New Equations for the Size Reconstruction of Sturgeon from Isolated Cranial and Pectoral Girdle Bones

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ABSTRACT Measurements on cranial and pectoral girdle bones of 56 museum specimens of modern sturgeon (*Acipenser sturio* and *A. oxyrinchus*) were used for the establishment of regression equations allowing back-calculation of size from isolated sturgeon remains. Different curve fittings (power, linear, logarithmic and exponential fit) were modeled to retain the most accurate regression. These were then applied to archaeological sturgeon remains (*A. sturio/A. oxyrinchus*) from Vlaardingen, a Dutch late Neolithic settlement. The back-calculated lengths obtained on the archaeological remains all stayed within the known size ranges of the two species and allowed making inferences on the possible place of capture of the fish. Copyright © 2014 John Wiley & Sons, Ltd.

Key words: *Acipenser oxyrinchus*; *Acipenser sturio*; archaeozoology; body length estimations; osteometry; Sturgeon

Introduction

Size estimation of fish remains found in archaeological contexts can be used to gain information on former fishing methods, exploited fishing grounds, selective consumer behavior and human impact on fish populations through time (Greenspan, 1998; Leach & Davidson, 2001), and it is also of use for the establishment of the minimum number of individuals (MNI) (Orchard, 2005). One of several methods described in the literature to estimate size is the visual comparison of archaeological remains with modern specimens of known size (Casteel, 1976; Brinkhuizen, 1989; e.g. Wheeler & Jones, 1989; Vanderhoeven *et al.*, 1993). Although simple and quick, this method is also fairly imprecise. Another approach is the proportional method, where a linear relationship between the size of individual bones (M) and a length measurement (e.g. total length TL) of modern fish is assumed (TL = b × M), which is then extrapolated to archaeological remains (e.g. Gehlbach & Miller, 1961). However, this method is rather inaccurate when archaeological remains are considered that belonged to significantly larger or smaller individuals than the

reference specimens (Casteel, 1976). A third and more accurate method is regression (Casteel, 1976), where fish size is predicted by measurements on skeletal elements by means of a regression formula, which is based on a reference collection consisting of modern fish (e.g. Leach *et al.*, 1996).

The elements selected for size estimation are mainly individual bones or, in rare cases, scales (Casteel, 1976; Frost & Lowry, 1981; Harvey *et al.*, 2000), and should ideally be easily identifiable, solid structures with distinct features. The measurements should be made between landmarks that are not easily damaged by taphonomic processes (Wheeler & Jones, 1989). For several fish species, proportional or regression relationships between fish size and different measurements on various bones are provided in the literature (e.g. Leach *et al.*, 1996; Harvey *et al.*, 2000; Thieren *et al.*, 2012b). For sturgeon (*Acipenser* spp.), however, such information is scarce.

Most of the sturgeon skeleton is cartilaginous, except for the rostrum and circumorbital region which are covered by dermal bones. Other ossified parts are the skull roof, the opercular series, parts of the braincase, the palatoquadrate, the lower jaw, the hyoid and gill arches, the fin rays, the pectoral girdle and the dermal scutes, which are found in five rows

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alongside the body. Consequently, only these ossified elements have chances of being found on archaeological excavations and may thus offer a possibility for size reconstruction. Thus far, the pectoral fin spine has been the most frequently used element for back-calculating size of sturgeons in archaeozoology and fisheries. For some sturgeon species, such as the beluga (*Huso huso*), the sterlet (*A. ruthenus*) and the diamond sturgeon (*A. gueldenstaedtii*), the width of the articular head of the fin spine has been used in the proportional method (Bartosiewicz & Takács, 1997; Bartosiewicz *et al.*, 2008) and in regressions (Tsepkin & Sokolov, 1970, as cited by Casteel, 1976 p. 115–116).

Desse-Berset (1994, 2011a) also took measurements on the pectoral fin spine to reconstruct the size of remains of *Acipenser sturio* from the protohistoric site of Jardin d'Hiver (Arles, France) to get an insight in the population structure and to evaluate possible fishing pressure. For modern specimens with known length and age, the antero-dorsal and the antero-ventral distances of the pectoral fin spines (M2 and M3 in Figure 1) were plotted. These measurements were taken at the first distinct break of the slope of the pectoral spine, right below the knuckle at the proximal extremity. The length/age data was cross-referenced with Magnin's (1963) age/size distribution of *A. sturio* from the Gironde to obtain a length and associated age for every modern specimen. By comparing the measurements from archaeological fin spines with the biplot for the modern specimens, an approximate length and age were estimated.

Balazik *et al.* (2010) regressed fork length on the 'average fin spine diameter' of the thin-sectioned spine base, to estimate the fork length of an Atlantic sturgeon (*A. oxyrinchus*) population of James river, over a period of four centuries. The average fin spine diameter was defined as the average of height and width, the latter measurement being in fact the anteroposterior distance if the position of the spine within the fish is considered.

Brennan and Cailliet (1989) analyzed the growth of modern white sturgeon (*A. transmontanus*) using yet another measurement, the 'fin spine section radius', to construct a regression equation for the total length. However, to establish the 'average diameter' and the 'section radius', the preparation of thin sections is required, which is not a standard procedure in archaeozoology and is therefore less user-friendly.

Next to the pectoral fin spine, other bony elements such as the parasphenoid, dentary, hyomandibula, subopercle, cleithrum, clavicle, dermopalatine and palapterygoid (terminology according to Hilton *et al.*, 2011) have been used for size reconstruction of different
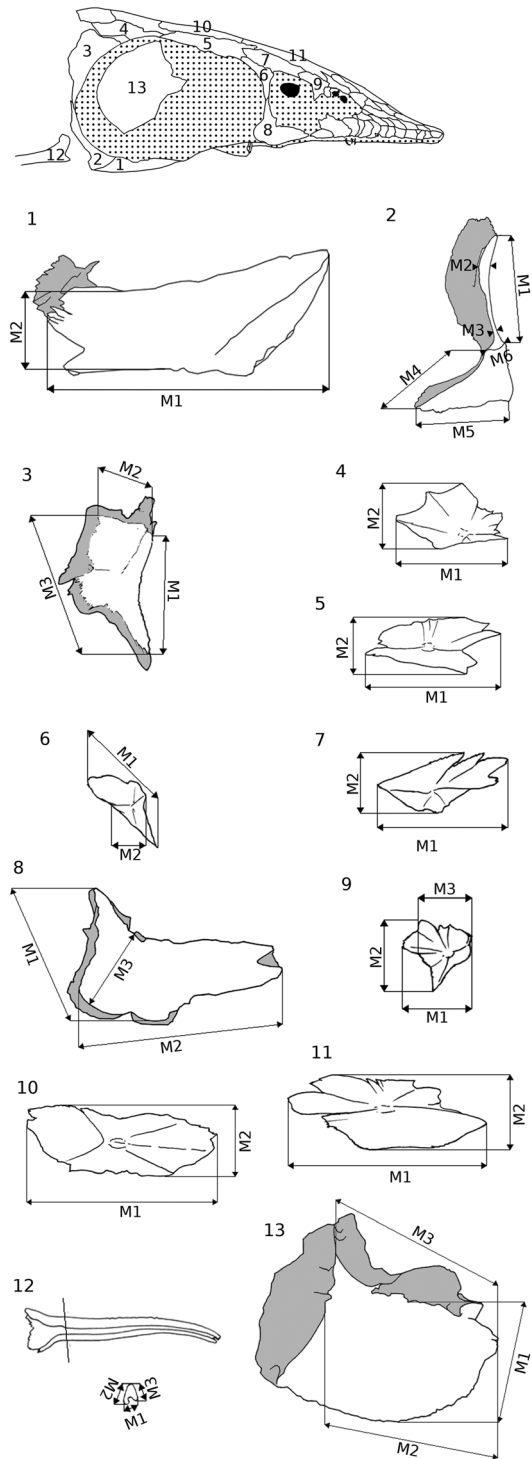

Figure 1. Right lateral view of the sturgeon skull and measurements indicated on the isolated bones. 1. clavicle; 2. cleithrum; 3. supracleithrum; 4. posttemporal; 5. dermopterotic; 6. postorbital; 7. dermosphenotic; 8. jugal; 9. supraorbital; 10. parietal; 11. frontal; 12. pectoral fin spine. Measurements are taken right below the knuckle at the proximal end of the spine at the first distinct break of the slope; 13. subopercle. Measurements are taken on the ornamented part of the bone only. Grey parts on elements 1, 2, 3, 8 and 13 are without ornamentation and thus not included in the measurements.

sturgeon species with both the proportional (Bartosiewicz & Takács, 1997) and the regression methods (Brennan & Cailliet, 1989; Desse-Berset, 1994, 2011b). Size has also been estimated with scute measurements, also both with the proportional method (van Maren, 1971) and with regression equations (Brennan, 1988; Brinkhuizen, 1989: 252-256; Debus, 1999; Desse-Berset, 2011b). However, since scute shape and size vary within one row, size reconstructions on isolated scutes will be less reliable unless their exact position within the row can be established. Vos-Kelk (1978) applied the proportional method to a number of unspecified skeletal elements, probably both scutes and elements of the skull and pectoral girdle.

The literature data mentioned above might give the impression that abundant tools are available to carry out body length reconstructions of sturgeon starting from their isolated bones. In reality, however, the actual regression equations or proportionality constants are rarely given, making it difficult to carry out back-calculations on other material. Only four publications give equations or proportionality constants for size reconstruction based on bones of the skull and pectoral girdle. These include the width of the clavicle, cleithrum, subopercle and the pectoral fin spine section of *A. transmontanus* (Brennan, 1988), the average spine diameter in *A. oxyrinchus* (Balazik *et al.*, 2010) and a measurement on the dentary of *A. sturio* and *A. oxyrinchus* (Desse-Berset, 2011b). The regressions provided by Bartosiewicz & Takács (1997) for measurements on the parasphenoid, dentary, hyomandibula, subopercle, preopercle, cleithrum, dermopalatine, pectoral fin spine and palapterygoid were obtained on *H. huso*.

While easily recognizable bones of the skull and pectoral girdle occur regularly in archaeological contexts, it appears that most of them have not yet been considered for size back-calculation thus far. Below, relationships are established between measurements on different bones of the head and pectoral girdle and the total length of sturgeon (*A. sturio* and *A. oxyrinchus* combined). The equations are then applied to a large sample of archaeological remains from a Neolithic site in the Netherlands.

Material and methods

Measurements were taken on skull bones and pectoral girdle elements of 56 European museum specimens of *A. sturio* and *A. oxyrinchus*, ranging in size between 17.7 and 300 cm TL. Since most of the examined sturgeon specimens were still intact and bones could not be extracted individually without damaging the fish,

measurements could only be made on the externally visible, ornamented parts of superficial bones. This excluded internal bones such as the parasphenoid, dentary and palatopterygoid from this study. The following bones were examined: cleithrum (cl), clavicle (clv), dermopterotic (dpt), dermosphenotic (dsp), frontal (fr), parietal (pa), supraorbital (so), posttemporal (pt), postorbital (po), jugal (j), subopercle (sop), supracleithrum (scl) and pectoral fin spine (pfs) (terminology according to Hilton *et al.* (2011)). Figure 1 gives an overview of these bones and the defined measuring distances.

Although some studies measure the articular head of the pectoral fin spine for size reconstruction (Bartosiewicz & Takács, 1997; Tsepkin & Sokolov 1970, as cited by Casteel, 1976 p. 115), this relatively fragile part of the bone is often damaged in archaeological fin spines. Therefore, we chose to use the lengths of the three sides at the base of the fin spine, which were also used by Desse-Berset (1994). Although the largest dimension of a particular bone often gives the most reliable estimate for the original fish size (Leach *et al.*, 1996), measurements applicable to incomplete bones are also included wherever possible, since archaeological remains are often fragmented. In case of paired bones, measurements were made on the right-sided element unless this was not possible due to the preservation state or difficult access to the element.

Multiple and simple least squares regression analysis, a common method for back-calculating size, was used to fit different curves to the data: linear ($y = a + bx$), exponential ($y = a*e^{bx}$), logarithmic ($y = a + b*\ln(x)$) and power curves ($y = ax^b$). The R^2-values (coefficient of determination) and the SEE's (standard error of estimate), two parameters indicating the accuracy of a regression, were used to evaluate each regression model. ANCOVA (analysis of covariance) was carried out to check the effect of the pooling of data from two morphologically similar cranial elements (parietal and frontal), as well as to test the validity of regression equations based on pooled data of *A. sturio* and *A. oxyrinchus*.

The established models were then applied to archaeological sturgeon remains from Vlaardingen, a Late Neolithic settlement in the Netherlands, excavated from 1959 to 1964 by the former Institute for Prae- and Protohistory (IPP), now the Amsterdams Archeologisch Centrum (AAC, University of Amsterdam). Radiocarbon dating showed that the settlement, which was located on a levee of a freshwater tidal creek, was occupied around 2900 BC (Clason, 1967; van Beek, 1990). Next to bones of domestic mammals, a large amount of remains of game, fowl and fish, especially sturgeon, were found. The sturgeon was identified as *A. sturio*, since at the time of the analysis, this was the only sturgeon species

thought to be indigenous to the Netherlands. Recently, however, archaeological *A. oxyrinchus* remains have been found in sites along the Atlantic façade of France (Desse-Berset, 2009; 2011a; Chassaing *et al.*, 2013) and along the Baltic Sea (Tiedemann *et al.*, 2007; Ludwig *et al.*, 2008, 2002, 2009), which implies that this species may also be expected to have occurred in the North Sea. Our own ongoing research confirms that this is indeed the case (Thieren *et al.*, 2012b).

Measurements on bones were taken with digital calipers to the nearest 0.1 mm. Data processing was performed using STATISTICA software (StatSoft Inc., 2013).

Results and discussion

Establishment of the regression equations

The individual measurements taken on the 56 *A. sturio* and *A. oxyrinchus* specimens are provided as Supplementary Data S1. Due to the poor preservation state of some of the sturgeons, not all measurements could be taken on each fish.

There is a strong correlation between the measurements on the different bones and the total length (TL) of the animals, despite the fact that some variation can be expected in the ornamented portion of the skull elements, as reported in shortnose sturgeon (*A. brevirostrum*) (Hilton *et al.*, 2011). Most of the relationships between the different measurements and the total length of the animal are highly significant, with correlation coefficients higher than 0.9 at the significance level α of 0.001, indicating a high predictive power. Two measurements on the cleithrum (M2 and M3) had low correlation coefficients of 0.82 and 0.62, respectively, and were therefore excluded from further analysis. Linear, exponential, logarithmic and power curves were fitted to the remaining data. For parietals and frontals, an additional regression model was constructed where no distinction was made between both, since it is sometimes difficult to distinguish these two bones when they occur isolated or fragmented in archaeological assemblages.

For all measurements on the different bones, the exponential and logarithmic fits proved unsatisfactory, based on the numerical statistical results and analysis of the residuals. For most bones and measurements, the R^2 and error statistics are very similar for the two remaining fitting types, i.e. the linear and power curves. However, only the power curves were retained since these are theoretically more likely in the context of allometric scaling (Table 1). In the case of the parietals and frontals, the validity of the curve fittings

based on the pooled data has been checked with ANCOVA, which showed no difference in curve fittings between both bones ($p > 0.05$). This indicates that data of parietals and frontals can be pooled.

No distinction was made between *A. oxyrinchus* and *A. sturio* for the final analysis, since models would then be based on a considerably lower number of individuals, thus decreasing the accuracy. Moreover, the species identification of most museum specimens included in the present study is based on the morphological criteria mentioned in Magnin (1964) and Kottelat & Freyhof (2007) and has not yet been genetically validated. Since *A. oxyrinchus* and *A. sturio* are closely related sister species (Peng *et al.*, 2007) that strongly resemble each other morphologically (e.g. Vecsei *et al.*, 2001), museum collections could, and do, contain undetected hybrid specimens (Chassaing *et al.*, 2013). Nevertheless, to gain some insights in the possible effect of species on the analysis, ANCOVA was performed with the morphological species identification as categorical factor. This analysis showed that regression lines did not differ significantly between both species ($p > 0.01$), which means the regression equations based on the pooled data from both species can be considered valid. This is in accordance with previous protocols carried out, for instance, by Desse & Desse-Berset (1996) or Van Neer & Lesur (2004).

Application to archaeological material

These models were then applied to archaeological sturgeon material from the Neolithic site of Vlaardingen of which a total of 318 measurable cranial and pectoral girdle bones were available. Only one measurement, the one which gave the model with the highest R^2 and lowest SEE, was used for each archaeological bone. The distribution of the reconstructed total lengths is presented in 25-cm length intervals in Figure 2. The minimum reconstructed total length is 67.5 cm, the maximum 355 cm, with a mean of 187.6 cm. This falls within the size ranges reported in the literature for the two species, varying between 3 and 4.5 m for *A. oxyrinchus* and between 3 and 6 m for *A. sturio* (Mohr, 1952; Vladykov & Greeley, 1963; Hochleithner & Gessner, 1999; Vecsei *et al.*, 2001). Our results differ somewhat from those of van Maren (1971), whose back-calculations on 80 specimens fell into a range of 72 and 267 cm, with a mean of 173 cm. Possibly, this can be explained by the different reconstruction methods and the extent of the reference collection. The proportional method on scutes was based on a single reference specimen whereas our regressions on cranial and pectoral girdle bones are based on 56 specimens. Moreover, it is

Table 1. Retained equations per bone and measurement, with correlation coefficients (r), coefficients of determination (R2), standard error of estimate (SEE) and the number of specimens on which the equations are based (n). Figure 1 gives an overview of the measuring distances

Bone	Measurement	r	R^2	SEE	Equation	n
Pectoral fin spine	M1	0.9743	0.952	13.66	$16.6327\,M1^{1.0134}$	28
Pectoral fin spine	M2	0.9211	0.944	27.10	$13.9741\,M2$	40
Pectoral fin spine	M3	0.9408	0.859	17.65	$13.8491\,M3^{0.9845}$	29
Posttemporal	M1	0.9581	0.938	16.45	$4.6407\,M1^{0.7902}$	43
Posttemporal	M2	0.9524	0.934	20.02	$3.5846\,M2^{1.0105}$	44
Posttemporal	M1 and M2		0.961	13.74	$3.7810\,M1^{0.4288}\,M2^{0.4883}$	43
Supracleithrum	M1	0.9719	0.964	13.76	$2.4373\,M1^{0.9917}$	49
Supracleithrum	M2	0.9012	0.926	27.03	$4.0351\,M2^{1.0147}$	49
Supracleithrum	M3	0.9675	0.964	14.85	$2.9901\,M3^{0.9345}$	38
Supraorbital	M1	0.9324	0.899	25.52	$5.3179\,M1^{0.9800}$	51
Supraorbital	M2	0.9453	0.926	23.05	$5.4958\,M2^{1.0700}$	49
Supraorbital	M3	0.9183	0.926	27.28	$12.4074\,M3^{0.8845}$	51
Supraorbital	M1 and M2 and M3		0.969	18.78	$5.3879\,M1^{0.3337}\,M2^{0.5427}\,M3^{0.1894}$	51
Postorbital	M1	0.9864	0.974	11.32	$3.0280\,M1^{1.0201}$	36
Postorbital	M2	0.9102	0.894	28.35	$8.2121\,M2^{1.0885}$	37
Dermosphenotic	M1	0.9640	0.956	18.06	$2.6351\,M1^{0.9722}$	36
Dermosphenotic	M2	0.9553	0.917	20.99	$7.6625\,M2^{0.9432}$	36
Dermosphenotic	M1 and M2		0.969	15.34	$3.4803\,M1^{0.6554}\,M2^{0.3336}$	36
Dermopterotic	M1	0.9434	0.922	20.71	$2.2744\,M1^{0.9580}$	45
Dermopterotic	M2	0.9519	0.922	18.45	$5.5551\,M2^{0.9522}$	45
Dermopterotic	M1 and M2		0.945	17.13	$3.2705\,M1^{0.4900}\,M2^{0.4893}$	45
Subopercle	M1	0.9587	0.958	19.56	$4.6561\,M1^{0.8701}$	53
Subopercle	M2	0.9750	0.970	15.24	$2.8525\,M2^{0.8907}$	52
Subopercle	M3	0.9338	0.926	24.40	$4.6870\,M3^{0.8290}$	50
Subopercle	M1 and M2		0.982	11.61	$3.2789\,M1^{0.3631}\,M2^{0.5352}$	52
Clavicle	M1	0.9723	0.971	13.27	$1.6656\,M1^{0.9978}$	38
Clavicle	M2	0.9144	0.920	23.16	$5.6473\,M2^{0.9254}$	39
Clavicle	M1 and M2		0.980	12.64	$2.1388\,M1^{0.7371}\,M2^{0.2649}$	38
Jugal	M1	0.9454	0.943	19.80	$2.1219\,M1^{1.1955}$	50
Jugal	M2	0.9412	0.888	33.82	$1.6779\,M2^{1.0998}$	52
Jugal	M3	0.9168	0.880	23.78	$6.7352\,M3^{1.0054}$	50
Jugal	M1 and M2		0.963	14.77	$1.6442\,M1^{0.6784}\,M2^{0.5167}$	48
Cleithrum	M1	0.9109	0.921	22.15	$3.9167\,M1^{0.9477}$	44
Cleithrum	M4	0.8836	0.825	21.43	$6.7438\,M4^{0.8879}$	37
Cleithrum	M5	0.9178	0.907	17.87	$5.6652\,M5^{0.9178}$	37
Cleithrum	M6	0.8841	0.879	21.60	$11.4734\,M6^{0.9453}$	36
Cleithrum	M1 and M6		0.964	12.33	$4.3833\,M1^{0.7136}\,M6^{0.3072}$	34
Parietal	M1	0.9687	0.941	17.08	$1.8339\,M1^{0.9284}$	48
Parietal	M2	0.9879	0.963	11.16	$5.2404\,M2^{0.9606}$	47
Parietal	M1 and M2		0.971	10.88	$3.4484\,M1^{0.3256}\,M2^{0.6399}$	47
Frontal	M1	0.9433	0.923	22.97	$1.6914\,M1^{0.9509}$	50
Frontal	M2	0.9434	0.949	23.61	$5.1121\,M2^{0.9530}$	49
Frontal	M1 and M2		0.964	18.07	$2.8511\,M1^{0.4232}\,M2^{0.5592}$	49
Parietal + frontal	M1	0.9556	0.932	20.13	$1.7626\,M1^{0.9395}$	49
Parietal + frontal	M2	0.9596	0.954	19.28	$5.2109\,M2^{0.9544}$	48
Parietal + frontal	M1 and M2		0.967	14.99	$3.0986\,M1^{0.3870}\,M2^{0.5854}$	48

unclear if the collection studied by van Maren (1971) was exactly the same as the one that was made available to us. Vos-Kelk (1978) only gives the mean back-calculated length (210 cm TL) and provides no details on minimum and maximum lengths, the type of skeletal elements or the number of examined specimens.

The size reconstructions obtained through our back-calculations and those of van Maren (1971) indicate that the Vlaardingen material mainly consists of larger animals of over 150 cm (in about 77.6% of the cases). Growth patterns, and thus size, are influenced by environmental factors and can therefore be population and time dependent (Balazik *et al.*, 2010). Nevertheless, in view of the evaluation of the possible place and season of capture, it is worth determining whether these sturgeon remains can be from spawning individuals or not. There are indications that size might be a more important trigger for spawning than age (Van Eenennaam & Doroshov, 1998). Spawning size also depends on gender and latitude, with lengths varying from 110–120 to 150 cm for male and from 120–150 to 180–200 cm for female *A. oxyrinchus* (Dadswell, 2006). The length distribution obtained on the Vlaardingen cranial material (Figure 2) with its peak of specimens in the 150–175 cm
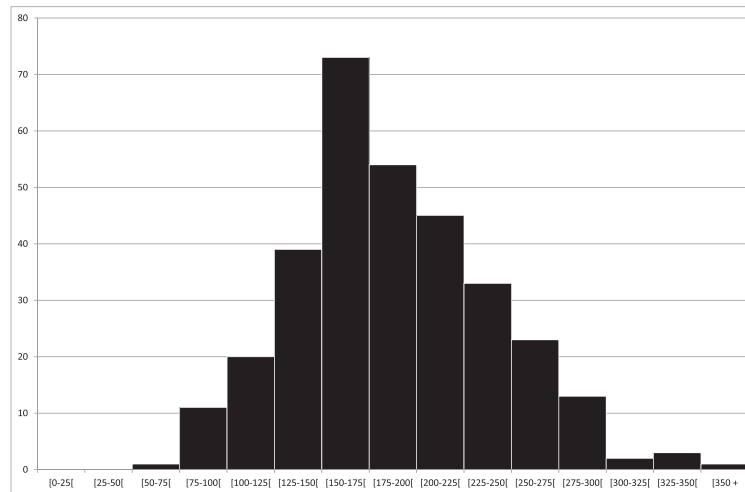
Figure 2. Histogram of the reconstructed total lengths of the Vlaardingen site, with length intervals in cm on the x-axis and the number of observations on the y-axis (n = 318).

TL class, and the presence of numerous fish larger than 175 cm suggests that probably most of the analysed sturgeon remains were from sexually mature animals that may therefore have been fished during their yearly spawning run.

The proportion of sturgeons of smaller dimensions at Vlaardingen is very low, but it is unclear if this is a biased distribution due to differential preservation, recovery methods or a combination of both. Bones of small sturgeons are indeed more difficult to recover than bones of larger individuals and they are also more fragile, thus decreasing their chance for preservation (Desse-Berset, 1994). An increase in total length of the sturgeon, and the resulting size increase of their bones should make it easier to recognize and to recover them, but according to Bartosiewicz & Bonsall (2008), it also would reduce preservation chances, since skeletal resorption exceeds bone formation during aging. This would imply that bones are easily destroyed and eroded beyond identifiability. However, Magnin (1963) states that A. sturio and A. oxyrinchus keep their scutes throughout their lives, with both size and thickness increasing, which agrees with our own observations on museum specimens. The most plausible explanation for the average large size of the sturgeon remains at Vlaardingen is that this was to a large extent determined by the recovery methods, i.e. hand-collecting in the trench, combined with a selection of the best preserved elements. However, it is also likely that the Vlaardingen people preferentially captured larger sturgeon on their spawning run. The contribution of smaller individuals remains unclear, but it is obvious that now and then fish of less than 1 m were captured. The presence of such juvenile specimens in

the assemblage could be indicative of fishing activities carried out in an estuary. Young sturgeon can reside in such an environment up to 4 years of age, and afterwards they live in the sea. However, up to 7 years of age, they can regularly migrate back to the estuary (the Saint John's migration) (Magnin, 1963; Acolas et al., 2011).

Conclusion

This study established relationships between measurements of different bones of the head skeleton and pectoral girdle and the total length of sturgeon (Acipenser sturio and A. oxyrinchus combined) for the back-calculation of size of archaeological sturgeon remains. Results show that these skeletal elements are suitable for size reconstruction, with standard errors of estimates in most cases less than 25 cm. It remains to be verified if the accuracy of the size prediction will increase with species specific models, although it can be expected that this increase would probably be limited. It should also be kept in mind that the relationships between skull bone measurements and total length may be population specific. However, due to the extinction of nearly all European sturgeon populations and the resulting dearth of comparative specimens, this will be difficult to verify. The models obtained in the present study were applied to a large assemblage of Neolithic sturgeon remains, and will be further used in the diachronic analysis of sturgeon remains from sites bordering the North Sea, dating between 4500 BC and postmedieval times (Thieren et al., 2012a).

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