channel ( $n = 30$ ), the French Atlantic façade ( $n = 193$ ), the Iberian Peninsula ( $n = 17$ ), the Mediterranean Sea ( $n = 2615$ ) and the Adriatic Sea ( $n = 1$ ). Size of the circles is proportional to the number of remains. Based on data from Garrido-Ramos *et al.* (1997, 2009), Ludwig *et al.* (2002, 2008, 2009*a, b*), de la Herrán *et al.* (2004), Tiedemann *et al.* (2007), Desse-Berset (2009, 2011*a*), Pagès *et al.* (2009), Robles *et al.* (2010), Desse-Berset & Williot (2011), Chassaing *et al.* (2013), Popović *et al.* (2014), Thieren *et al.* (2016) and this study.

species identifications were based on mtDNA only. Of the few hybrid animals identified in the literature on the basis of their nDNA and mtDNA, this study only uses the mtDNA identification.

Combining the information from the present study with data from the literature, an overview can be made of the occurrence of both sturgeon species in Europe during the Holocene. The species identifications based on splanchnocranial elements and dermal bones with a reconstructed  $L_T > 1$  m are shown in Fig. 5. These data are combined with all previously morphologically or genetically examined archaeological sturgeon remains and with information from museum specimens from the Mediterranean, the North and Baltic Sea, the English Channel, the Iberian Peninsula and the north-east Atlantic Ocean, (Garrido-Ramos *et al.*, 1997, 2009; Ludwig *et al.*, 2002, 2008, 2009*a, b*; de la Herrán *et al.*, 2004; Desse-Berset, 2009, 2011*a*; Robles *et al.*, 2010; Desse-Berset & Williot, 2011; Chassaing *et al.*, 2013; Haerter *et al.*, 2014; Popović *et al.*, 2014; Thieren *et al.*, 2016). Lake Ladoga, located in north-western Russia and connected to the Baltic, was not included in this overview. This is because this population has not yet been studied thoroughly (Ludwig *et al.*, 2002, 2009*a*; D. Popović, pers. comm.).

The proportion of *A. oxyrinchus* increases northwards, compared with *A. sturio* (Fig. 5). In the Mediterranean Sea, only *A. sturio* has been found, while in the Baltic Sea, the sturgeon population almost exclusively seems to have existed of animals with *A. oxyrinchus* mtDNA or skeletal morphology. *Acipenser sturio* probably colonized the North Sea after the Last Glacial Maximum or the Younger Dryas cold interval from the south. During that cold period, the Iberian Peninsula and Mediterranean and Adriatic rivers may have acted as refugia, as is suggested by the decreasing genetic diversity with increasing latitude (Chassaing *et al.*, 2011). Moreover, the oldest archaeological marine sturgeon bone, presumed to be *A. sturio*, is found in the Iberian Peninsula and dated to the Solutrean (20 000–15 000 BC). This means that the remaining extant Gironde population represents a relic of a population with an original distribution centre located more to the south (Chassaing *et al.*, 2011; Ludwig *et al.*, 2011). The Holocene colonisation of the North Sea by *A. sturio* might have been influenced by competition with *A. oxyrinchus* (Chassaing *et al.*, 2011). Besides possible competition (*e.g.* for food or spawning grounds), environmental conditions, such as temperature, may also have played a role. *Acipenser sturio* is reported only to spawn at water temperatures of at least 20° C, while *A. oxyrinchus* has a broader tolerance, ranging from 13.3 to 26.0° C (Ludwig & Gessner, 2007). This could also explain why *A. oxyrinchus* seems to have been more successful in northern regions, as shown in Fig. 5.

#### DIACHRONIC CHANGES IN THE ABUNDANCE OF *ACIPENSER* SPP. AND THEIR SIZES

Although there is a decrease through time in absolute numbers of acipenserid bone elements available for analysis (Table SI, Supporting information), it is not possible to quantify accurately the decline of *Acipenser* spp. through time as several factors will have influenced their occurrence at archaeological sites. Besides species' abundance, other factors such as fishing techniques, choice of fishing grounds and fishing season and (in later times) fishing rights, will have had an influence on the number of *Acipenser* spp. caught and consequently, on the amount of bone remains finally deposited at archaeological sites. Other factors, such as differential preservation and recovery methods, are unlikely to have significantly influenced the number of sturgeon remains. Because of their large size and robustness, preservation chances of *Acipenser* spp. bones are high and chances of overlooking them during excavations are limited, even when only hand collecting has been applied. Smaller sturgeon specimens, however, may still be underrepresented in some sites, as a result of differential preservation or recovery methods.

Most of the acipenserid remains available for study date back to the Neolithic, while finds from more recent time periods are poorly represented. In the case of the Metal Ages, this could be explained by the fact that, in the study region, settlement sites with good faunal preservation are scarce for this period (Table SI, Supporting information), although it cannot be excluded that sturgeon had already become rare at that time. In the Roman period, numbers of finds are also low, except in three of the nine sites studied. Considering the medieval and postmedieval periods, with their numerous sites usually yielding extensive ichthyofaunal assemblages, it seems clear that the low numbers found must be a result of the rarity of the species (Table SI, Supporting information). Both natural factors and human influence may explain the decrease in

*Acipenser* spp. abundance. Overfishing may have started relatively early, as shown in the Baltic region where the medieval sites of Gdansk and Ralswiek document an early decrease in sturgeon percentages between the 8–9th and the 12th centuries (Benecke, 1986). Although overfishing must have played a major role in the eventual extinction of sturgeon in the North Sea basin, habitat degradation and habitat loss will also have been important factors (Williot & Castelnaud, 2011). In The Netherlands, waterworks, such as damming, can be considered as one of the main causes for the decline of Dutch populations of *Acipenser* spp. Boddeke (1971) points to the medieval polderization around 1000 AD, causing significant loss of sturgeon spawning and nursery grounds, as the start of the Dutch sturgeon decline; whereas according to Nienhuis (2008), man-made hydrological changes affecting migrating fish species go back as far as the Roman period. Next to habitat loss, habitat degradation, e.g. through pollution, will have influenced abundance of *Acipenser* spp. Although human waste is often assumed to become an important factor after the Industrial Revolution, earlier traces from anthropogenic pollution are evident (Brännvall *et al.*, 2001). Also deforestation, beginning in the Neolithic together with agricultural activities (Nienhuis, 2008), have influenced river hydrology (Vos, 2015) and consequently altered spawning and nursery grounds (Hoffmann, 1996). Natural processes, such as rising seawater levels and the alteration of river courses must also have had an effect on the abundance of *Acipenser* spp. In general, in the case of the North Sea, the natural hydrological conditions may have been more favourable for acipenserid species during the Neolithic than during later periods.

The reconstructed  $L_T$ , based on 637 bones from the skull and the pectoral girdle (Fig. 2), all fall within the known maximum size ranges of *A. sturio* (between 3 and 6 m) and *A. oxyrinchus* (between 3 and 4.5 m) (Mohr, 1952; Bain, 1997; Hochleithner & Gessner, 1999; Vecsei & Peterson, 2000; Vecsei *et al.*, 2001). Overall, the size of the *Acipenser* spp. analysed seems to remain constant through time, except for the Roman period, when they appear to be smaller compared with the other periods and for the Modern Era, when they seem to be larger. In general, differences in size distributions through time may relate to fishing pressure, but they can also be the result of changes in fishing methods, exploited fishing grounds, environment, genetic variability or competitive interactions (Shin *et al.*, 2005). Although temporal overfishing could be a plausible explanation for the Roman size decrease, a difference in exploited fishing grounds between Valkenburg (the site yielding 91% of the Roman finds) and the earlier, Neolithic sites is more likely. According to the reconstructed  $L_T$ , the sturgeons from the Neolithic excavations were adult animals, probably caught in fresh water during their spawning run, whereas the Valkenburg fish were mostly juveniles, most likely caught in the estuary.

Other fish species found in the Neolithic excavations attest freshwater fishing. In Neolithic sites from which the bulk of the remains with reconstructed lengths are derived, such as Vlaardingen, Hekelingen III and Molenaarsgraaf, mainly freshwater fishes were found including pike *Esox lucius* L. 1758 and European catfish *Silurus glanis* L. 1758 (Clason, 1967; Brinkhuizen, 1979; Prummel, 1987). Moreover, structures that can be interpreted as fishing weirs have been found in Hekelingen III and Vlaardingen (Boddeke, 1971; Bakels & Zeiler, 2009), which indicate the catch of migrating species of fishes. In the Roman site of Valkenburg, freshwater, anadromous and marine fishes were found (Clason, 1999), suggesting fishing activities in both continental and marine environments.

The larger sturgeon sizes observed in the later periods compared with the Roman (Valkenburg) dataset are possibly biased by the low number of available reconstructed lengths from the Middle Ages and the Modern Era. It can be argued that sturgeon caught in later periods, which by then must have been already rare, were vagrant animals that possibly were especially targeted.

Summarizing, the analysis of >7000 acipenserid remains from archaeological sites in The Netherlands, Belgium, the U.K. and France, dating from the Mesolithic to Late Modern times, documents a population decline through time in the North Sea. No diachronic trend is observed, however, in the reconstructed fish lengths that can be seen as possible evidence for overfishing. The data presented here indicate the sympatric occurrence of *A. sturio* and *A. oxyrinchus* from at least the Neolithic (the fourth millennium BC) onwards, with *A. oxyrinchus* always being more prevalent. Comparison of the North Sea data with those from other parts of Europe show a gradient in the proportion of both species with an absence of *A. oxyrinchus* in the Mediterranean and *A. sturio* becoming less prevalent from the coast of the Iberian peninsula towards the North Sea and the Baltic.

Finally, previous work on North Sea museum specimens and archaeological sturgeon bones (Thieren *et al.*, 2016) has shown that the remains of hybrid individuals cannot be recognised on a morphological basis. The present study could, therefore, not take hybridisation between both species into account. The material studied, however, has the potential to document the genetic composition of ancient *Acipenser* spp. populations in Europe, as part of a more extensive molecular analysis.

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## Supporting Information

Supporting Information may be found in the online version of this paper:

TABLE SI Approximate numbers of *Acipenser* spp. elements identified in this study (ES), evaluated against the total numbers of fish remains identified (LF), and compared with the *Acipenser* spp. elements mentioned in literature (LS) (Table SII, Supporting information). Finds are ordered chronologically, with site codes corresponding to Table SII (Supporting information). Archaeological and historical periods are defined as followed: Mesolithic: c. 9000–5300 BC; Neolithic: 5300–2000 BC; Bronze Age: 2000–800 BC; Iron Age: 800–57 BC; Roman Period: 57 BC–402 AD; Middle Ages: 5th–15th century AD; Modern Era: 16th–18th century AD. Numbers in brackets indicate the total number of sturgeon finds examined per period. (NA: data not available; S: sieved; HC: hand collected).

TABLE SII Overview of the different excavations producing *Acipenser* spp. remains with respective site names and, eventually, codes, site descriptions, historical and

chronological dating and references. Archaeological and historical periods are defined as followed: Mesolithic: c. 9000–5300 BC; Neolithic: 5300–2000 BC; Bronze Age: 2000–800 BC; Iron Age: 800–57 BC; Roman Period: 57 BC–402 AD; Middle Ages: 5th–15th century AD; Modern Era: 16th–18th century AD.

TABLE SIII Overview of the archaeological *Acipenser* spp. remains examined (following Hilton *et al.* 2011), comprising bones of the skull roof and circumorbital region (the post-temporal, extrascapulars, dermopterotic, parietal, frontal, dermosphenotic, nasal, postorbital, supraorbital and jugal); the braincase with the parasphenoid; the opercular series (the subopercle and branchiostegals); the palatoquadrate and its ossifications (the dermopalatine, ectopterygoid, quadrate, palatopterygoid, autopalatine and quadratojugal); the lower jaw (the dentary and prearticular); the hyoid arch (the hyomandibula, interhyal, ceratohyal and hypohyal); the gill arches (the basibranchials, hypobranchials, ceratobranchials and pharyngobranchials); the pectoral fin and girdle (supracleithrum, cleithrum, clavicle and pectoral fin spine); the caudal fin and fin supports (the fulcra, fin rays and rhomboid scales of the caudal fin) and the scutes (lateral, dorsal and ventral scutes and non-identifiable scutes)

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