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Human palaeodiet at Zamostje 2, central Russia: Results of radiocarbon and stable isotope analyses

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ABSTRACT

Only 21 human remains have been identified at Zamostje 2, despite extraordinarily good conditions for organic preservation, and the recovery of thousands of animal bones from layers dating from the Late Mesolithic to the Middle Neolithic (c.6500–4000 cal BC). Almost all the human remains are fragments of the cranium, maxilla, mandible, which are potentially reworked from earlier depositions, uphill or upstream of Zamostje 2, or isolated teeth. Disregarding naturally shed deciduous teeth, these remains have been attributed to between 5 and 14 individuals, ranging in age from 6 to 7 years to mature adult. We report AMS radiocarbon (^{14}C) dating and dietary stable isotopes, δ^{13}C and δ^{15}N, for all the human bones, and δ^{13}C and δ^{15}N values from 63 prehistoric animal bones from Zamostje 2, including 18 fish and 7 dogs. Using the faunal isotope data, we construct isotope signatures for different food groups, which we use to interpret the human δ^{13}C and δ^{15}N values. Based on ^{14}C ages and dietary stable isotopes, we propose that the human bones represent 10–12 individuals, most of whom date to the Late Mesolithic occupation at Zamostje 2; one is somewhat earlier in the Mesolithic, one (probably from the nearby site, Zamostje 1) may date to the Middle Neolithic, and two (one from Zamostje 1, one un-provenanced) date to the Late Neolithic or Eneolithic. The earliest and latest individuals may have obtained most of their dietary protein intake from fish, but Late Mesolithic individuals probably had more mixed diets. Palaeodiet reconstruction is complicated by unusual δ^{13}C and δ^{15}N values for local fish in the Late Mesolithic, which are reflected in δ^{13}C and δ^{15}N values from dogs.

1. Introduction

1.1. Human remains, diet reconstruction and radiocarbon dating

Archaeological evidence (particularly organic artefacts, such as nets and fishing fences, as well as faunal remains) shows that prehistoric hunter-gatherer communities in northern and eastern Europe regularly relied on fishing for subsistence. There is also increasing interest in archaeobotanical evidence of wild plant foods. While we may observe trends in archaeozoological or archaeobotanical data, however, it is difficult to quantify the overall importance of different food sources, and impossible to detect differences between individual diets. Analysis of dietary stable isotopes in human remains is an essential complementary approach.

Radiocarbon dating and dietary stable isotope analysis of unburnt human bone is possible when a significant proportion of the bone's original organic content ('collagen') is preserved. Collagen is synthesised primarily from dietary protein. Once a bone is fully formed, collagen is gradually remodelled over time; thus collagen in an adult human bone represents food consumed over a number of years. Dietary stable isotope ratios, such as δ^{13}C and δ^{15}N, tend to vary systematically between species in the same environment, depending on each species'

position in the local food web. In the northern European forest zone, plants generally have low $\delta^{15}N$ and moderate $\delta^{13}C$ values, terrestrial animals have somewhat higher $\delta^{13}C$ and $\delta^{15}N$ values, and freshwater fish tend to have even higher $\delta^{15}N$ values and often lower, or even much lower, $\delta^{13}C$ values than terrestrial animals and plants (e.g., Fischer et al., 2007). Stable isotope ratios in human collagen will reflect the relative importance of isotopically distinct food groups. If the isotopic signatures of food sources are known, Bayesian statistical programs can be used to estimate (with appropriate uncertainties) the contribution of each food group to the overall diet of each consumer (e.g. human), based on that individual's stable isotope values.

Quantitative diet reconstruction is essential when human bones are dated directly, as carbon in aquatic ecosystems is typically depleted in radiocarbon (^{14}C) compared to atmospheric CO_2, which means that fish give misleadingly old ^{14}C ages ('reservoir effects'). When fish is one of the main protein sources in human diets, human ^{14}C ages may be hundreds of years older than the ^{14}C ages of contemporaneous organic artefacts (e.g., Fernandes et al., 2015; Shishlina et al., 2017; Wood et al., 2013; Zagorska et al., 2018). Disarticulated human remains found in cultural layers (archaeological deposits accumulated over a significant period of time) are particularly difficult to date, as their find context may be almost irrelevant (e.g., Meadows et al., 2018b).

Considering the geographic extent of the north-eastern European forest zone (between the Baltic and the Urals), and the time-depth of hunter-gatherer-fisher archaeology in this region (c.10,000–3000 cal BC), there have been relatively few palaeodiet studies using dietary stable isotopes (e.g., Eriksson et al., 2003; Shishlina et al., 2016; Tõrv, 2018), some of which involve only a handful of individuals (e.g., Antanaitis-Jacobs et al., 2009; Iacumin et al., 2004; Piezonka et al., 2013), providing insufficient evidence to detect geographic or temporal trends in human diets, or to distinguish typical from atypical individuals. Where isotope analyses have taken place, the scarcity or absence of relevant local reference data has sometimes meant that diet reconstruction is still a speculative exercise. The situation in north-eastern Europe is readily contrasted with the much more intensively studied hunter-gatherer-fisher communities in the Baikal region of Siberia (e.g., Katzenberg et al., 2012) and with the relatively well-studied prehistoric cemeteries in the steppe region of south-eastern Europe (e.g., Lillie et al., 2011). This contrast is largely a reflection of the poor visibility of prehistoric human remains in the forest zone (poor organic preservation is also a significant factor in e.g. Finland). New isotope results from directly dated prehistoric human remains, particularly when accompanied by detailed local reference data, are therefore essential to our understanding of hunter-gatherer-fisher subsistence strategies. This paper presents results from all human bones identified at Zamostje 2, one of the most important prehistoric sites in central Russia.

1.2. Zamostje 2

Vladimir Lozovski's excavations at Zamostje 2, on the banks of the River Dubna, c.100 km north of Moscow (Fig. 1), revealed a sequence of five main archaeological layers in gyttja on the edge of a former lake, containing domestic waste and some *in-situ* fishing installations, but no burials. The site, which spans the Late-Final Mesolithic and Early-Middle Neolithic, was occupied regularly throughout c.6500-4000 cal BC. The lower Late Mesolithic layer may date from c.6600/6500 cal BC onwards, and the upper Late Mesolithic layer lasted until c.5900/5800 cal BC, with no evidence of a significant hiatus between these two layers. A Final Mesolithic layer fills the gap before the start of the Early Neolithic, marked by the appearance of Upper Volga style pottery, which can be dated to c.5700/5600 cal BC; the Middle Neolithic layer is poorly dated, but may cover much of the 5th millennium cal BC (Meadows et al. in prep.).

Throughout the sequence, there is abundant archaeological and archaeozoological evidence that fishing was a major part of the

subsistence economy (e.g., Radu and Desse-Berset, 2013). For example, fishing fences, fish-traps and even nets have been directly dated to both the Late Mesolithic and Neolithic phases. There are fish scales in food-crusts on pottery, and fish-bones in Mesolithic coprolites. However, there is also a rich archaeobotanical record (Berihuete Azorin and Lozovskaya, 2014), and terrestrial fauna (elk (*Alces alces*) and beaver (*Castor fiber*)) were heavily exploited throughout the sequence (Chaix, 2003). Thus the relative importance in different phases of plant and animal foods, or of terrestrial and aquatic species, is an obvious topic for research.

In this paper, we report ^{14}C ages, $\delta^{13}C$ and $\delta^{15}N$ values from all disarticulated human bones identified during the Zamostje 2 excavations, and $\delta^{13}C$ and $\delta^{15}N$ values from 63 animal bones from Zamostje 2, including 18 fish and 7 dogs. We use the faunal isotope data to suggest isotope signatures for different food groups, and thus to interpret the human dietary stable isotopes. Based on our human diet reconstructions, we also propose a chronological interpretation of the ^{14}C ages from human remains.

1.3. Human remains at Zamostje 2

Out of many thousands of bones and teeth recovered since excavations began in 1989, only 22 have been identified as human, but loose human bones were found in all five cultural layers. In terms of their taphonomic history, eight naturally shed deciduous teeth may have been lost or discarded by the residents of Zamostje 2, but they are too small for ^{14}C and stable isotope analysis. The remaining fragments were deposited after the death of the individual concerned, and they may have been redeposited one or more times after burial, as they are all disarticulated. The only post-cranial elements are an adult humerus (No12), and a fused proximal epiphysis from a femur (No15); although No15 was identified as human by morphometric analysis, its dietary stable isotopes cast doubt on this attribution, and biomolecular analysis (ZooMS) has now identified it as bear (*Ursus* sp.). Three human mandibles and two maxillae, with some surviving teeth, have been attributed to five different individuals; dental analyses by A V Zubova and T A Chikisheva (2015 unpublished) confirm that all age groups are represented. The remaining bones are small cranial fragments, none of which conjoin. Thus on morphometric criteria the Zamostje 2 human bone assemblage (including fragments Nos 13 and 16, now known to come from a nearby site, Zamostje 1) was derived from at least five, and perhaps as many as 13 individuals. In some cases, ^{14}C ages differentiate bones that on morphometric grounds alone could have been derived from the same individual (see below).

Fragment No7, a small piece of occipital bone, is unusual, in that it has a clear network of cut-marks (striations) on its internal surface, as well as fainter evidence of smoothing of the edges (Fig. 2). Based on experimental analyses (Lozovskaya unpublished data), the striations are regarded as manufacturing traces, made with a stone tool with a retouched denticulated edge. Use-wear traces have not been observed. None of the other human remains display any abrasion or evidence of intentional modification, and there is nothing to indicate why they were found in the gyttja layers, together with food waste, artefacts, and occasionally *in-situ* fishing or boating equipment.

1.4. Faunal remains at Zamostje 2

Elk and beaver are by far the most abundant terrestrial species throughout the sequence of cultural layers, with elk likely to have provided much more meat than beaver (Chaix, 2003; Moubarak-Nahra et al., 2014). Other terrestrial taxa (e.g. wild boar (*Sus scrofa*), reindeer (*Rangifer tarandus*)) have been recorded, but are numerically insignificant, and can be ignored for the purpose of diet reconstruction. The only domestic animal is the dog (*Canis familiaris*), which was apparently eaten by humans (Chaix, 2013). Abundant fish remains include a broad range of species and age/size classes; the most abundant taxa are pike

Fig. 1. Map of north-eastern Europe, showing sites mentioned in the text (Karin Göbel, ZBSA; base map Eriksson et al., 2003)

(*Esox lucius*), perch (*Perca fluviatilis*), and various cyprinids, such as roach (*Rutilus rutilus*), tench (*Tinca tinca*), ide (*Leuciscus idus*), bream (*Abramis brama*) and crucian carp (*Carassius carassius*) (Radu and Desse-Berset, 2013). A wide variety of birds has been identified (Mannermaa, 2013), but when the number of identifications and meat weight of each species are considered, consumption of birds is unlikely to have had much impact on human isotope values.

1.5. Food plants at Zamostje 2

The seeds and fruits of forest trees and shrubs were an important addition to the diet. The most ubiquitous remains of edible plants are of bird cherry (*Prunus padus*), viburnum (*Viburnum opulus*) and raspberry (*Rubus idaeus*), whose seeds number in the hundreds (Berihuete Azorin and Lozovskaya, 2014: 76). They occur in both the Mesolithic and Neolithic layers; raspberry seeds are more numerous in Mesolithic sediments, but charred viburnum berries are found in food-crust on Early

Fig. 2. Internal surface of human skull fragment No7, showing cut-marks (photo: O Lozovskaya). The clean cut edge (left) is the result of sampling for this study.

Table 1
Analytical results from human remains.

label	element sampled	provenance, expected date	laboratory code	^{14}C age (BP)	maximum date (cal BC)	collagen yield (%)	C (%)	N (%)	atomic C:N	δ^{13}C (‰)	δ^{15}N (‰)
№1	cranium[a]	Zamostje 2 1989 season unstratified	KIA-53294†	7636 ± 43	6590–6420	9.1	43.0	15.8	3.2	−20.8	12.6
№2	cranium[b]	Zamostje 2 1989 season unstratified	KIA-53295†	3673 ± 32	2150–1950	7.0	42.0	14.9	3.3	−22.0	12.1
№3	cranium[a]	Zamostje 2 1991 season II-3-B13, early Neolithic	KIA-51432[d]	7415 ± 39	6390–6220	9.7	49.5	18.3	3.2	−21.1	12.7
№4	cranium[a]	Zamostje 2 1991 season II-3-ДІ3, early Neolithic	KIA-51433[d]	7442 ± 39	6410–6230	11.2	43.3	15.9	3.2	−20.9	13.7
№5	cranium[b]	Zamostje 2 1995 season II-4-A11, early Neolithic	KIA-51097[d]	7655 ± 49	6600–6430	11.8	43.6	16.3	3.1	−20.5	12.2
№6	cranium[a]	Zamostje 2 1996 season II-6-B9, final Mesolithic	KIA-51434[d]	7567 ± 39	6480–6370	8.5	43.8	16.2	3.2	−20.2	13.4
№7	cranium, dense network of scratches on internal surface[b]	Zamostje 2 1996 season II-7-B9, late Mesolithic upper layer	KIA-51096[d]	7094 ± 38	6050–5890	13.5	44.2	16.3	3.2	−19.7	10.4
№8	root of left second permanent molar, from adult female mandible	Zamostje 2 1990 season II-7-B3, late Mesolithic upper layer	KIA-51435[d]	7663 ± 44	6600–6440	9.2	44.0	16.0	3.2	−19.3	12.9
№9	maxilla, adult <25y	Zamostje 2 1998 season trench, late Mesolithic lower layer	KIA-53296[e]	7581 ± 41	6500–6380	12.7	43.4	16.1	3.2	−20.6	12.3
№12	humerus, young woman	Zamostje 2 2000 season II-9-A9, between lower and upper late Mesolithic layers	KIA-53297[e]	8332 ± 46	7530–7190	10.6	43.3	16.0	3.2	−21.7	11.2
№13	right mandible, female? no teeth, perhaps >50y	Zamostje 1 1990 season II-3-29, middle-late Neolithic	KIA-53298[e]	4827 ± 33	3700–3520	13.1	43.4	16.1	3.2	−22.8	11.4
№14	mandible, child 1.5-2y	Zamostje 2 1991 season II-1-B1', unstratified	KIA-53299[e]	7624 ± 41	6590–6420	13.2	42.6	15.6	3.2	−19.7	14.3
№15	fused proximal femur epiphysis, brown bear[c]	Zamostje 2, 1990 (?) season layer 6 (?), late Mesolithic upper level	KIA-53300[e]	7094 ± 40	6050–5890	9.3	42.5	15.7	3.2	−20.7	6.6
№16	maxilla with canine, premolars; maxilla sampled	Zamostje 1 1990 season II-?-24/29, middle-late Neolithic	KIA-53301	5442 ± 35	rejected	1.3	–	–	–	–	–

[a] Osteological morphometric analysis cannot attribute №1, 3, 4, 6 to different individuals, whereas AMS and IRMS results suggest that №1 and 6 are from different individuals, whereas AMS results show that these samples are from 3 different individuals to №3 and 4, but cannot distinguish №1 from №6, or №3 from №4

[b] Osteological morphometric analysis cannot attribute №2, 5, 7 to different individuals, whereas AMS results show that these samples are from 3 different individuals

[c] Previously identified as human; ZooMS analysis at BioArCh, University of York, re-identified it as a bear.

[d] EA-IRMS analysis at isolab GmbH.

[e] EA-IRMS analysis at BioArCh, University of York.

Neolithic pottery (Lozovskaya and Lozovski, 2014: Fig. 2). Charred and waterlogged remains of yellow water lily (*Nuphar lutea*) are among the most numerous of botanical macro-remains; leaves, roots and seeds are edible. Goosefoot (*Chenopodium* sp.) was also widespread in all layers, especially in the Early Neolithic (Berihuete Azorin, 2018); these are ruderal plants indicating dry habitat conditions; seeds and leaves of most Chenopodiaceae are edible and are widely used for food. Hazelnut shells are found rarely, and only in the Neolithic.

2. Methods

2.1. Human remains

Fourteen presumably human bone fragments (Table 1) were sampled for ^{14}C dating and dietary stable isotope analysis, to test whether they were broadly of the same date as the cultural layer in which they were found, and ideally to compare the diets of Mesolithic and Neolithic individuals. Collagen was extracted at the Leibniz-Labor, Kiel, Germany by demineralising the crushed bone in HCl to remove bioapatite and secondary carbonates, dissolving secondary organic compounds in an NaOH solution, re-acidifying the insoluble residue in HCl, and gelatinising it by in a weakly acidic solution at 85 °C for 17 h. The collagen solution was then filtered through a pre-baked 0.45 μm pore silver filter, to remove any insoluble particles, and freeze-dried.

Part of the collagen was then dated at the Leibniz-Labor, by Accelerator Mass Spectrometry (Nadeau et al., 1998). Some of the remaining collagen from each sample was sent for EA-IRMS (Elemental Analysis-Isotope Ratio Mass Spectrometry), either to isolab GmbH, Schweitenkirchen, Germany (for measurement of %C, %N, %S, δ^{13}C, δ^{15}N and δ^{34}S; (Sieper et al., 2006)), or the BioArCh research centre, University of York, United Kingdom (for measurement of %C, %N, δ^{13}C and δ^{15}N; details below). At least two collagen aliquots were analysed for each sample, with consistent results. All stable isotope results (δ^{13}C, δ^{15}N and δ^{34}S) are expressed in parts per mill (‰) relative to the respective standards, Vienna PeeDee Belemnite for δ^{13}C, air N_2 for δ^{15}N, and Canyon Diablo Troilite for δ^{34}S ($\delta = [(R_{sample}/R_{standard}-1)] \times 1000$, where R = ^{13}C/^{12}C, ^{15}N/^{14}N, and ^{34}S/^{32}S).

2.2. Faunal remains

We sampled 64 prehistoric faunal remains from Zamostje 2, including 19 beaver, 16 elk, 1 reindeer, 1 otter, 20 fish and 7 dogs. Each sample consisted of a single bone, presumed to represent a different individual. None of these samples was dated directly. The elk and beaver bones were selected from all occupation layers (Late Mesolithic through to Middle Neolithic), but the majority of those analysed were from the upper Late Mesolithic layer. Almost all the fish bones analysed were from upper Late Mesolithic and Final Mesolithic layers. The dog samples were all from the upper Late Mesolithic layer. Thus most of the faunal samples can be dated to the late 7th-early 6th millennium – coincidentally the same period as most of the human remains (see below).

Collagen from elk, beaver, dog and fish samples was extracted using standard procedures (Brown et al., 1988; Jørkov et al., 2007; Longin, 1971; Richards et al., 1998), and analysed by EA-IRMS at the BioArCh research centre, University of York. Each sample was mechanically cleaned, weighed out (200–800 mg), immersed in HCl solution (0.6 M) and refrigerated at 4 °C until demineralized. The acid-insoluble fractions were then rinsed with distilled water and gelatinised with 0.001 M HCl solution at 80 °C during 48 h. The samples were first filtrated using polyethylene Ezee Filters (9 mL, pore size 60–90 μm; Elkay Laboratories Ltd.) to remove the large insoluble particulate matter. The supernatants were then ultrafiltered (30 kDa, Amicon® Ultra-4 Centrifugal Filter Units, Millipore, Billerica, MA, USA), frozen at −20 °C for 48 h and lyophilized. Collagen was weighed out into tin capsules (0.9–1.1 mg) and analysed in duplicate by EA-IRMS using a Sercon GSL analyzer

coupled to a Sercon 20–22 Mass Spectrometer. Instrumental precision on repeated measurements was ± 0.2‰ (standard error of the mean), Accuracy was calculated by measurements, in each run, of international standard reference materials (IAEA 600, IAEA N2, IA Cane).

Collagen preparation and purification on some samples of beaver, elk, reindeer and otter (ZMS-1 to ZMS-10) was performed following a protocol based on Longin (1971) and modified by Bocherens et al. (1997). In brief, the extraction procedure includes demineralization in 1 M HCl, soaking in 0.125 M NaOH, and a final step of solubilization in acidified water (pH = 2) before freeze-drying. C and N measurements were made at the Institut des Sciences de l'Evolution of Montpellier 2 University in France (VG-Optima). Analytical error, based on within-run replicate measurement of laboratory standards (egg albumin, keratin, alanine amino acid, modern collagen), was ± 0.1‰ for δ^{13}C, and ± 0.2‰ for δ^{15}N. Sulfur elemental and isotopic measurements were conducted at the Department of Geosciences of Tübingen University, using a NC2500 CHN elemental analyzer coupled to a Thermo Quest Delta + XL mass spectrometer. Samples were calibrated to δ^{34}S values relative to CDT of NBS 123, NBS 127, IAEA-S-1 and IAEA-S-3. The reproducibility is ± 0.4‰ for δ^{34}S, and the error on %S measurement is 5%.

2.3. Botanical remains

A small number of charred plant remains from the archaeological strata, and several modern *Viburnum* berries collected close to Zamostje 2, were dried and weighed out into tin capsules (0.9–1.1 mg) without additional pretreatment. Samples were analysed in duplicate by EA-IRMS using a Sercon GSL analyzer coupled to a Sercon 20–22 Mass Spectrometer at the BioArCh research centre, University of York, following procedures outlined above.

3. Results

3.1. Human remains

Analytical data from human bones are reported in Table 1. Collagen yields were mostly very good (average 10% of the starting weight), indicating that the bones were well-preserved and suitable for isotopic analysis (Dobberstein et al., 2009). The elemental analyser C and N results (%C, %N, atomic C:N ratio) are normal for collagen and again indicate good preservation (DeNiro, 1985). The C and N isotope data (^{14}C, δ^{13}C and δ^{15}N) should therefore be reliable. One sample, No16, gave only 1.3% collagen by weight, and although a plausible ^{14}C age was obtained (KIA-53301, 5442 ± 35 BP), there was not enough collagen left for EA-IRMS analyses, and we therefore regard this ^{14}C age as unreliable. No16's provenance is also unclear; it now appears to have been found at a nearby site, Zamostje 1. Two samples gave relatively recent ^{14}C ages: No13 (KIA-53298, 4827 ± 33 BP) and No2 (KIA-53295, 3673 ± 32 BP) (Fig. 3). No13, now also attributed to Zamostje 1, was expected to provide a Middle Neolithic date, but even with no allowance for dietary reservoir effects, a calibrated date of 3700–3520 cal BC appears too late for the Lyalovo culture. No2 was from Zamostje 2, but was unstratified, and evidently is not associated with any of the archaeological strata.

The remaining samples, all found at Zamostje 2, yielded Mesolithic ^{14}C ages, regardless of stratigraphic position (all except Nos 1 and 14 were from archaeological layers). The oldest result came from the humerus (No12, KIA-53297, 8332 ± 46 BP); this bone may be significantly older than the start of Mesolithic occupation at Zamostje 2. The ^{14}C age of the cut-marked bone, No7, is almost unique in appearing to fit its stratigraphic position, suggesting that this bone was not redeposited. All the human ^{14}C ages are regarded as potentially misleadingly old, given the abundant evidence of fish consumption.

In terms of dietary stable isotopes, it is notable that the outliers (aside from No15, the bear) are the samples whose ^{14}C ages also stand
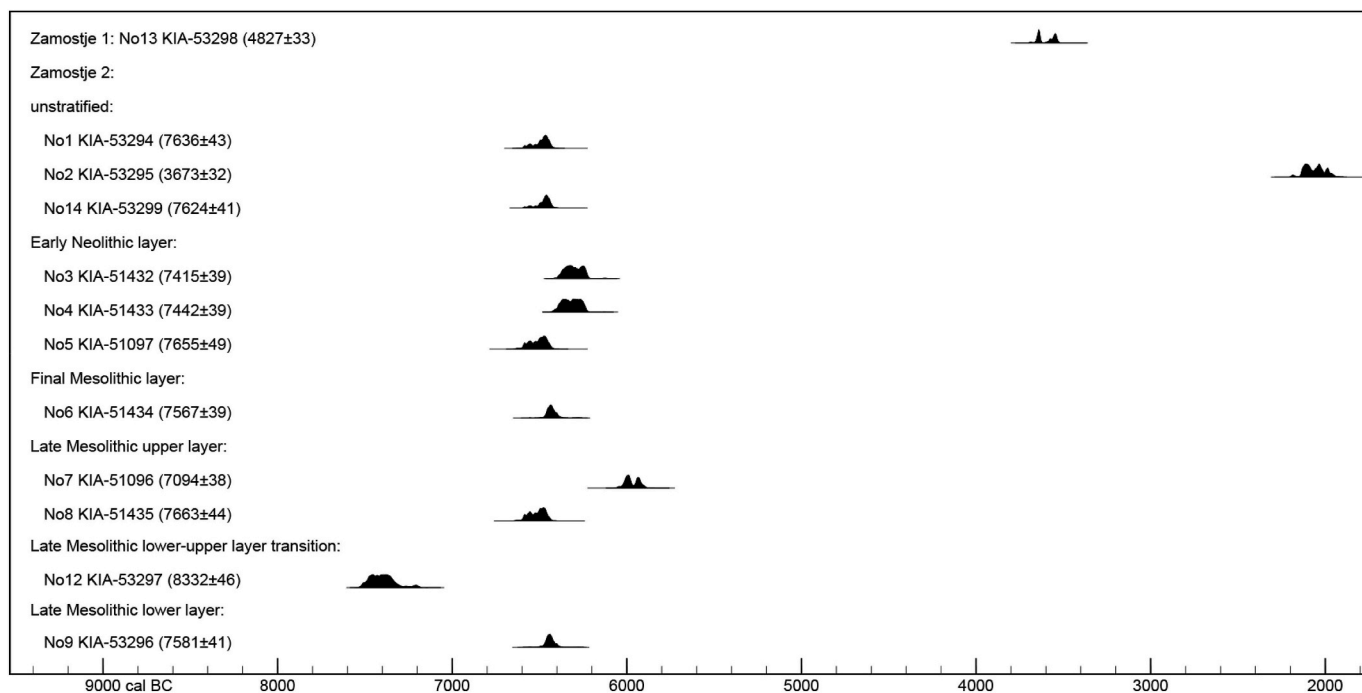
Fig. 3. Calibrated dates of human remains, grouped by stratigraphic position (Table 1), without correction for possible dietary reservoir effects. These calibrations only provide termini post quos for deposition, but everything above No7 appears to be re-deposited, unless dietary reservoir effects were extremely high; Nos 8 and 12 also seem older than expected, based on other dates from the Late Mesolithic layers (Meadows et al. in prep.).
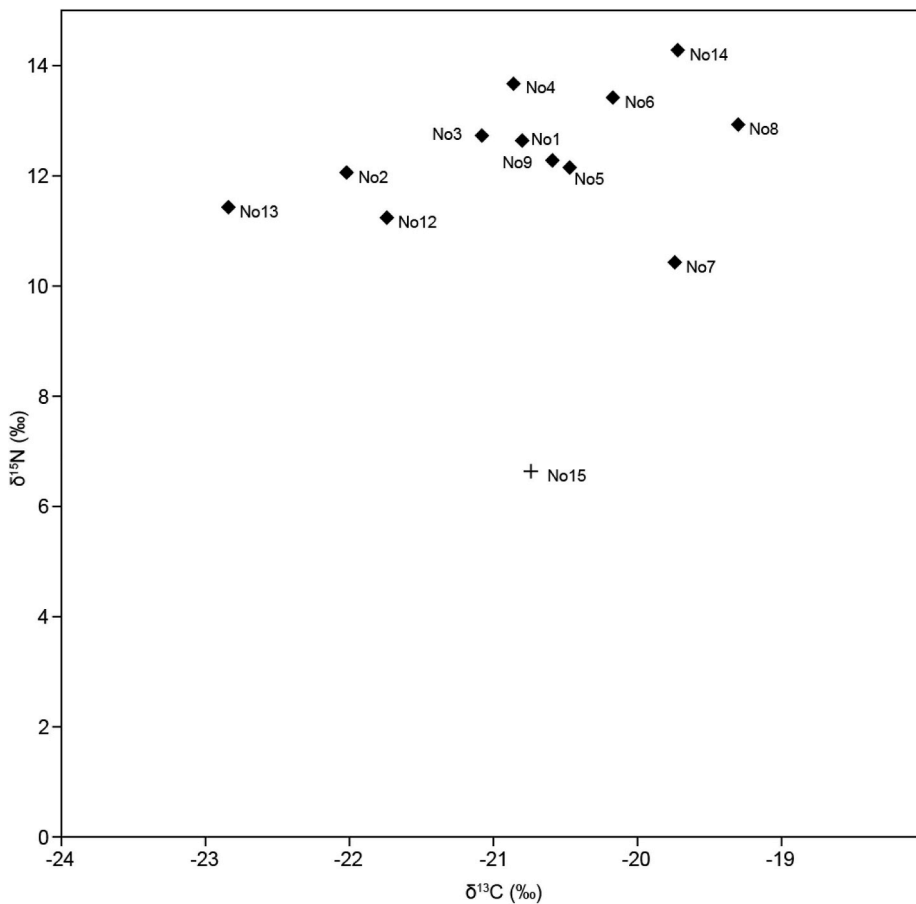

Fig. 4. Zamostje human stable isotope data (Table 1). Note that No15 has been identified as a bear.
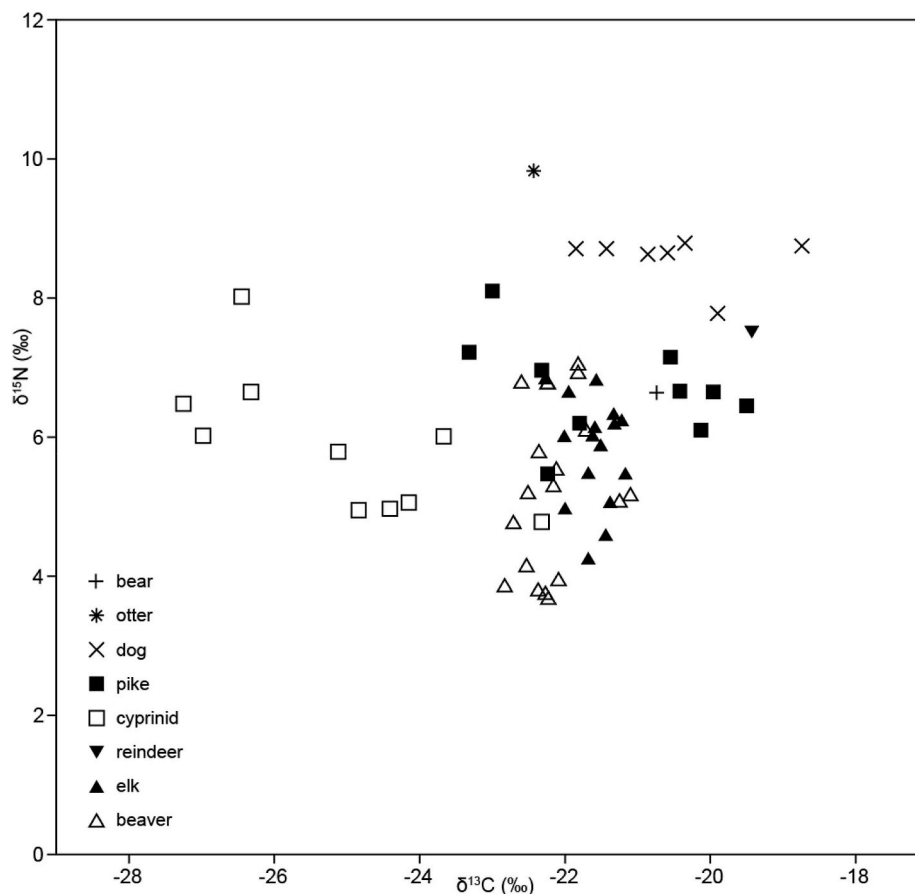
Fig. 5. Faunal stable isotope data, collagen from individual bones found in the late-final Mesolithic layers at Zamostje 2 (Table 2).

out: Nos 2, 12 and 13 have the lowest $\delta^{13}C$ values, while No7 has the lowest $\delta^{15}N$ value (Fig. 4). The typical Late Mesolithic human has a moderate $\delta^{13}C$ value (-21 to $-19‰$) and a high $\delta^{15}N$ value (12–14‰).

3.2. Faunal remains

All 19 beaver and 16 elk samples gave good collagen yields and C:N values. In both species, the $\delta^{13}C$ values are tightly clustered (Fig. 5); average beaver $\delta^{13}C$ values ($-22.2 \pm 0.5‰$) are marginally more negative than elk ($-21.6 \pm 0.3‰$). This may reflect physiological differences, as elk are ruminants and beavers are not. $\delta^{15}N$ values are more scattered, but again the average values for the two species are similar (beaver $5.3 \pm 1.2‰$; elk $5.8 \pm 0.8‰$). These $\delta^{15}N$ values appear slightly higher than those from Mesolithic-Neolithic Minino, about 400 km north of Zamostje near Vologda in northern Russia (beaver $4.5 \pm 0.8‰$, n = 5; elk $4.2 \pm 1.0‰$, n = 10) (Wood et al., 2013). The elk values for both isotopes are also higher than those of elk from Eneolithic-Bronze Age Shagara, about 250 km south-east of Za-mostje ($\delta^{13}C$ $-22.7 \pm 0.3‰$, $\delta^{15}N$ $4.3 \pm 0.2‰$, n = 9) (Shishlina et al., 2016), emphasising the importance of obtaining local reference data for palaeodiet studies. The Zamostje reindeer isotope values ($\delta^{13}C$ $-19.4‰$, $\delta^{15}N$ $7.5‰$) are higher than those of elk, as expected given their dietary preferences (Drucker et al., 2010).

Two fish taxa were analysed: pike (n = 10) and undifferentiated cyprinids (n = 10). Fish-bone collagen yields (average 3%) were lower than for mammal bones (average 9%), but only two samples, one pike and one cyprinid, were rejected, on account of their elevated C:N values. There is no systematic difference between pike and cyprinids in either collagen yields or C:N values, and therefore no reason to question the validity of the isotopic data. We would normally expect pike, as

predators of cyprinids, to show a typical trophic-level increase, relative to cyprinids, of 1–2‰ in $\delta^{13}C$ and at least 3‰ in $\delta^{15}N$ (e.g. Schmölcke et al. 2016), but at Zamostje 2 pike have much higher $\delta^{13}C$ values than cyprinids ($-21.2 \pm 1.4‰$ vs $-25.5 \pm 1.3‰$), but very similar $\delta^{15}N$ values ($6.8 \pm 0.6‰$ vs $6.0 \pm 1.0‰$) (Fig. 5). Again, these results highlight the importance of local reference data for palaeodiet studies; compared to pike from Shagara ($\delta^{13}C$ $-25.3 \pm 1.3‰$, $\delta^{15}N$ $10.5 \pm 1.0‰$, n = 7) (Shishlina et al., 2016), the Zamostje 2 pike have c.4‰ higher $\delta^{13}C$ values and c.4‰ lower $\delta^{15}N$ values. Our results effectively imply that, in addition to cyprinids, pike also consumed a higher-$\delta^{13}C$, low-$\delta^{15}N$ food, which has not been identified, but might be e.g. a crustacean or mollusc seldom consumed by the cyprinids. Radu and Desse-Berset (2013) noted that pike bones at Zamostje 2 were predominantly from immature fish. Pike have flexible and opportunistic feeding habits, which change with age and size (Craig, 2008), and the isotope results suggest that these young pike had not developed a fully piscivorous diet.

Isotope data from carnivorous mammals (Fig. 5) need to be interpreted against this background. Results from the single otter analysed ($\delta^{13}C$ $-22.4‰$, $\delta^{15}N$ $9.9‰$) are easily explained by a trophic-level shift from the average of all the local fish values ($\delta^{13}C$ $-23.3‰$, $\delta^{15}N$ $6.4‰$), as expected for a fully aquatic peak predator. The dog results (average $\delta^{13}C$ $-20.5 \pm 1.0‰$, $\delta^{15}N$ $8.6 \pm 0.4‰$, n = 7) are more complex. Considering how tightly the herbivore $\delta^{13}C$ values are clustered, the wide range of $\delta^{13}C$ values from dogs is inexplicable without a substantial aquatic component in most dog diets, whereas the narrow range of dog $\delta^{15}N$ values reflects the similarity in average $\delta^{15}N$ between the various potential meat sources. In fact, the dog $\delta^{15}N$ values are surprisingly low, considering the other faunal data, and may mean that dogs also consumed either plant foods (presumably human food waste) or molluscs, crustaceans etc. from the base of the aquatic food chain.

Table 2
Carbon and nitrogen analytical results from faunal remains.

label	taxon	collagen yield (%)	C (%)	N (%)	atomic C:N	δ^{13}C (‰)	δ^{15}N (‰)
1597	beaver	9.3	41.9	14.9	3.3	−22.1	5.6
1600	beaver	7.6	41.9	15.1	3.2	−21.7	6.1
1601	beaver	8.2	42.0	14.9	3.3	−21.8	7.1
1602	beaver	8.3	41.4	15.1	3.2	−22.2	5.3
568	beaver	10.8	42.5	15.3	3.2	−22.2	3.7
577	beaver	10.4	41.5	15.0	3.2	−22.2	6.8
846	beaver	6.4	39.8	13.8	3.4	−22.7	4.8
71	beaver	6.4	42.4	15.1	3.3	−22.2	6.8
74	beaver	7.3	41.4	15.0	3.2	−22.4	5.8
76	beaver	11.1	42.2	15.1	3.3	−22.5	4.2
Z 1	beaver	9.7	42.6	15.3	3.3	−21.8	6.9
Z 2	beaver	8.2	41.8	15.1	3.2	−22.1	4.0
Z 3	beaver	10.9	44.1	16.0	3.2	−22.8	3.9
Z 4	beaver	11.2	43.2	15.5	3.3	−22.6	6.8
Z 5	beaver	8.3	42.8	15.6	3.2	−22.5	5.2
ZMS-2	beaver	3.3	37.1	13.4	3.2	−22.3	3.8
ZMS-3	beaver	5.4	41.4	14.9	3.2	−21.3	5.1
ZMS-4	beaver	5.7	41.3	14.3	3.4	−22.4	3.8
ZMS-5	beaver	4.0	35.1	12.9	3.2	−21.1	5.2
Z 44	elk	8.3	42.7	14.9	3.3	−21.3	6.3
Z 45	elk	9.3	43.8	15.7	3.3	−21.6	6.0
Z 46	elk	10.7	43.7	15.6	3.3	−21.3	6.2
Z 47	elk	12.2	43.7	15.6	3.3	−21.6	6.8
Z 48	elk	13.2	43.4	15.6	3.3	−22.0	5.0
Z 49	elk	12.7	44.3	15.8	3.3	−21.7	5.5
Z 50	elk	13.6	40.6	14.4	3.3	−22.0	6.7
Z 51	elk	14.8	46.8	16.6	3.3	−21.5	5.9
Z 52	elk	11.8	41.2	14.9	3.2	−22.0	6.0
Z 53	elk	12.0	43.7	15.7	3.3	−22.3	6.9
Zam-Elk-01	elk	11.5	43.4	15.5	3.3	−21.6	6.2
Zam-Elk-02	elk	12.2	42.8	15.3	3.3	−21.2	5.5
ZMS-1	elk	9.2	38.3	14.0	3.2	−21.4	4.6
ZMS-6	elk	6.1	39.1	14.5	3.2	−21.2	6.3
ZMS-7	elk	6.6	39.2	14.3	3.2	−21.7	4.3
ZMS-8	elk	3.3	38.5	14.0	3.2	−21.4	5.1
ZMS-10	reindeer	7.7	38.1	14.4	3.1	−19.4	7.5
Z 31	cyprinid	3.9	19.3	6.7	3.4	−24.2	5.1
Z 32	cyprinid	2.9	22.6	7.6	3.5	−24.4	5.0
Z 33	cyprinid	3.2	29.3	10.1	3.4	−24.8	5.0
Z 35	cyprinid	2.9	27.5	9.7	3.3	−23.7	6.0
Z 36	cyprinid	3.6	23.1	7.9	3.4	−26.3	6.7
Z 37	cyprinid	3.1	27.2	9.5	3.3	−25.1	5.8
Z 38	cyprinid	2.7	22.3	7.4	3.5	−27.0	6.0
Z 39	cyprinid	3.4	30.1	10.1	3.5	−26.5	8.0
Z 40	cyprinid	3.6	31.0	10.8	3.3	−27.3	6.5
Z 21	pike	2.0	31.9	11.5	3.2	−23.0	8.1
Z 22	pike	2.1	21.9	7.4	3.5	−21.8	6.2
Z 23	pike	2.9	35.2	11.8	3.5	−20.1	6.1
Z 24	pike	2.5	24.4	8.4	3.4	−22.3	7.0
Z 25	pike	3.2	32.5	11.4	3.3	−20.0	6.7
Z 26	pike	4.3	34.0	12.1	3.3	−20.6	7.2
Z 28	pike	3.3	30.8	10.4	3.5	−23.3	7.2
Z 29	pike	3.8	31.6	10.9	3.4	−20.4	6.7
Z 30	pike	1.0	35.3	12.6	3.3	−19.5	6.5
ZMS-9	otter	9.0	37.6	13.5	3.3	−22.4	9.8
Z 14	dog	13.4	43.7	15.9	3.2	−21.9	8.7
Z 15	dog	10.8	43.1	15.1	3.3	−20.9	8.6
Z 16	dog	16.5	44.0	15.9	3.2	−20.6	8.7
Z 17	dog	14.9	43.3	15.6	3.2	−18.7	8.8
Z 18	dog	12.9	41.9	15.1	3.2	−21.4	8.7
Z 19	dog	15.2	42.9	15.6	3.2	−20.4	8.8
Z 20	dog	14.3	43.0	15.6	3.2	−19.9	7.8

Samples ZMS 1–10 from Tübingen University; all other data from University of York.

3.3. Botanical remains

EA-IRMS results for botanical samples are shown in Table 3. Charring may have affected results from the archaeological samples, but no acceptance criteria are regularly applied to plant remains (Metcalfe and Mead, 2018), and the validity of results is difficult to assess. Modern *Viburnum* berries gave consistently lower %N and δ^{15}N values than the archaeological remains, which may be due to a combination of inter-

specific differences, (absence of) charring, and change over time in baseline isotope values. However, Selva et al. (2012) report similarly low δ^{15}N values for modern *Vaccinium* berries, and large inter-specific differences between various wild plant foods in Białowieza Forest, Poland (δ^{13}C range > 10‰, δ^{15}N range > 6‰), so the Zamostje 2 results may reflect real variability in the isotopic signatures of wild plant foods, rather than differential preservation. Herbivores and humans would have consumed a wide range of plant species, in varying proportions,

Table 3
Carbon and nitrogen analytical results from plant samples.

label	taxon	age	condition	C (%)	N (%)	atomic C:N	$\delta^{13}C$ (‰)	$\delta^{13}C$ (‰) corrected[a]	$\delta^{15}N$ (‰)
ZpL2	*Viburnum opulus*	modern	dried	34.9	0.3	158.9	−23.4	−21.4	−1.1
ZpL3	*Viburnum opulus*	modern	dried	36.6	0.2	209.6	−27.5	−25.5	−5.3
ZpL4	*Viburnum opulus*	modern	dried	40.3	0.2	195.3	−25.2	−23.2	−2.6
ZpL5	*Viburnum opulus*	modern	dried	36.9	0.2	203.5	−25.6	−23.6	−6.2
ZpL6	*Viburnum opulus*	modern	dried	37.8	0.3	149.5	−26.3	−24.3	−2.8
ZpL7	*Viburnum opulus*	modern	dried	47.7	0.6	97.6	−25.6	−23.6	−0.2
ZpL8	*Viburnum opulus*	modern	dried	38.5	0.3	179.0	−24.8	−22.8	−4.1
ZpL9	*Viburnum opulus*	modern	dried	37.2	0.2	194.4	−24.7	−22.7	−4.4
ZpL10	waterlily (*Nuphar lutea*)	archaeological	charred	33.9	1.0	38.9	−25.7	−25.7	4.0
ZpL11	bird cherry (*Prunus padus*)	archaeological	charred	49.7	1.2	49.1	−28.0	−28.0	1.6
ZpL12	*Viburnum opulus*	archaeological	charred	33.1	1.5	25.1	−27.4	−27.4	12.4

[a] For comparison with archaeological samples, $\delta^{13}C$ values of modern samples are raised by 2‰, to compensate for the lower $\delta^{13}C$ of modern atmospheric CO_2 as a result of fossil fuel use (the "^{13}C Suess effect").

thereby averaging out much of the variability in plant isotope values (hence the clustering and similarity of beaver and elk isotope values). It is difficult to estimate useful average plant values for human diet reconstruction, however, particularly as we have no data for potentially important food plants, such as underground storage organs of e.g. *Typha* and *Phragmites* (Brown et al., 2013).

3.4. Sulfur

Collagen from four human (Nos 3, 4, 6, 8) and four herbivore bones (3 elk, 1 beaver) was analysed for %S and $\delta^{34}S$ (Table 4). In some situations, sulfur isotope values vary systematically between terrestrial and freshwater ecosystems, and $\delta^{34}S$ in humans may therefore serve as a proxy for consumption of terrestrial or aquatic species. However, the sulfur content of collagen is relatively low (0.28% in mammals; Nehlich and Richards, 2009) and sulfur is therefore more vulnerable to contamination from the burial environment than C and N (particularly at Zamostje 2, where the sulfur content of gyttja is relatively high (M Kulkova pers comm)). Nehlich (2015) and Nehlich and Richards (2009) recommend accepting $\delta^{34}S$ values from mammal collagen if %S is between 0.15% and 0.35%, the C:S ratio is 600 ± 300 and the N:S ratio is 200 ± 100. The elk samples meet all three criteria, while the beaver bone fails all three, and has a much lower $\delta^{34}S$ value than the elk. Only one of the human samples, No6, meets all three criteria; No8 meets two criteria and Nos 3 and 4 fail all three, suggesting that collagen is contaminated with sulfur from the burial environment. Fig. 6 shows that $\delta^{34}S$ is negatively correlated with %S (Spearman's r = −0.793, p = 0.0189), which means that most of the variation in $\delta^{34}S$ reflects differences in the level of contamination, rather than differences in diet. As $\delta^{34}S$ values in samples meeting the Nehlich and Richards (2009) acceptance criteria are very similar, it is also possible that there is no real difference in $\delta^{34}S$ between terrestrial and aquatic species at Zamostje 2. We have therefore not used the $\delta^{34}S$ data for diet reconstruction.

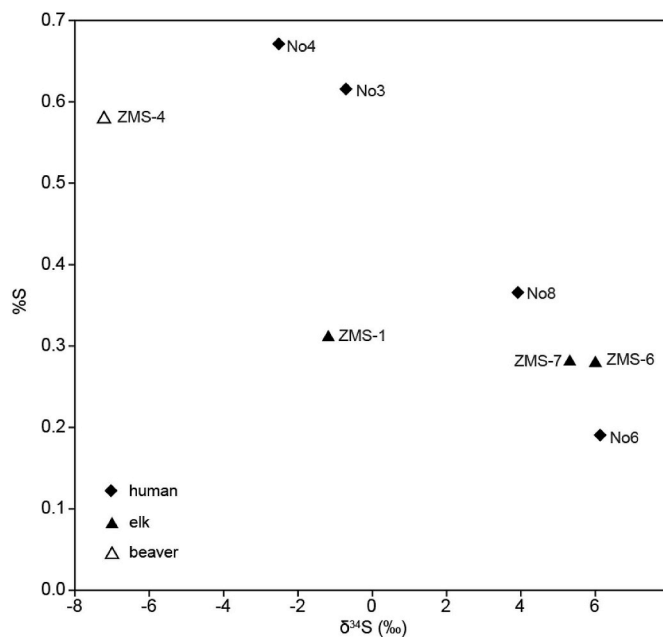**Fig. 6.** $\delta^{34}S$ versus %S in collagen from human and faunal samples (Table 4), showing that excess %S (above the expected 0.28%) is associated with large shifts in $\delta^{34}S$. These samples are quite tightly clustered in terms of $\delta^{13}C$ and $\delta^{15}N$, which again implies that $\delta^{34}S$ is probably not a reliable palaeodiet proxy. Nos 3 and 4 are potentially fragments of the same skull, but were found close together, and the similarity in their $\delta^{34}S$ and %S values could be due to similarity in their burial environment.

4. Discussion

4.1. Zamostje 2 dietary stable isotopes in context

Our results are not the first dietary stable isotope data from

Table 4
Sulfur analytical results.

label	taxon	collagen yield (%)	C (%)	N (%)	S (%)	atomic C:N	atomic C:S	atomic N:S	$\delta^{34}S$ (‰)
ZMS-1	elk	14.8	46.8	16.6	0.31	3.3	380	118	−1.1
ZMS-4	beaver	5.7	41.3	14.3	0.58	3.4	190	56	−7.2
ZMS-6	elk	12.0	43.7	15.7	0.28	3.3	371	117	6.0
ZMS-7	elk	13.6	40.6	14.4	0.28	3.3	330	104	5.3
No3	human	9.7	49.5	18.3	0.62	3.2	215	68	−0.7
No4	human	11.2	43.3	15.9	0.67	3.2	172	54	−2.5
No6	human	8.5	43.8	16.2	0.19	3.2	619	196	6.2
No8	human	9.2	44.0	16.0	0.37	3.2	321	100	4.0

Beaver and elk results from Tübingen University; human samples analysed by isolab GmbH, Schweitenkirchen.
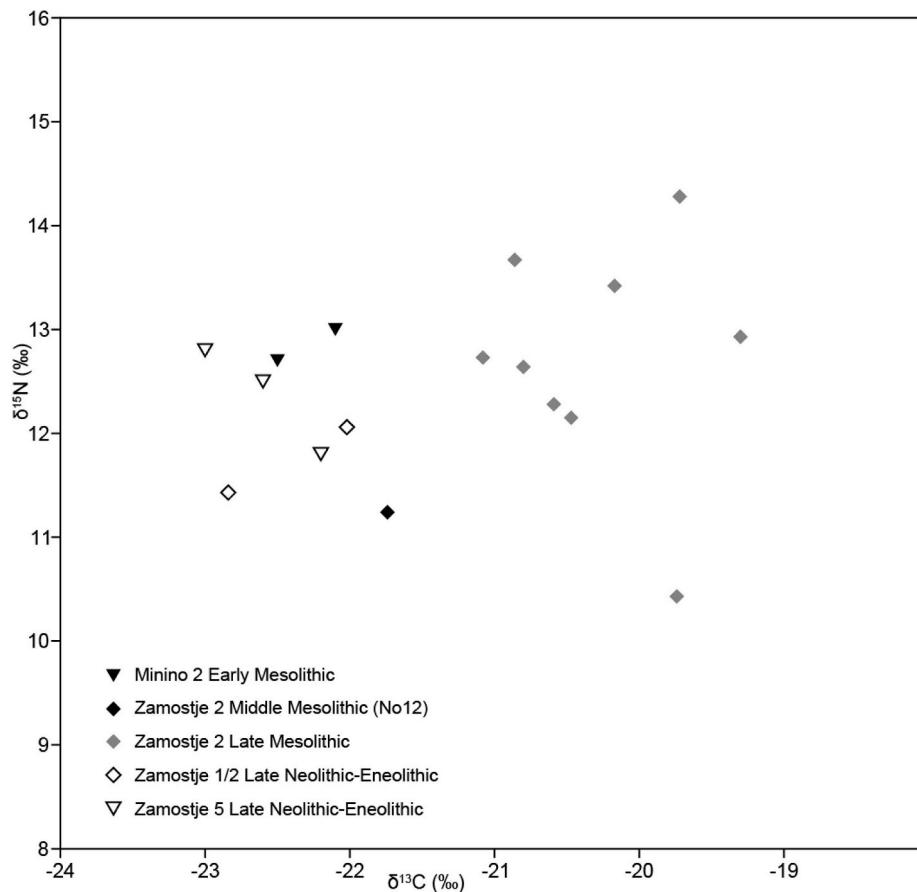
Fig. 7. Dietary stable isotope results from prehistoric human remains found at or nearby Zamostje 2 (Table 1 and Iacumin et al., 2004; Minino 2 (14/1, 14/2), Zamostje 5 (14/3, 14/4, 14/5)).

prehistoric human remains in the Zamostje area. Within a study of oxygen isotopes in animal bones across a wider region, Iacumin et al. (2004) analysed some human samples, including five from "Zamost'e", and reported collagen $\delta^{13}C$ and $\delta^{15}N$, as well as $\delta^{18}O$ from bone carbonate and phosphate. The provenance details of these samples were not published, and the bones were not dated directly, but two were from burials at Minino 2, and three were from Zamostje 5; differences in $\delta^{18}O$ between the Minino 2 and Zamostje 5 individuals support the idea that the former belong to an earlier, colder period (Iacumin pers comm). These burials were presumably associated with Early Mesolithic artefacts at Minino 2, 150–200m west of Zamostje 2, and Late Neolithic-Eneolithic finds at Zamostje 5, 100m downstream of Zamostje 2 (Gracheva et al., 2015). The isotopic similarities between the oldest sample at Zamostje 2 (No12) and the Minino 2 individuals, 14/1 and 14/2, and between the Late Neolithic-Eneolithic Nos 2 and 13 and the Zamostje 5 individuals (Fig. 7), are therefore unsurprising.

It is remarkable, however, that all the Late Mesolithic $\delta^{13}C$ and $\delta^{15}N$ results from Zamostje 2 fall outside the range of data from Minino 2 and Zamostje 5. The Late Mesolithic human isotope results also stand out compared to data from Eneolithic-Bronze Age Shagara and Mesolithic-Neolithic Minino (Vologda region) (Shishlina et al., 2016; Wood et al., 2013). Two Middle Neolithic individuals at Sakhtysh IIa, 200 km north-east of Zamostje, gave the combination of relatively high $\delta^{13}C$ and $\delta^{15}N$ results found in the Late Mesolithic at Zamostje 2 (Piezonka et al., 2013), but otherwise this pattern appears to be unusual at inland sites in north-eastern Europe. Four Late Mesolithic individuals from Olenii Ostrov in Karelia gave even higher $\delta^{13}C$ and $\delta^{15}N$ values (average $-20.2 \pm 0.3‰$, $14.4 \pm 1.3‰$; (Wood et al., 2013)), but in this case we may assume that freshwater seal was the main food source, which does not help to explain the Zamostje 2 results. The most comparable

$\delta^{13}C$ and $\delta^{15}N$ values to those at Late Mesolithic Zamostje 2 are from 14 burials at Vasilievka II, a Late Mesolithic cemetery in the steppe zone in southern Ukraine (Lillie and Jacobs, 2006).

When terrestrial and aquatic protein sources have clearly different $\delta^{13}C$ and $\delta^{15}N$ signatures, human $\delta^{13}C$ and $\delta^{15}N$ values tend to fall on a "mixing line" between hypothetical endpoints based on purely terrestrial and purely aquatic diets, and human $\delta^{13}C$ and $\delta^{15}N$ may therefore be highly correlated. This is particularly evident at coastal sites, but can also be seen at inland sites, particularly if results from infants are omitted (e.g. at Lake Baikal, Siberia (Katzenberg et al., 2012); Shagara, central Russia (Shishlina et al., 2016); Lake Burtnieks, Latvia (Meadows et al., 2018a); Friesack, Germany (Meadows et al., 2018b)). In male burials at Vasilievka II, on the Dnieper rapids, $\delta^{13}C$ and $\delta^{15}N$ are almost perfectly correlated (Lillie and Jacobs, 2006, Fig. 2), presumably reflecting differential consumption of sturgeon (*Acipenser* spp.), as at Mesolithic sites in the Danube Gorges (Cook et al., 2001). At Zamostje 2, however, there is no sign of correlation between Late Mesolithic human $\delta^{13}C$ and $\delta^{15}N$ values. This does not mean that there were no differences in diet between individuals, but rather that terrestrial and aquatic foods are not isotopically distinct enough for differences in fish consumption to produce a regular pattern of human $\delta^{13}C$ and $\delta^{15}N$ values. Diet reconstruction is therefore more challenging at Zamostje 2 than at some of the other sites mentioned.

4.2. Food sources

One explanation for the unusual pattern among human $\delta^{13}C$ and $\delta^{15}N$ values at Zamostje is that pike average $\delta^{13}C$ values are higher and $\delta^{15}N$ values are lower than expected, given the cyprinid results. This situation may not be unique. ^{14}C and EA-IRMS data from carbonised

food remains on early Neolithic pottery hint at the existence of fish with similar isotopic signatures at Sakhtysh IIa (Piezonka et al., 2016). Several fish-bones dated to the late 6th millennium cal BC from Preobrazhenka 6, in south-western Siberia, yielded much higher $\delta^{13}C$ values and lower $\delta^{15}N$ values than modern or Bronze Age fish from other sites in the region. The mechanism accounting for these isotope values is not understood, but it may be related to environmental change and differences in climate. However the pike isotope values are to be explained, it is impossible to ignore them, as young pike was clearly one of the main fish exploited at Zamostje 2 (Radu and Desse-Berset, 2013). Whether or not mature pike would have had more typical $\delta^{13}C$ and $\delta^{15}N$ values (lower $\delta^{13}C$ than terrestrial mammals, $\delta^{15}N$ 3–4‰ higher than cyprinids), the Late Mesolithic human isotope data are more consistent with a focus on young pike.

Another question is the role of dogs as a food source for humans, given the observation by Chaix (2013) that dog bones from Zamostje 2 frequently reveal butchery marks. Intuitively, dogs are unlikely to have been as important to human diets as wild food resources, either in terms of overall food intake or specifically as a protein source, but they are sufficiently isotopically distinct (due to their higher $\delta^{15}N$ values) that their potential contribution to human isotope values must be considered. Any consumption of dog meat would help to account for the high $\delta^{15}N$ values in humans (Fig. 8).

Given the relatively low $\delta^{15}N$ values in fish collagen, in fact, it is difficult to account for some of the higher $\delta^{15}N$ values in human samples without some dog consumption. Traditionally, a $\delta^{15}N$ trophic-level shift of +3–5‰ was assumed between diet and human collagen (Bocherens and Drucker, 2003; Hedges and Reynard, 2007), although O'Connell et al. (2012) proposed a +6‰ $\delta^{15}N$ shift between dietary protein and human bone collagen. If we assume a +5‰ $\delta^{15}N$ trophic-level shift, and that fish flesh was 1–2‰ enriched relative to bone

collagen (Fischer et al., 2007), human $\delta^{15}N$ values above 13‰ (Nos 4, 6, 14) would imply an almost completely aquatic diet (No14 was a young child, and its elevated $\delta^{15}N$ value may be due to a nursing effect, but Nos 4 and 6 were adults).

Wild plant foods were probably fundamental to subsistence, for the basic reason that wild animals in this environment do not store enough fat to meet human energy needs throughout the year. Necessarily, therefore, plant foods provide relatively little protein, and therefore may have only a minor effect on collagen isotope values, as collagen is made mainly from dietary protein, particularly in high-protein diets (Fernandes et al., 2012). Nevertheless, if wild plant foods provided more than half of the overall food intake, as suggested at Shagara (Shishlina et al., 2016), Lake Burtnieks (Meadows et al., 2018a) or Friesack (Meadows et al., 2018b), their impact on human $\delta^{13}C$ and $\delta^{15}N$ values cannot be ignored.

With limited local reference data for the edible parts of wild plant foods, we could infer average $\delta^{13}C$ and $\delta^{15}N$ values in plants consumed by humans by assuming that terrestrial herbivores consumed isotopically similar plants. Allowing for a $\delta^{13}C$ trophic-level shift of +5‰ and a $\delta^{15}N$ trophic-level shift of +3–5‰ from plants to elk/beaver collagen, local plants consumed by elk and beaver may have had average $\delta^{13}C$ and $\delta^{15}N$ of −27‰ and +2‰ respectively. A human vegan would therefore have had collagen $\delta^{13}C$ and $\delta^{15}N$ values around −22‰ and 7–8‰ respectively. Alternatively, plant foods consumed by the bear, No15 ($\delta^{13}C$ −20.7‰, $\delta^{15}N$ 6.6‰), may better represent the plant component of human diets, although physiological differences between humans and bears could lead to different isotope values in human vegans.

A largely carnivorous diet would produce a similar $\delta^{13}C$ value in humans to a largely vegan diet, even if energy macronutrients (fat and carbohydrate) contribute to collagen isotope values (Fernandes et al.,
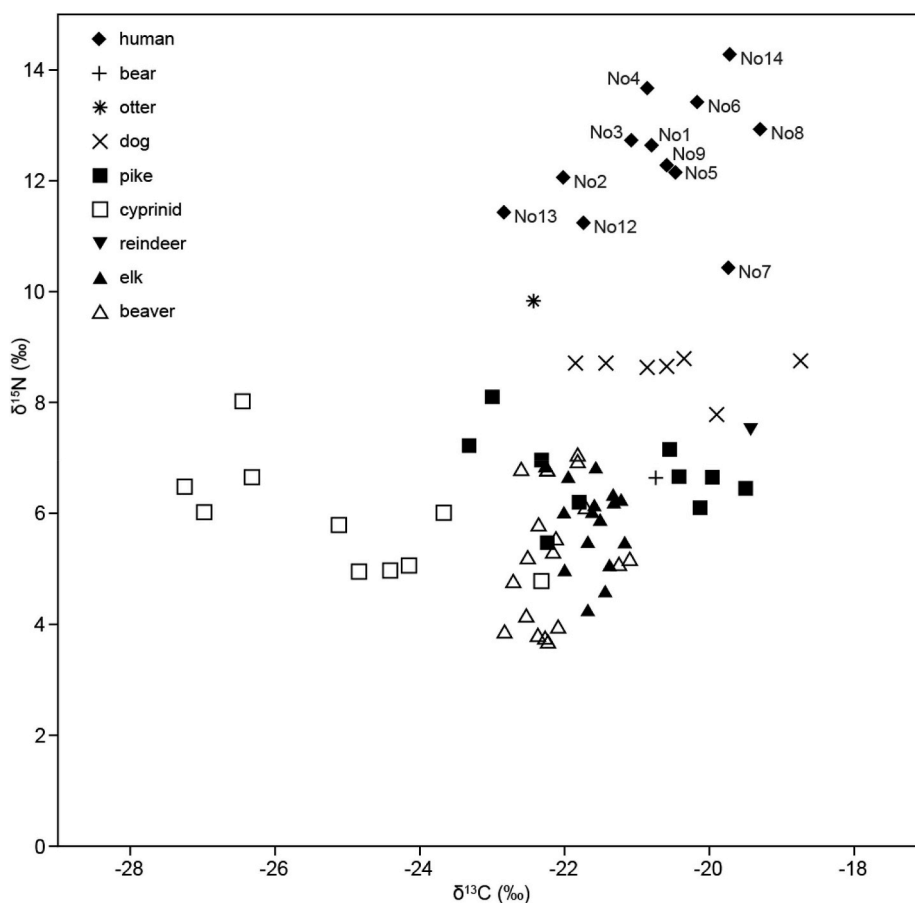

Fig. 8. Dietary stable isotope results from prehistoric human remains found at or nearby Zamostje 2, compared to values in Late Mesolithic fauna from Zamostje 2.

2012). Given that N is found only in protein, however, the higher protein content of meat and fish means that the average δ^{15}N of dietary protein in omnivore diets would approach that in meat and fish if flesh made up a quarter of overall food intake, so human δ^{15}N should be quite sensitive to low levels of meat consumption. The relatively low δ^{15}N for No7, the cut-marked skull, implies either that this individual consumed very little flesh (e.g. c.10% of overall food intake), or that local faunal collagen δ^{15}N is misleading, if this individual came from elsewhere (e.g. the δ^{15}N of elk collagen is higher at Zamostje than at Shagara, and No7's estimated meat consumption would therefore be higher if Shagara elk isotope values were applied). Small differences in δ^{15}N between individuals with relatively high δ^{15}N values probably reflect differences in the sources of animal protein (e.g. higher trophic level fish, dogs) rather than the amount of flesh consumed, as these individuals cannot have met their energy needs without significant plant-food consumption.

4.3. Quantitative diet reconstruction

Bayesian mixing models attempt to quantify the relative importance of different food sources by calculating all possible combinations of intakes of available foods that would result in the observed human dietary stable isotopes. Programs such as SIAR (Parnell et al., 2010) and FRUITS (Fernandes et al., 2014) have been used on comparable assemblages, with food-source isotope values based on either local reference samples or data from literature (e.g., Boethius and Ahlström, 2018; Fernandes et al., 2015; Meadows et al., 2018a; Meadows et al., 2018b; Shishlina et al., 2016; Tõrv and Meadows, 2015). Mixture modelling requires a subjective assessment of what constitute separate food groups (e.g. plants, terrestrial herbivores, fish) and how to construct such groups (e.g. at Zamostje 2, we might assign an 80% weighting within the terrestrial herbivore food group to elk meat, given the relative abundance and size of elk).

For mixture modelling to give meaningful results, food groups need to be isotopically fairly homogenous, and distinct from each other. At Zamostje 2, for example, fish δ^{13}C values are so variable that it would be logical to treat pike and cyprinid as separate food groups. Increasing the number of food groups (without increasing the number of isotopes analysed) leads to less precise estimates, however, and given that elk δ^{13}C values are intermediate between those of pike and cyprinids, it would still be difficult to distinguish elk meat consumption from consumption of both fish taxa in equal proportions. On the other hand, fish δ^{15}N values are similar to each other and only slightly higher than elk δ^{15}N values, whereas dog δ^{15}N values are distinctly higher, suggesting that dogs could constitute an isotopically distinct food group. FRUITS permits users to impose constraints on the modelled mixtures – for example, that dogs were less important to human diets than fish or terrestrial resources, which would allow some role for dog consumption without ignoring the fundamental problem that it would have been more efficient for humans to have eaten most of the catch themselves, rather than feeding it to their dogs. In an unrouted FRUITS model (i.e. one which does not consider the role of energy macronutrients in collagen isotope values) in which there are only three food groups (terrestrial, fish and dogs), dog is estimated to have provided up to c.20% of protein intake for individuals with high δ^{15}N values, if dog consumption is restricted to being less than fish and terrestrial food intake. Various parameter values that are not tightly constrained (e.g. the protein content of plant foods, the δ^{15}N diet-collagen offset) would significantly affect these estimates.

For illustrative purposes, we have created a simple routed FRUITS model (following e.g. Fernandes et al., 2015), in which dog consumption is disregarded and isotope values for plant, terrestrial herbivore and fish protein and energy components (Fig. 9) are derived from the average faunal collagen isotope values, weighted 80/20 for elk vs beaver, and 50/50 for cyprinids and pike (this weighting implies that perch, the other major fish taxon identified, may had intermediate
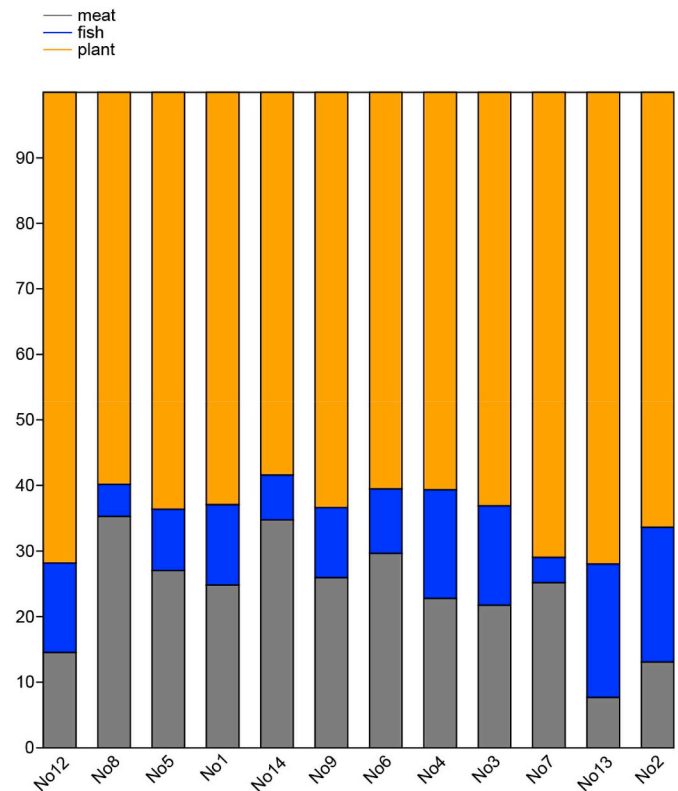

Fig. 9. Estimated overall food intake, median shares for terrestrial herbivore meat, fish, and plant foods; output of the simple routed FRUITS model. Samples arranged from oldest to youngest in ^{14}C age. FRUITS parameter specifications: Diet-collagen offsets: 5.0 ± 0.5‰ for both δ^{13}C and δ^{15}N; Dietary routing: δ^{13}C 75 ± 5% from dietary protein, 25 ± 5% from energy macronutrients, δ^{15}N 100% from dietary protein; Food isotope values: meat protein δ^{13}C −23.7 ± 0.5‰, δ^{15}N 7.7 ± 0.5‰, meat energy δ^{13}C −31.7 ± 0.5‰; fish protein δ^{13}C −27.3 ± 0.5‰, δ^{15}N 8.4 ± 0.5‰, fish energy δ^{13}C −35.3 ± 0.5‰; plant protein δ^{13}C −28.9 ± 0.5‰, δ^{15}N 1.7 ± 0.5‰, plant energy δ^{13}C −26.4 ± 0.5‰; Concentrations: meat 75 ± 3% protein; fish 80 ± 2% protein; plant 10 ± 1% protein; protein intake restricted to 10–40% of overall diet.

isotope values between cyprinids and pike). While the uncertainties in individual diet estimates are relatively large, the model output (e.g. Fig. 9) suggests that all the Late Mesolithic individuals consumed more terrestrial herbivore meat than fish (median estimates are typically meat 20–30% of overall diet and 50–60% of protein intake, fish 10–20% of overall diet and 20–30% of protein intake), whereas the roles of meat and fish were reversed in the older Mesolithic sample (No12) and the two Late Neolithic-Eneolithic samples (Nos 2, 13). However, this model applies the same isotope values for each food group in all periods, and if the high δ^{13}C values in pike only occurred in the Mesolithic, it would over-estimate fish consumption in the later periods. Fish or meat intake could also be over-estimated for No14, whose high δ^{15}N may include a nursing effect (breast milk is isotopically enriched relative to the mother's diet, and recently weaned children therefore give higher δ^{15}N values than older children with similar diets).

4.4. Chronological implications

The ^{14}C ages of human bones – particularly of hunter-gatherer-fishers – can be misleadingly old, due to dietary reservoir effects. There are many examples of large reservoir effects (e.g. 400–500 ^{14}C years) in human bones from prehistoric burials at inland sites, where closely associated terrestrial samples have also been dated, from the Danube
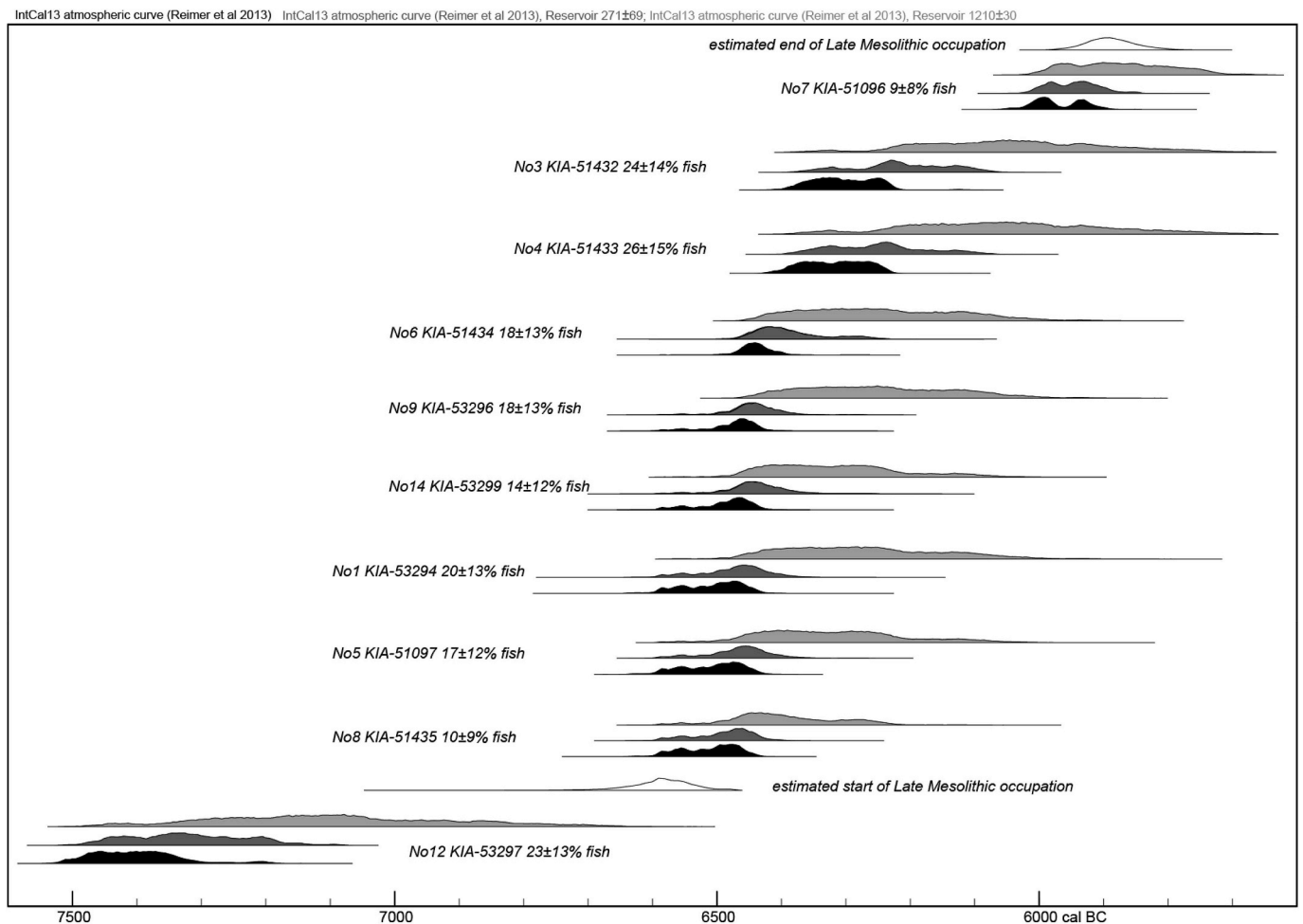
Fig. 10. Illustration of potential dating of Mesolithic human remains from Zamostje 2, based on the diet reconstructions produced by the basic FRUITS model, and different magnitudes of the local freshwater reservoir effect. Black: FRE = 0 (i.e. sample cannot be older than this date); dark grey: FRE = 271 ± 69y (minimum local FRE value, based on food-crust results in (Meadows et al., 2015), i.e. samples are probably more recent than this date); light grey: FRE = 1210 ± 30y (modern value at Friesack 4, Germany (Meadows et al., 2018b), selected as an example of a relatively large FRE; samples are probably older than this date). Sample labels show the FRUITS-estimated fish contribution to collagen carbon isotope values, which is greater than the fish contribution to overall food intake shown in Fig. 8, because fish is rich in protein. Results were calibrated with OxCal v4 (Bronk Ramsey, 2009), using OxCal's Reservoir function to apply the estimated FREs to the IntCal13 calibration curve (Reimer et al., 2013) and the Mix_Curves function to calibrate each radiocarbon result with the proportion of aquatic carbon shown in the sample label, as per e.g. (Meadows et al., 2016).

(Cook et al., 2001) to the Dnieper Rapids (Lillie et al., 2016), the middle Volga (Shishlina et al., 2017), the Baikal region (Schulting et al., 2014, 2015), and northern Russia (Wood et al., 2013). With (redeposited) disarticulated human remains, contextual dating can only reveal maximum reservoir effects, assuming that a human bone is not more recent than the layer in which it was found (Berzins et al., 2014).

When human bones may also be intrusive, we cannot use the dates of other samples to constrain potential dietary reservoir effects; instead, estimates of reservoir effects in fully aquatic species, and of the proportional contribution of aquatic species to the carbon content of human bone collagen, can be used to propose reservoir-effect corrections (e.g., Meadows et al., 2018b). This approach, unlike the regression-based approach permitted when paired samples of contemporaneous terrestrial and human bone can be dated (e.g., Schulting et al., 2014), requires accurate dietary reconstruction, which is problematic at Zamostje. Even if the simple FRUITS model discussed above is valid, it yields large uncertainties in the fish contribution to carbon-isotope values in each human bone (e.g., No4, 25 ± 15%). Moreover, there are currently no data for local freshwater reservoir effects (FRE) during the Mesolithic, which may have been significantly different between cyprinid and pike, considering their stable isotope signatures.

[14]C ages of food-crusts on pottery suggest that the local FRE at

Zamostje 2 in the Early Neolithic was moderate, but not negligible, with one fish-derived food-crust dating 271 ± 69 ^{14}C years older than a contemporaneous plant fibre (Meadows et al., 2015). While it is dangerous to extrapolate from a single sample, dietary reservoir effects at Zamostje 2 may have been relatively modest, compared to the examples listed above, particularly in the Late Mesolithic. Fig. 10 shows possible calibrated dates for individual samples (following e.g. Meadows et al., 2018b), assuming no FRE (black), a very modest local FRE (dark grey), or a much higher FRE (light grey), and the same individual diet reconstructions, derived from the simple FRUITS model. Whilst these FRE values, and indeed the diet reconstructions, are not robust estimates, Fig. 10 gives a more realistic idea of the minimum and maximum date of each sample than Fig. 3.

We therefore suggest that even if the local FRE was much greater than expected,

- No12, the humerus, predates the Late Mesolithic layer in which it was found.
- all other human bones, apart from No16 (Middle Neolithic?), No2 and No13 (Late Neolithic-Eneolithic) correspond in date to the Late Mesolithic occupation of Zamostje 2 (c.6500–5900 cal BC)
- only No7, the cut-marked cranium, apparently dates to the

beginning of the 6th millennium

- Nos 2, 5, and 7, which could not be securely attributed to different crania by morphometric analysis, must represent three different individuals on the basis of their ^{14}C ages
- given their ^{14}C ages and isotope results, Nos 3 and 4 may well be fragments of a single cranium, but cannot belong to the same individual as Nos 1 and 6 (which, however, could also belong to a single individual)
- taking into account morphometric and isotopic evidence, at least 10–11 human individuals are represented altogether, but if we omit those now attributed to Zamostje 1 (Nos 13 and 16), and the Eneolithic No2, only 7–8 Mesolithic individuals are represented at Zamostje 2
- most of the Late Mesolithic remains probably predate the peak of the 8.2ka cold event, dated by Vinther et al. (2006) to 6284-6190 cal BC, but Nos 3 and 4 may postdate this event, and No7 must.

5. Conclusions

This study presents ^{14}C ages and dietary stable isotopes (δ^{13}C and δ^{15}N) for 13 prehistoric human remains. Nine of these bones were dated to the Late Mesolithic period at Zamostje 2, one to the Middle Mesolithic, one (perhaps) to the Middle Neolithic, and two to the Late Neolithic-Eneolithic. We also report δ^{13}C and δ^{15}N for 63 animal bones (beaver, elk, reindeer, otter, bear, pike, cyprinid, and dog), and δ^{34}S for four human and four herbivore bones. δ^{13}C and δ^{15}N results should be reliable, but δ^{34}S values appear to be affected by contamination from the burial environment. Palaeodiet reconstruction is thus based on δ^{13}C and δ^{15}N only.

The unusual δ^{13}C and δ^{15}N values from Mesolithic pike bones are reflected in dietary stable isotopes from almost all the loose human remains dated to the Late Mesolithic phases of occupation, and in some of the dog bones. It is unclear why Mesolithic pike (and perhaps other fish, such as perch) have elevated δ^{13}C and lower δ^{15}N values compared to pike at other prehistoric sites in the northern European forest zone, or whether this phenomenon was more widespread and continued into later periods; there may be a localised environmental explanation, such as water depth, which affected isotope values in the main food sources for young pike during the Late Mesolithic. Its consequence is that human δ^{13}C and δ^{15}N values are difficult to interpret in terms of the dietary importance of fish or terrestrial herbivores, as the isotopic signature of fish is broadly defined and overlaps with that of terrestrial herbivores. An additional complication at Zamostje 2 is that dogs may have been consumed regularly by humans, and dogs themselves appear to have consumed fish regularly.

A simple Bayesian mixing model, based on the averaged isotope data from fish and terrestrial herbivores, suggests that in the Late Mesolithic, humans consumed more elk and beaver flesh than fish, whereas fish was more important than meat in the one Middle Mesolithic sample, and in two Late Neolithic-Eneolithic individuals. This interpretation assumes that faunal isotope values were the same in each phase, which may not be valid. Our Middle Mesolithic and Late Neolithic-Eneolithic results are compatible with the δ^{13}C and δ^{15}N values and proposed dating of five prehistoric individuals from two nearby sites analysed in a previous study (Iacumin et al., 2004).

One Late Mesolithic cranial fragment, No7, bears clear cut-marks, demonstrating deliberate post-mortem manipulation, possibly in order to use it as a bowl or cup. Isotopically, this individual is unique, having apparently had an almost completely terrestrial diet, and it may therefore be anomalous in this period, both at Zamostje 2 and in the forest zone in general. It is also almost the only human bone at Zamostje 2 which was not apparently older than the cultural layer in which it was found. No7 therefore appears to have been a freshly used and discarded artefact, whereas skull fragments without cut-marks may be derived from burials upstream of the site, which were eroded gradually over the course of the 6th millennium, with a few fragments becoming trapped

in Mesolithic and Neolithic layers at Zamostje 2. Skull fragments are particularly prone to fluvial transport (Turner et al., 2002).

Nevertheless, these burials apparently coincided with the later-7th millennium occupation at Zamostje 2, and in dietary terms they appear to be local. Although Zamostje may have become a more specialised fishing site in later phases, the broad-based diets of Mesolithic inhabitants are consistent with the model of Brown et al. (2013), in which floodplain sites are predicted to provide hunter-gatherer-fishers access to the widest range of food resources, providing sufficient amounts of all essential nutrients throughout the year, and thus permitting long-term survival in the absence of sophisticated food storage technologies.

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