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ORIGINAL PAPER

Reconstructing Subneolithic and Neolithic diets of the inhabitants of the SE Baltic coast (3100–2500 cal BC) using stable isotope analysis

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Abstract We present 9 accelerator mass spectrometry (AMS) dates and 41 carbon and nitrogen stable isotope measurements on bone and tooth collagen from the Šventoji Subneolithic/Neolithic sites and the Benaičiai cemetery, both in NW Lithuania. These data have led to a revised chronology and to the creation of a comprehensive stable isotope baseline for the Subneolithic and Neolithic periods at the SE Baltic coast. The Benaičiai cemetery has been AMS redated from the Late Bronze Age to the Neolithic, i.e., 2600/2500 cal BC. After a freshwater radiocarbon effect (FRE)/marine radiocarbon effect (MRE) correction to the AMS dates of isolated human bones found at the Šventoji sites, a date range of 3100–2600 cal BC was established. Stable isotope data obtained from isolated human bones from Subneolithic coastal sites indicate that these originated from a local "lagoonal" people who relied heavily on freshwater fish species despite the proximity to the Littorina Sea. Seals and terrestrial animals were only of secondary importance in terms of diet. A non-routed dietary model, with zooarchaeological priors included, created with the Bayesian package FRUITS gave results that were consistent with expected FRE/MRE offsets. Stable isotope data of two Benaičiai graves indicate a sharp dietary shift towards terrestrial protein that occurred between 2700 and 2500 cal BC in the Šventoji River basin. This is contemporaneous with the arrival of both Corded Ware Culture stockbreeders and the beginning of a natural and significant reduction in the productivity of lagoonal lake ecosystems.

Keywords SE Baltic · Carbon and nitrogen stable isotopes · Subneolithic · Neolithic · Diet

Introduction

The mode of subsistence followed by Subneolithic (=ceramic Mesolithic) and Neolithic coastal groups within the Baltic Sea region remains a topic of debate. Several researchers agree that Ertebølle populations in the west Baltic relied exclusively on wild food resources, mainly aquatic, while a dramatic change in diet towards terrestrial foods occurred simultaneously with cultural changes occurring ca. 4000 cal BC (e.g., Richards et al. 2003; Fischer et al. 2007; Sørensen 2014). However, there are also arguments for a more gradual change and for a chronological overlap of Mesolithic and Neolithic cultures (e.g., Brinch Petersen 2015). The Southeast Baltic experienced a different neolithization trajectory with a much later emergence of a Neolithic culture (3200–2700 cal BC) accompanied by the formation of economies of mixed type (e.g., Rzucewo Culture). A Neolithic culture was established at the Curonian Lagoon at ca. 3200 cal BC and only ca. 500 years later advanced 50 km northwards into the Šventoji paleolagoon (Piličiauskas

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2016). Zooarchaeological evidence reveals a high reliance on both marine and freshwater foods during the Subneolithic and during at least first half of the Neolithic (Żurek 1954; Makowiecki 2003; Rimantienė 2005; Heron et al. 2015). However, no stable isotope analyses on human bone collagen have been previously conducted for the SE Baltic as it has been generally assumed that there are no Stone Age cemeteries on the SE Baltic coast. Furthermore, isolated human bones found within the cultural layers of Subneolithic/Neolithic wetland sites (3100–2500 cal BC) have not been recognized as potential material for isotopic paleodiet studies (Antanaitis-Jacobs et al. 2009).

In 2014–2015, the chronology of the Benaičiai cemetery graves, as well as of the isolated human bones found at Šventoji Subneolithic/Neolithic sites, both located in NW Lithuania, SE Baltic (Fig. 1), were re-examined. In addition, stable carbon and nitrogen isotope analyses were conducted on the human remains and on a wide variety of zooarchaeological remains recovered at Šventoji Subneolithic sites to construct a local food-web isotopic baseline. Marine (MRE) and freshwater radiocarbon effects (FRE) for the Šventoji region have recently been studied (Piličiauskas and Heron 2015) allowing to test the accuracy of isotope-based diet reconstruction from known human dietary FRE/MRE offsets. A similar recent study

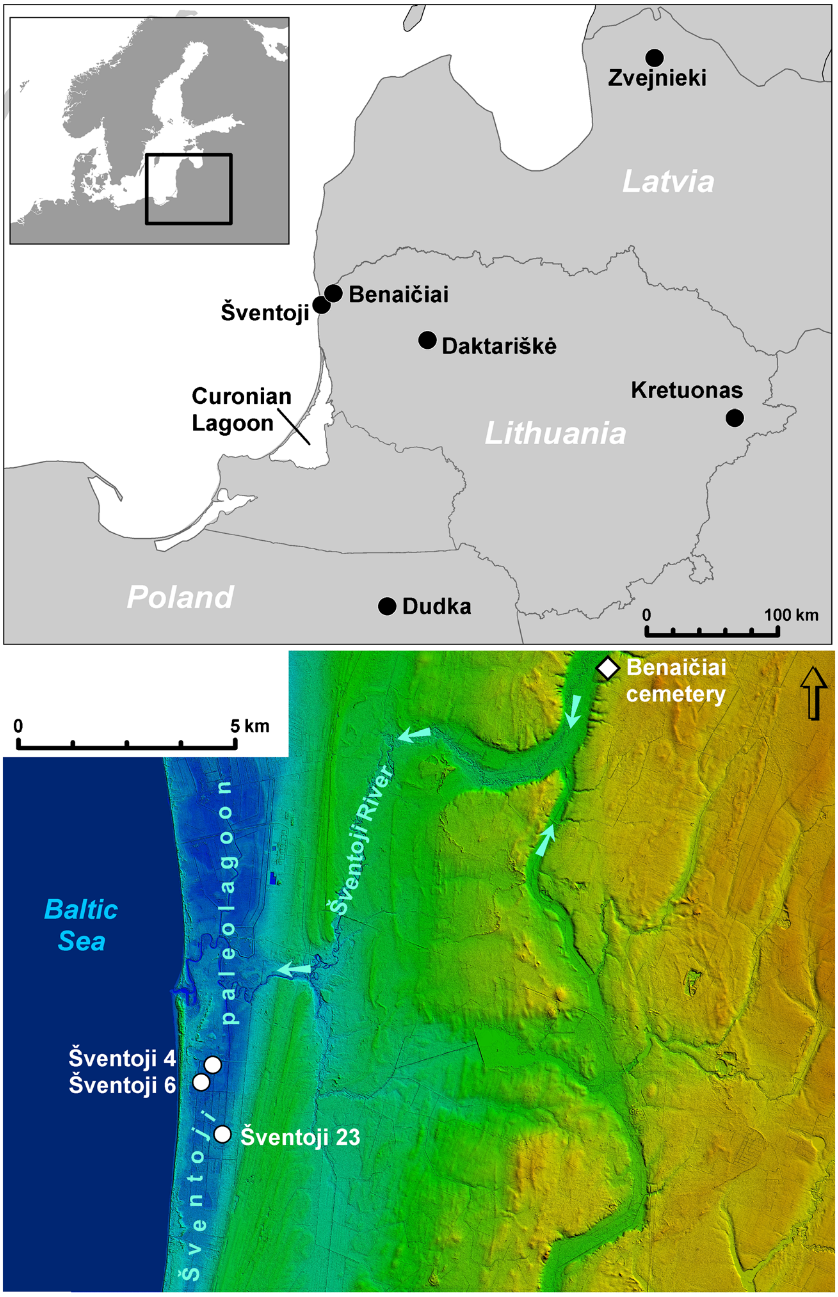

Fig. 1 Location of studied and referenced Mesolithic-Neolithic sites in the SE Baltic. A shaded relief map shows the lower reaches of the Šventoji River based on LIDAR data

provided satisfactory results for the Neolithic cemetery of Ostorf located in northern Germany (e.g., Fernandes et al. 2015).

Sites and materials

The Benaičiai cemetery (NW Lithuania, Fig. 1) is located 10 km from the Baltic Sea coast (Fig. 1). As no dramatic changes in relative sea level have occurred in the Šventoji region during the last 5000 years, it is expected that during the Neolithic period, the distance to the sea was similar to that of present day (Piličiauskas et al. 2015). During 4000–2500 cal BC, Benaičiai was connected to the Šventoji lagoonal sites by the Šventoji River which has a modern length of 68 km (Fig. 1). Benaičiai is a site with structures and artifacts assigned to different chronologies and containing several cremated and inhumation graves. The grave (no. 3) of a 0–1-year-old infant containing a flint blade, a goat pelvis bone, and a bone awl was dated to the Late Bronze Age, i.e. 910–800 cal BC (Merkevičius 2005). Another inhumation (grave No. 1), heavily damaged during gravel extraction, was of a > 40 year old female who was most likely buried in a crouched position together with a bone awl and 3 or 4 amber pendants (Merkevičius 2002). Grave artifacts and burial customs at Benaičiai are typically Neolithic, casting doubt on the original chronology of the graves. Both of these skeletons (Nos. 1 and 3) were subjected to AMS radiocarbon dating and stable isotope analysis in this study.

At Šventoji (NW Lithuania, Fig. 1) isolated human bones were found during extensive archeological excavations of waterlogged refuse layers of Subneolithic and Neolithic fishing stations as well as from dwelling sites dating to 3100–2500 cal BC. Sites were situated in the shallow water near to the shoreline and in the deepest parts of the ancient lagoon which was filled with sediments and overgrown between 2400 and 2000 cal BC. The lagoon was fed with freshwater by the Šventoji River.

Šventoji 4 is a key site for studying cultural change and the study of aquatic radiocarbon reservoir effects given the excellent preservation of artifacts and ecofacts including organic materials within the freshwater gyttja. This site was excavated extensively between 1967 and 2006 (Juodagalvis and Simpson 2000; Rimantienė 2005). According to data from the newest research in 2014, Šventoji 4 has two Subneolithic and one Neolithic (Globular Amphora Culture (GAC)) horizons dating to 3110/3000–3020/2930, 2800/2720–2720/2650, and 2720/2650–2700/2620 cal BC, respectively (Piličiauskas 2016). These horizons were formed by human debitage, including fishing and boating equipment that was abandoned directly at the fishing stations and perhaps transported there intentionally from distant onshore dwelling sites. Only a single piece of a human skull, from a >50-year-old male, is known from a total excavation area of 2254 m^2. The skull fragment was found in the shallowest part of the trench where Subneolithic and Neolithic horizons are stratigraphically indistinguishable.

The Šventoji 6 site was located 300 to 500 m from the Šventoji 4 site (Fig. 1). It contains similar materials dating to the same time period as those from the Šventoji 4 site. However, in the Šventoji 6 site, Subneolithic and Neolithic artifacts are mixed within the same horizon situated on a shoal part of the lagoon instead of a deep bed. During 1982–1988 and 1997, an area of 2001 m^2 was investigated at Šventoji 6 (Juodagalvis and Simpson 2000; Rimantienė 2005). Only two human bones were found, a fragment of a maxilla and a metacarpal. Both, however, were not mentioned within early publications and were identified only recently.

Unlike the two Šventoji sites described previously, the Šventoji 23 site is an onshore dwelling site, although with a refuse layer deposited at the littoral immediate adjacent to a dwelling area with wooden piles and fireplaces (Fig. 1). An area of 1268 m^2 was investigated during 1970–1971. Excavations of a waterlogged refuse layer at Šventoji 23 yielded the most valuable human skeletal material—two mandibles and one maxilla. These belong to a 25–35-year-old male, an adult of unknown age, and a 7–11-year-old child. Bone and molar teeth were subjected to carbon and nitrogen analysis. The site contains pointed base pottery which is very similar to the Subneolithic vessels at Šventoji 4 dated to 3100–2700 cal BC. However, some of the radiocarbon dates from Šventoji 23 are much younger and therefore conflicts with the typological date for this site (Rimantienė 2005). To address this discrepancy, a burnt hazelnut shell, charcoal from several fireplaces, and human bones were radiocarbon dated.

Šventoji 26 is a Subneolithic dwelling site dated to 3900–2600 cal BC according to pottery typology (Piličiauskas 2016). Only one human bone fragment, a femoral diaphysis, was recovered from the site. This bone was subjected to stable isotope analysis and AMS radiocarbon dating. This bone was not described or identified in previous publications (e.g., Rimantienė 2005).

In total, human bones and teeth from seven individuals[1] from Šventoji Subneolithic/Neolithic sites were analyzed in this study. In addition, animal and fish bones found at the same or synchronous sites and not treated with any preservatives were analyzed for the establishment of a local food-web isotopic baseline. To avoid misleading interpretations caused by diachronic changes of stable isotopes ratios it is essential to use local and synchronous humans and animal bones in isotope-based diet reconstruction (Hedges and Reynard 2007). In addition to already published stable isotope results of 32 Subneolithic animals, fish, and birds at Šventoji (Antanaitis-Jacobs et al. 2009; Heron et al. 2015), we

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[0] Including AMS-undated humans due to poor collagen preservation, as well as individuals AMS dated to the modern period.

analyzed 56 new samples including several modern fish samples from the adjacent Curonian lagoon. Modern fish samples were analyzed in order to understand the potential ecological differences between the Šventoji and Curonian ancient lagoons as no prehistoric fish bones were available from the latter.

Methods

For analysis of carbon and nitrogen stable isotopes, after a lipid extraction using a 2:1 chloroform/methanol mix, bone collagen was extracted using the method described in Longin (1971) with some modifications (DeNiro and Epstein 1978; Chisholm et al. 1983), while dentin collagen extraction followed the procedure outlined by Wright and Schwarcz (1999). Stable isotope analysis was performed at the Colorado Plateau Stable Isotope Laboratory (CPSIL) using a Thermo-Electron DELTA V Advantage isotope ratio mass spectrometer with a CONFLO III using a Carlo Erba NC2100 Elemental Analyzer. The standard for δ^{15}N is AIR (atmospheric nitrogen), and the standard for δ^{13}C is Vienna Pee Dee Belemnite (VPDB). Precision of analysis was determined by completing duplicate sample analyses (10%), which for δ^{13}C was ±0.09‰, and for δ^{15}N was ±0.07‰. Accuracy was assessed using a laboratory standard (NIST peach leaves), which gave an average δ^{13}C value of −26.17 ± 0.03‰ and an average δ^{15}N value of 1.67 ± 0.01‰ for 11 analyses.

A non-weighted offset-dependent concentration-independent protein diet model was created using the Bayesian statistical package FRUITS (Fernandes et al. 2014) in order to obtain numeric estimates on the dietary protein contributions from lagoonal fish (freshwater species), marine food (almost exclusively seals), and terrestrial animals (herbivores and boars) to human bone collagen at the Šventoji Subneolithic sites (Electronic supplementary material no. 1). Animal collagen isotopic values were taken as reference for food values and as animal food collagen to consumer collagen offsets (Table 1). Only two isotopic proxies ($\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$) were included in the model. Generated model estimates are represented as 68% credible intervals.

AMS radiocarbon measurements were made at the Poznań Radiocarbon Laboratory. All wood or charcoal samples were pretreated using the acid-alkali-acid (AAA) method described by Brock et al. (2010). For the bones, extraction of collagen was performed using the methods proposed by Longin (1971), as described previously, with additional modifications (Piotrowska and Goslar 2002). The extracted collagen was ultrafiltered using precleaned Vivaspin™ 15 MWCO 30 kD filters (Brown et al. 1988; Bronk Ramsey et al. 2004). The same skeletal material was sampled for AMS radiocarbon dating and EA-IRMS, although different extraction methods were used for each.

All dates in this study were calibrated using the OxCal 4.2 software and IntCal13 atmospheric calibration curve (Bronk Ramsey 2009; Reimer et al. 2013). Dates are presented with a 68.2% probability range when calibrated.

Results

Fourteen human and forty-six animal samples were analyzed for stable isotopes, and 39 of these (13 humans and 26 animals) yielded sufficient collagen for analysis. These samples include seven humans (five of them were sampled several times), seven fish (including four modern), three seals, three dogs, and twelve other terrestrial mammals. Two individuals from the Benaičiai cemetery were also sampled and analyzed twice unintentionally, and repeated values are also presented, although mean values were used when discussing diet. All results including previously published stable isotope values for the Šventoji region are given in Table 2.

For fresh bone samples, the average collagen yield is 20% to 25% collagen by weight (Schoeninger et al. 1989). The minimum acceptable collagen yield for archeological samples varies from values greater than 1% (White and Schwarcz 1989; White et al. 1993), greater than 2% (DeNiro and Weiner 1988), and more conservative values above 5–6% (Schoeninger and DeNiro 1982; Tuross et al. 1988). The minimum threshold value used for this research is 2%, following DeNiro and Weiner's (1988) study, although values of greater than 1% were also considered if other indicators signified good collagen preservation.

Other measures of collagen preservation include concentrations of carbon (%C) and nitrogen (%N) (Ambrose 1990), and atomic C/N ratios (DeNiro 1985; Katzenberg 2008). Based on values from modern animals, acceptable %C and

Table 1 Bone collagen δ^{13}C and δ^{15}N values and offsets between food and consumers used for dietary modeling. The offset value for $\delta^{13}C_{collagen}$ has been taken from Bocherens and Drucker (2003) while the difference between wolf and mean value of herbivores and boars δ^{15}N value was taken as reference for the offset value for $\delta^{15}N_{collagen}$

Food group	$\delta^{13}C_{collagen}$	$\delta^{15}N_{collagen}$	Trophic enrichment for $\delta^{13}C_{collagen}$	Trophic enrichment for $\delta^{15}N_{collagen}$
Freshwater fish	−21.6 ± 0.9 (*n* = 5)	11.2 ± 1.2 (*n* = 5)	1 ± 0.2	4.1 ± 0.9
Seals	−16.4 ± 0.6 (*n* = 15)	12.4 ± 1.1 (*n* = 15)		
Herbivores and boars	−22.7 ± 0.9 (*n* = 18)	4.9 ± 0.9 (*n* = 18)		

Table 2 Carbon and nitrogen stable isotope results and supportive information (–Subneolithic (SBN), Neolithic (NEO), Early Bronze Age (EBA), and modern (MOD))

No.	Age	Site	Species	Description	δ^{13}C	δ^{15}N	C/N	% collagen	%C	%N	Reference
1	NEO	Benaičiai	Human	Grave no. 1, female >40, mandible	−21.2	9.8	3.2	5.8	37.4	13.6	This study
2	NEO	Benaičiai	Human	Grave no. 1, mandible, repeated measurements	−21.2	9.9	3.2	5.1	37.5	13.5	This study
3	NEO	Benaičiai	Human	Grave no. 3, infant 0–1, skull	−21.3	10.9	3.2	15.1	44.5	16.1	This study
4	NEO	Benaičiai	Human	Grave no. 3, skull, repeated measurements	−21.4	10.6	3.3	12.9	39.7	14.2	This study
5	SBN/NEO	Šventoji 2/4	Human	Skull	−20.1	15.6	3.2	6.6	42.3	15.3	This study
6	SBN	Šventoji 6	Human	Maxilla	−19.5	14.1	3.3	9.6	41	14.2	This study
7	SBN	Šventoji 23	Human	Grave 1, M1 tooth	−19.3	15.1	3.3	15.3	44.8	16.1	This study
8	SBN	Šventoji 23	Human	Grave 1, mandible	−18.9	15.0	3.3	17.1	44.9	15.7	This study
9	SBN	Šventoji 23	Human	Grave 1, M3 tooth	−18.1	15.6	3.2	13.9	44.5	16.4	This study
10	SBN	Šventoji 23	Human	Grave 2, M1 tooth	−19.6	16.0	3.3	9.5	41.8	14.7	This study
11	SBN	Šventoji 23	Human	Grave 2, maxilla	−20.3	14.4	3.4	17.5	41.8	14.4	This study
12	SBN	Šventoji 23	Human	Grave 3, M1 tooth	−21.2	15.3	3.2	10.3	42.9	15.5	This study
13	SBN	Šventoji 23	Human	Grave 3, mandible	−21.0	15.0	3.3	12.3	33.7	11.8	This study
14	SBN	Šventoji 26	Human	Femur	Insufficient collagen			0.2			This study
15	SBN	Šventoji 6	Dog (*Canis lupus familiaris* L.)	Skull, adult	−20.3	13.2	3.3	11.7	43	15.4	This study
16	SBN	Šventoji 6	Dog (*C. lupus familiaris* L.)		−20.7	13.3	3.4				Antanaitis-Jacobs et al. (2009)
17	SBN	Šventoji 23	Dog (*C. lupus familiaris* L.)		−19.2	12.8	3.6				Antanaitis-Jacobs et al. (2009)
18	SBN	Šventoji 43	Dog (*C. lupus familiaris* L.)	Mandibular P4, adult	−23.8	13.9	3.5	2.2	12.5	4.2	This study
19	MOD?	Šventoji 43	Dog (*C. lupus familiaris* L.)	Mandibular P4, adult	−16.6	13.4	3.3	0.8	41.1	14.7	This study
20	SBN	Šventoji 43	Dog (*C. lupus familiaris* L.)	Mandibular molar, adult	Insufficient collagen			0.2			This study
21	SBN	Šventoji 23	Wood grouse (*Tetrao urogallus* L.)		−21.9	2.2	3.6				Antanaitis-Jacobs et al. (2009)
22	SBN	Šventoji 2/4	Auroch/bison (*Bos primigenius* B./*Bison bonasus bonasus* L.)	Maxilla, adult	−22.6	5.1	3.1	19.2	39.8	15.0	This study
23	SBN	Šventoji 43	Auroch/bison (*B. primigenius* B./*B. bonasus bonasus* L.)	Metacarpus, adult	−23.0	5.6	3.7	1.7	28.7	9.0	This study
24	SBN	Šventoji 43	Auroch/bison (*B. primigenius* B./*B. bonasus bonasus* L.)	Calcaneus, adult	−22.4	3.4	3.3	2.9	24.0	8.6	This study
25	SBN	Šventoji 3	Beaver (*Castor fiber* L.)		−22.1	5.4	3.4				Antanaitis-Jacobs et al. (2009)
26	EBA	Šventoji 9	Beaver (*C. fiber* L.)	Femur, adult	−22.9	4.5	3.2	16.1	41.2	15.3	This study
27	SBN	Šventoji 43	Beaver (*C. fiber* L.)	Tooth, adult	Insufficient collagen			0.7			This study
28	SBN	Šventoji 43	Beaver (*C. fiber* L.)	Tooth, adult	Insufficient collagen			0.8			This study
29	SBN	Šventoji 1B	Elk (*Alces alces* L.)		−23.1	3.6	3.4				Antanaitis-Jacobs et al. (2009)
30	SBN	Šventoji 2/4	Elk (*A. alces* L.)		−23.6	4.9	3.3				Antanaitis-Jacobs et al. (2009)
31	SBN	Šventoji 43	Elk (*A. alces* L.)	Phalanx , adult	−23.5	4.4	3.3	1.8	37.4	13.1	This study
32	EBA	Šventoji 41B	Horse (*Equus ferus ferus* B./*E. ferus caballus* L.)	maxillary premolar/M, adult	−22.3	4.4	3.3	11.3	34	12.2	This study
33	SBN	Šventoji 43	Horse (*E. ferus ferus* B.)	Talus, subadult/adult	−24.7	5.7	3.5	1.0	25.7	8.5	This study
34	SBN	Šventoji 43	Horse (*E. ferus ferus* B.)	Tibia, adult	−23.2	4.9	3.2	12.2	39.8	14.6	This study
35	SBN	Šventoji 43	Roe deer (*Capreolus capreolus* L.)	Mandibular M2, adult	Insufficient collagen			0.8			This study
36	SBN	Šventoji 43	Roe deer (*C. capreolus* L.)	Maxillary M2, adult	Insufficient collagen			0.6			This study
37	SBN	Šventoji 43	Roe deer (*C. capreolus* L.)	Mandible, adult	−23.5	4.5	3.2	12.8	40.9	14.8	This study
38	SBN	Šventoji 1B	Boar/pig (*Sus scrofa scrofa* L./*Sus scrofa domesticus* L.)		−21.8	4.1	3.4				Antanaitis-Jacobs et al. (2009)
39	SBN	Šventoji 3	Boar/pig (*S. scrofa scrofa* L./*S. scrofa domesticus* L.)		−21.7	5.5	3.4				Antanaitis-Jacobs et al. (2009)
40	SBN	Šventoji 3	Boar/pig (*S. scrofa scrofa* L./*S. scrofa domesticus* L.)		−21.3	3.8	3.3				Antanaitis-Jacobs et al. (2009)
41	SBN	Šventoji 6	Boar/pig (*S. scrofa scrofa* L./*S. scrofa domesticus* L.)		−21.6	5.3	3.4				Antanaitis-Jacobs et al. (2009)
42	SBN	Šventoji 43	Boar/pig (*S. scrofa scrofa* L./*S. scrofa domesticus* L.)	Humerus, adult	−22.2	6.9	3.2	16.1	44.8	16.3	This study
43	SBN	Šventoji 43	Boar/pig (*S. scrofa scrofa* L./*S. scrofa domesticus* L.)	Scapula, >1 year	No peaks			1			This study
44	MOD?	Šventoji 43	Boar/pig (*S. scrofa scrofa* L./*S. scrofa domesticus* L.)	Mandibular M_2, adult	−18.3	11.2	3.6	1.7	14.6	4.9	This study
45	SBN	Šventoji 43	boar/pig (*S. scrofa scrofa* L./*S. scrofa domesticus* L.)	Talus, subadult/adult	−23.3	5.6	6.3	0.7	6.3	1.2	This study
46	SBN	Šventoji 3	Brown bear (*Ursus arctos* L.)		−21.4	4.5	3.3				Antanaitis-Jacobs et al. (2009)
47	SBN	Šventoji 6	Brown bear (*U. arctos* L.)		−20.9	4.4	3.5				Antanaitis-Jacobs et al. (2009)
48	SBN	Šventoji 43	Brown bear (*U. arctos* L.)	Mandibular M2, adult	−21.4	5.7	3.3	3.5	28.1	10.1	This study
49	SBN	Šventoji 3	Fox (*Vulpes vulpes* L.)		−18.5	11.4	3.4				Antanaitis-Jacobs et al. (2009)
50	SBN	Šventoji 43	Fox (*V. vulpes* L.)	Maxillary molar, adult	Insufficient collagen			0.9			This study
51	SBN	Šventoji 43	Fox (*V. vulpes* L.)	Maxillary molar, adult	Insufficient collagen						This study
52	SBN	Šventoji 52	Wolf (*Canis lupus lupus* L.)	Mandible, adult	−20.9	9.0	3.2	12.6	41	14.7	This study

Table 2 (continued)

No.	Age	Site	Species	Description	$\delta^{13}C$	$\delta^{15}N$	C/N	% collagen	%C	%N	Reference
53	SBN	Šventoji 2/4	Mallard (*Anas platyrhynchos* L.)		−24.8	7.2	3.3				Antanaitis-Jacobs et al. (2009)
54	SBN	Šventoji 23	Mallard (*A. platyrhynchos* L.)		−21.1	7.8	3.5				Antanaitis-Jacobs et al. (2009)
55	SBN	Šventoji 2/4	Perch (*Perca fluviatilis* L.)	Preopercular	−20.0	10.6	3.3	3.5	36.0	12.7	This study
56	SBN	Šventoji 2/4	Pike (*Esox lucius* L.)		−21.6	12.6	3.3				Antanaitis-Jacobs et al. (2009)
57	SBN	Šventoji 2/4	Pike (*E. lucius* L.)	Dentary	−22.1	9.5	3.3	2.3	38.5	13.8	This study
58	SBN	Šventoji 43	Pike (*E. lucius* L.)	Vertebrae	Insufficient collagen						This study
59	SBN	Šventoji 2/4	Pikeperch (*Sander lucioperca* L.)		−21.8	12.6	3.5				Antanaitis-Jacobs et al. (2009)
60	SBN	Šventoji 2/4	Pikeperch (*S. lucioperca* L.)	Dentary	−22.6	10.9	3.4	1.3	39.9	13.6	This study
61	SBN	Šventoji 2/4	Flounder (*Platichthys flesus* L.)		−16.6	11.6	3.3				Antanaitis-Jacobs et al. (2009)
62	SBN	Šventoji 23	Gray seal (*Halichoerus grypus* F.)		−16.5	12.7	3.5				Antanaitis-Jacobs et al. (2009)
63	SBN	Šventoji 43	Harp seal (*Phoca groenlandica* E.)	Humerus, adult	−16.9	11.7	3.4	2.0	23.7	8.2	This study
64	SBN	Šventoji 43	Harp seal (*P. groenlandica* E.)	Radius, adult	−19.5	11.2	4.9	1.8	7.3	1.8	This study
65	SBN	Šventoji 1B	Harbor seal (*Phoca vitulina* L.)		−15.5	13.1	3.3				Antanaitis-Jacobs et al. (2009)
66	SBN	Šventoji 2/4	Harbor seal (*P. vitulina* L.)		−16.1	12.0	3.4				Antanaitis-Jacobs et al. (2009)
67	SBN	Šventoji 6	Harp seal (*P. groenlandica* E.)		−16.6	13.3	3.4				Antanaitis-Jacobs et al. (2009)
68	SBN	Šventoji 43	Ringed seal (*Phoca hispida* S.)	Ulna, adult	−16.5	12.7	3.3	3.1	28.2	10.0	This study
69	SBN	Šventoji 1B	Ringed seal (*P. hispida* S.)		−16.5	11.1	3.4				Antanaitis-Jacobs et al. (2009)
70	SBN	Šventoji 2/4	Ringed seal (*P. hispida* S.)		−18.7	13.9	3.4				Antanaitis-Jacobs et al. (2009)
71	SBN	Šventoji 2/4	Ringed seal (*P. hispida* S.)		−15.8	12.4	3.3				Antanaitis-Jacobs et al. (2009)
72	SBN	Šventoji 6	Ringed seal (*P. hispida* S.)		−17.1	12.6	3.4				Antanaitis-Jacobs et al. (2009)
73	SBN	Šventoji 2/4	Seal (Phocidae)		−16.3	12.2	3.4				Antanaitis-Jacobs et al. (2009)
74	SBN	Šventoji 2/4	Seal (Phocidae)	Adult	−16.6	12.0	3.2		47.1	17	Heron et al. (2015)
75	SBN	Šventoji 2/4	Seal (Phocidae)		−17.7	10.6	3.4				Antanaitis-Jacobs et al. (2009)
76	SBN	Šventoji 2/4	Seal (Phocidae)	Adult	−16.3	15.5	3.4		48	16.6	Heron et al. (2015)
77	SBN	Šventoji 2/4	Seal (Phocidae)	Adult	−15.3	13.1	3.2		45.8	16.7	Heron et al. (2015)
78	SBN	Šventoji 3	Seal (Phocidae)	Tibia, adult	−15.6	11.3	3.2	23.7	40.6	15	This study
79	SBN	Šventoji 23	Otter[b] (*Lutra lutra* L.)		−16.5	13.8	3.4				Antanaitis-Jacobs et al. (2009)
80	MOD	Curonian Lagoon	Bream (*Abramis brama* L.)	Modern, caught in 2014, vertebrae	−24.3	12.0	3.2	16.2	44.7	16.3	This study
81	MOD	Curonian Lagoon	Pikeperch (*S. lucioperca* L.)	Mmodern, caught in 2014, vertebrae	−24.6[a]	15.2	4.2	12.5	47.7	13.3	This study
82	MOD	Curonian Lagoon	Vimba (*Vimba vimba* L.)	Modern, caught in 2014, vertebrae	−23.5	12.1	3.2	10.6	40.5	14.8	This study
83	MOD	Curonian Lagoon	Sea trout (*Salmo trutta trutta* L.)	Modern, caught in 2014, vertebrae	−19.1[a]	12.1	4.2	13.2	46.9	13.0	This study

[a] Due to a higher lipid content, as observed from C/N values, $\delta^{13}C$ values for the pikeperch and sea trout were normalized using the following equation after Post et al. (2007): $\delta^{13}C_{normalized} = (\delta^{13}C_{untreated}) + ((-3.32) + (0.99 \times C/N))$. These values were not, however, used for modeling

[b] This bone was classified as otter by Antanaitis-Jacobs et al. (2009). However, carbon and nitrogen stable isotope values raise doubts on the species identification as these match isotopic values observed for seals (Fig. 2)

%N ranges for archeological human bone collagen are 15% to 47% for %C and 5% to 17% for %N (Ambrose 1990). The acceptable range for atomic C/N ratios in an archeological collagen sample is 2.9 and 3.6 (DeNiro 1985). We note that modern fish bones, depending on species, can contain much higher lipid content, therefore potentially affecting C/N ratios. Although lipids were extracted for all bone samples, we applied the equation developed by Post et al. (2007) to correct for lipid effects on isotope values in aquatic tissues for those modern samples whose C/N values were above the acceptable range, indicating higher lipid content. C/N ratios and %C and %N values were given more consideration as indicators of preservation than collagen yield due to possible samples losses during preparation procedures. Thirty-six samples, 13 human and 23 animal, fall within an acceptable range of a reference C/N ratio between 2.9 and 3.6, and only these were further used in dietary modeling (Table 2). Two modern fish samples whose original C/N ratios were higher than the acceptable range were included in this study after the values were corrected for high lipid content.

All AMS radiocarbon dates obtained for the present study are listed in Table 3. One sample, however, the human bone from the Šventoji 26 site, did not yield sufficient collagen. The Benaičiai cemetery gave two Neolithic dates within a range of 2620–2490 cal BC. Two dates from the Šventoji sites appeared to be modern, while the remaining seven revealed ages relevant to Subneolithic and Neolithic materials uncovered at the same sites (Table 3).

Discussion

Animal stable isotope data and diets at Šventoji

The results from the present stable isotope research combined with previously reported analyses (Antanaitis-Jacobs et al. 2009; Heron et al. 2015) provide data on 21 species, excluding humans, for the Šventoji Subneolithic sites. In addition, we report isotopic data on some modern fish (from the adjacent Curonian Lagoon) and supposed historical animals (pig and dog from Šventoji 43 site) in order to better reconstruct the ancient food-web isotopic baseline (Fig. 2).

Subneolithic herbivores present bone collagen δ^{15}N values within a range of 3.4‰ to 5.7‰ at Šventoji. Bears and boars demonstrate almost identical trophic level with a single boar outlier having a considerably elevated δ^{15}N value (6.9‰).

Table 3 New AMS radiocarbon dates and sample descriptions for the Benaičiai cemetery and Šventoji sites

No.	Site	Researcher	Year of excavation	Date (BP)	% collagen	δ13C	Description
1	Benaičiai	Merkevičius	2000	Poz-66,923 (4025 ± 30)	1.9	−18	Grave no. 1, human mandible
2	Benaičiai	Merkevičius	2002	Poz-61,591 (4040 ± 30)	8.7	−17.7	Grave no. 3, human infant skull
3	Šventoji 4	Rimantienė	1993	Poz-61,577 (4330 ± 80)	2.7	−40.7	Human skull fragment
4	Šventoji 6	Rimantienė	1982–1988	Poz-71,524 (4655 ± 35)	7.4	−18.4	Human maxilla fragment, adult
5	Šventoji 6	Rimantienė	1982–1988	Poz-61,578 (290 ± 30)	2.5	−16.2	Human metacarpal
6	Šventoji 23	Rimantienė	1970–1971	Poz-61,579 (4580 ± 30)	11	−20.2	Grave 1. Human mandible, 25–35 year male
7	Šventoji 23	Rimantienė	1970–1971	Poz-61,581 (4740 ± 35)	12	−14.7	Grave 2. Human maxilla, adult
8	Šventoji 23	Rimantienė	1970–1971	Poz-61,582 (4730 ± 35)	7.7	−25.6	Grave 3. Human mandible, 7–11-year-old child
9	Šventoji 23	Rimantienė	1970	Poz-71,985 (4380 ± 35)			Charcoal among Late Subneolithic ceramics
10	Šventoji 23	Rimantienė	1970–1971	Poz-66,908 (145 ± 30)			Partly burned pine branch from hearth no. 6
11	Šventoji 23	Rimantienė	1971	Poz-66,907 (4350 ± 35)			Burnt hazelnut shell
12	Šventoji 26	Juodagalvis	2003	Not enough collagen, 0.2%N and 3.8%C			Human femur

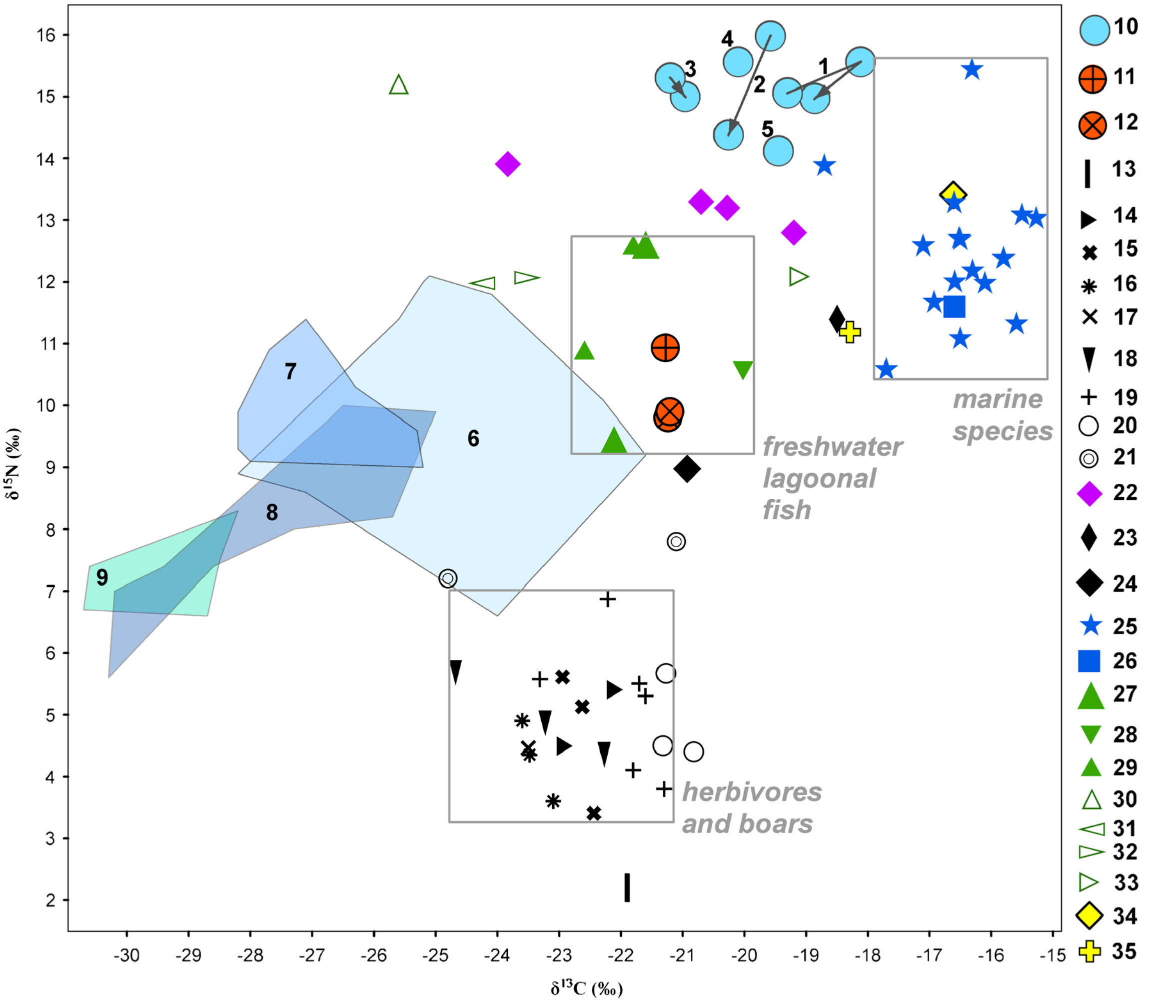

Fig. 2 Carbon and nitrogen stable isotope values of humans and animals at Šventoji, Benaičiai and modern Curonian Lagoon plotted against to Latvian and Polish freshwater fish data from inland lakes and rivers. Data from Antanaitis-Jacobs et al. (2009) has also been included. *1*, Šventoji 23 "grave 1" (M1–M3 mandible); *2*, Šventoji 23 "grave 2" (M1 maxilla); *3*, Šventoji 23 "grave 3" (M1 mandible); *4*, Šventoji 4 (skull); *5*, Šventoji 6 (maxilla); *6*, Central Poland Iron Age freshwater fish (Reitsema et al. 2010); *7–9*, Subneolithic fish from Riņņukalns in N Latvia: freshwater predatory, eels, and freshwater cyprinids, respectively (Schmölcke et al. 2015); *10*, Šventoji Subneolithic humans; *11*, Benaičiai Neolithic infant; *12*, Benaičiai Neolithic female; *13*, wood grouse; *14*, beaver; *15*, auroch/bison; *16*, elk; *17*, roe deer; *18*, horse; *19*, boar; *20*, brown bear; *21*, anatidae; *22*, dog; *23*, fox; *24*, wolf; *25*, seals; *26*, flatfish; *27*, pike; *28*, perch; *29*, pikeperch; *30–33*, modern pikeperch, bream, vimba, and sea trout from the Curonian Lagoon; *34* and *35*, eighteenth–nineteenth-century AD (?) dog and pig

Isotope signals (δ^{13}C −18.3‰; δ^{15}N 11.2‰) indicative of a strong marine dietary component are observed in a molar tooth of boar or pig found at the Šventoji 43 Subneolithic site (Fig. 3). However, it most likely originated from a historical village instead of a Stone Age settlement, as it was found within macroscopically undisturbed peat, although only slightly below a plowed zone. The only carnivore sample is a wolf from the Šventoji 52 site, exhibiting a δ^{15}N value (9‰) one trophic position above herbivores. Isotopic results are only available for predatory fish from the Šventoji paleolagoon (Šventoji 4, a lower Subneolithic horizon B), consisting of pike, pikeperch, and perch having a δ^{13}C mean value of −21.6 ± 1‰ and a δ^{15}N mean value of 11.2 ± 1.4‰ ($n = 5$). Following a δ^{13}C correction of 2‰ for the *Suess effect* (Marino and McElroy 1991; Rubino et al. 2013), the δ^{13}C signals of modern bream and vimba (−24.6‰ and −23.5‰) caught at the still existing Curonian Lagoon, ca. 50 km southward from Šventoji, fall within a range common for freshwater species at the Šventoji paleolagoon (−22.6‰ to −20‰). If compared with stable isotope signals of inland freshwater species in Poland and especially in Latvia, less negative δ^{13}C values are evident for the lagoons (Fig. 2). Most likely, the sea fingerprint on lagoonal fish is caused by a positive correlation between δ^{13}C and water salinity (Robson et al. 2015). Seals (ringed, harp, harbor, and gray) do not demonstrate significant inter-species dietary differences. The only marine fish with known stable isotope values in Šventoji is a flounder (δ^{13}C −16.6‰; δ^{15}N 11.6‰) and these are similar to that observed in seals. δ^{13}C collagen values of dogs (−16.6‰ to −23.8‰) indicate that they were fed, or ate freshwater fish,

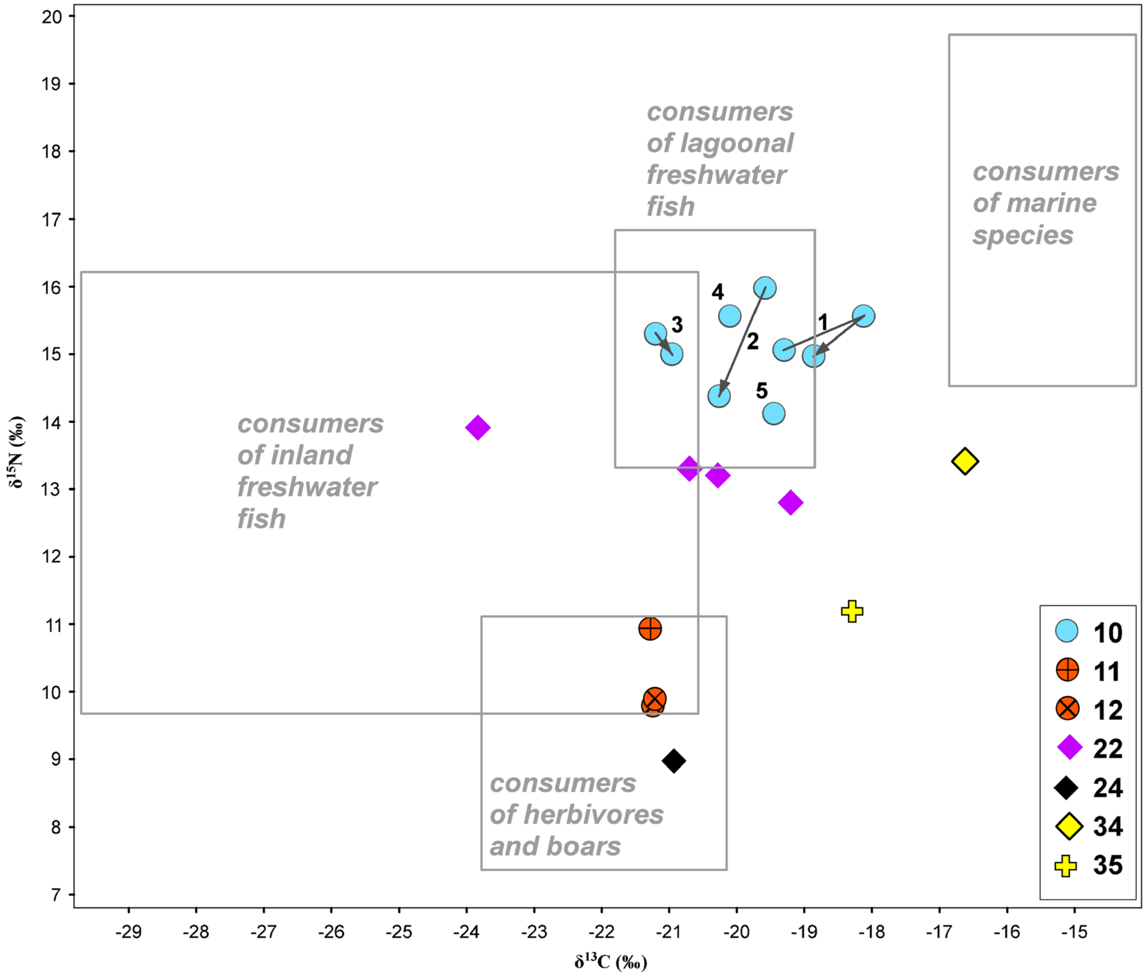

Fig. 3 Šventoji and Benaičiai human stable isotope collagen values plotted against the expected consumers' areas (*gray squares*) with a trophic level shift of approximately 1‰ for δ^{13}C and 4.1‰ for δ^{15}N. Symbols are explained in Fig. 2

and some of them probably had access to marine foods (e.g., δ^{13}C −16.6‰ and −19.2‰). A single dog from Šventoji 43 Subneolithic site (δ^{13}C −23.8‰; δ^{15}N 13.9‰) most probably ate only inland freshwater fish rather than lagoonal fish (Fig. 3), and it might be therefore considered of non-local origin. Extraordinary variability in dogs' stable isotope values has also been documented for the Zvejnieki Mesolithic-Subneolithic cemetery in northern Latvia (Eriksson and Zagorska 2003). The dog molar from the Šventoji 43 site with the strongest marine stable isotope signals (δ^{13}C −16.6‰; δ^{15}N 13.4‰) most likely originated from the same historical village as the previously described pig molar (δ^{13}C −18.3‰; δ^{15}N 11.2‰). Both teeth were found in the same upper horizon of the cultural layer with some later intruded objects.

Subneolithic human protein diet at Šventoji

When reconstructing Subneolithic human protein diet, it is necessary to determine the isotopic offsets between consumer's collagen and their diet. While δ^{13}C usually has a +1‰ value along higher trophic levels, δ^{15}N offsets may vary between +3‰ and +5‰ (Hedges and Reynard 2007 and references cited therein). The δ^{15}N value of 9‰ for the wolf is 4.1‰ higher than the mean value of local herbivores and boars at Šventoji (4.9 ± 0.9‰, *n* = 18). The 4.1 ± 0.9‰ value was taken as reference for human collagen δ^{15}N offset towards dietary protein (Fig. 3).

Human bone collagen stable isotope signals (ranging from −21‰ to −18.8‰ δ^{13}C and from 14.1‰ to 15.6‰ for δ^{15}N) confirm that freshwater fish species from the Šventoji paleolagoon represented the main source of protein for Šventoji coastal people during Subneolithic (Fig. 3). These data offer corroborating evidence to support the zooarchaeological evidence consisting of an extraordinarily large number of freshwater fish bones found at some fishing and dwelling sites (Stančikaitė et al. 2009; Piličiauskas 2016), as well as with aquatic biomarkers and single compound stable isotope data from food residues in ceramic vessels (Heron et al. 2015). Zooarchaeological data suggests that seals and forest animals may have contributed to the diet of the Šventoji peoples but would not represent a major part of the diet given that less negative δ^{13}C values would be expected for purely

Table 4 Estimates by the FRUITS non-routed model no. 1 and FRE/MRE corrections under scenarios no. 1 and 2

	Šventoji 23–1		Šventoji 23–2		Šventoji 23–3		Šventoji 4		Šventoji 6	
	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Estimates with no priors										
Freshwater fish	34	20	49	22	62	19	56	20	37	21
Seals	47	15	25	14	17	11	28	15	37	15
Terrestrial animals	18	12	26	15	21	14	16	11	26	14
Estimates with priors (fish intake) > (seal intake) > (animal intake)										
(a) Freshwater fish	58	12	65	15	72	14	67	14	59	14
(b) Seals	31	9	23	9	19	9	23	9	28	9
(c) Terrestrial animals	12	8	12	8	9	7	10	7	14	8
(d) AMS date, BP	4580	30	4740	35	4730	35	4330	80	4655	35
Scenario no. 1 (FRE = 320 ± 42 years; MRE = 190 ± 43 years)										
(e) FRE offset (FRE × a/100)	190	45	210	55	230	54	210	61	190	51
(f) MRE offset (MRE × b/100)	60	22	40	20	40	19	40	20	50	21
(g) FRE/MRE offset (e + f)	250	50	250	59	270	57	250	64	240	55
(h) Corrected age, BP (d–g)	4330	58	4490	69	4460	67	4100	100	4420	65
Corrected age, cal BC (68.2%)	3020–2900		3340–3100		3330–3025		2870–2500		3310–2920	
Scenario no. 2 (FRE = 510 ± 72 years; MRE = 190 ± 43 years)										
(i) FRE offset (FRE × a/100)	300	74	330	90	370	88	340	86	300	83
(j) MRE offset (MRE × b/100)	60	22	40	20	40	19	40	20	50	21
(k) FRE/MRE offset (i + j)	360	77	370	92	410	90	380	88	350	86
(l) Corrected date, BP (d–k)	4220	83	4370	98	4320	97	4000	120	4310	93
Corrected age, cal BC (68.2%)	2910–2670		3310–2890		3260–2760		2850–2310		3095–2760	

FRE and MRE used from Piličiauskas and Heron (2015). For FRE/MRE corrections, only estimates from the model with priors were used

seal consumers and much lower δ^{15}N would be expected for purely forest hunters.

According to the FRUITS model, lagoonal freshwater fish contribution mean values vary from 34 ± 20% to 62 ± 19% among five individuals, and in three out of five cases are higher than estimated marine contributions which vary from 17 ± 11% to 47 ± 15% (Table 4; Fig. 4a). Terrestrial animal protein contribution to human bone collagen was estimated to be between 16 ± 11% and 26 ± 15%. One approach to reduce the ambiguity in estimates is to introduce prior information namely from archeological or zooarchaeological data. At Šventoji, the significance of lagoonal fishing is attested by numerous findings of fishing equipment, including those for highly productive mass catches, i.e., fish weirs and nets. Enormous numbers of freshwater fish bones have been recovered from fishing stations conglomerating into densely packed horizons and spreading several hundred meters in length alongside underwater slopes (e.g., Šventoji 4; Rimantienė 2005; Piličiauskas et al. 2012). Another observation emerging from zooarchaeological studies is that seal bones outnumber terrestrial animal bones in every Subneolithic site at Šventoji (Stančikaitė et al. 2009; Piličiauskas 2016). Therefore, prior information established from zooarchaeological data was added to the model. It may be assumed that the contribution from the lagoonal freshwater fish to human collagen was bigger than that of terrestrial animals, as well as than that of the seals. Another zooarchaeological prior added to the model was that the dietary contribution from seals to human collagen is bigger than that of the terrestrial animals (see Electronic supplementary material no. 1 for all parameters). Zooarchaeological data provides information on group diet; however, since the Šventoji individuals show similar isotopic values, the applied prior are likely valid. According to estimates generated employing the model that included the priors, lagoonal fish protein contributed from 58 ± 12% to 72 ± 14% to human collagen, seals from 19 ± 9% to 31 ± 9%, and terrestrial animal from 9 ± 7% to 14 ± 8% (Fig. 4). Comparison between of model estimates generated with and without priors shows that the priors increased freshwater protein contribution mean values by 10–24% while diminishing terrestrial animal protein contributions by 6–14%. The priors altered marine protein contribution values significantly only in two cases (Šventoji 23, ind. 1 and Šventoji 6), lowering them by 16% and 9%, respectively (Table 4).

The sensitivity of model estimates for the non-routed FRUITS model was tested by varying diet-to-consumer offset values. Varying the offset from diet to consumer for $\delta^{15}N_{collagen}$ by 1‰ resulted in a 2% change in aquatic contribution towards human collagen, while a change of diet to consumer offset for $\delta^{13}C_{collagen}$ by 0.5‰ represented a 1% change in the aquatic contribution towards human collagen

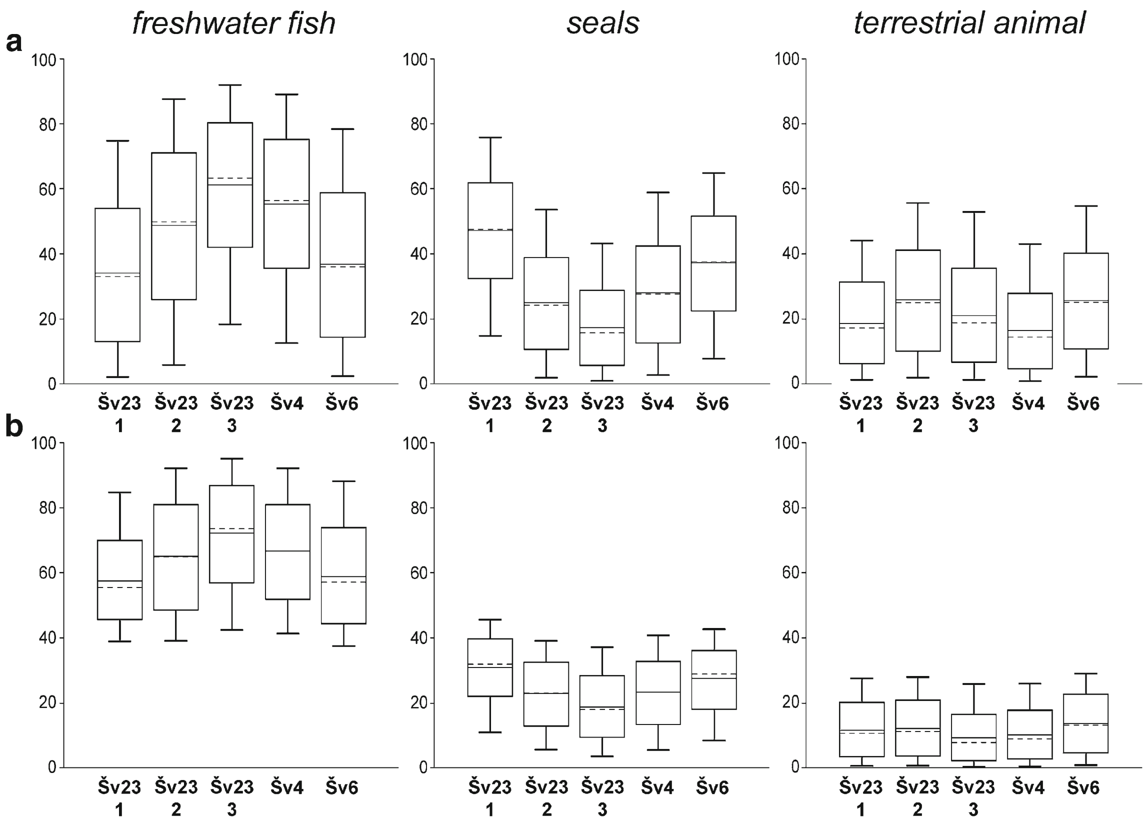

Fig. 4 Dietary protein contributions modeled for individuals at Šventoji 23, 4 and 6 sites by the non-routed FRUITS model (estimates are given in Table 4); **a** without and **b** with priors (fish intake) > (seal intake) > (animal intake). *Boxes* represent a 68% credible interval while the *whiskers* represent a 95% credible interval

(Table 5). If zooarchaeological priors are removed, then the sensitivity of the model outputs increases and changes to offset values represent 0–2% (changing δ^{15}N) and 5–8% (changing δ^{13}C) in total aquatic contributions to human collagen, respectively (Table 5). Nonetheless, the model remains quite robust.

Intra-individual C and N stable isotope variation at Šventoji 23

Collagen extracted from bone and teeth dentin are formed during different development periods of an individual's life. Tooth enamel and dentin are static structures, and once a tooth

Table 5 Testing the sensitivity of dietary protein contributions by modifying isotopic diet-to-consumer offset values for $\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$

	[1]Isotopic offset	Modeled contributions (means)		
	For $\delta^{13}C_{collagen}$	Freshwater fish	Seals	Terrestrial animals
(Fish) > (seal) > (animal)	0.5 ± 0.2	56	33	11
	1 ± 0.2	58	31	12
	1.5 ± 0.2	60	28	11
No priors	0.5 ± 0.2	34	47	18
	1 ± 0.2	41	40	20
	1.5 ± 0.2	48	31	20
	for $\delta^{15}N_{collagen}$	Freshwater fish	Seals	Terrestrial animals
(Fish) > (seal) > (animal)	3.1 ± 0.9	60	31	10
	4.1 ± 0.9	58	31	12
	5.1 ± 0.9	56	31	14
No priors	3.1 ± 0.9	46	40	14
	4.1 ± 0.9	41	40	20
	5.1 ± 0.9	35	38	37

Estimates for Šventoji 23 individual no. 1 were created using the non-routed FRUITS model. Contribution estimates for extreme and mid-isotopic offset values are given when zooarchaeological priors are introduced and absent is formed these structures do not remodel, therefore retaining the isotopic signature throughout a person's life. Bone, on the other hand, is a dynamic tissue that continually remodels during life. Bone collagen isotopic signature represents average of diet for up to the last 10–20 years before the death (Price and Burton 2001a), however individual age and bone type may have increase bone turnover rates (Hedges et al. 2007). Therefore, the potential to learn about individual life histories arises when analyzing stable isotopes of different skeletal parts (Eriksson and Lidén 2013). In addition to the mandibles and maxilla, molar tooth dentin was analyzed for Šventoji 23 individuals (Table 2; Fig. 2). The mandibular M1 and M2 teeth of a 25–35 year old male ('grave 1') revealed collagen-to-dentine offsets of up to 0.6 and 1.2‰ for δ^{15}N and δ^{13}C respectively. The M3 tooth δ^{13}C collagen value (−18.1‰) is elevated compared with that of M1 tooth (−19.3‰) as well as of bone (−18.9‰). As the crown of M3 forms between 10.5 and 15.5 years of age (Eriksson and Lidén 2013, and references cited therein), the observed stable isotope variation could be the result of an increased marine component in diet during teenage years. However, in the context of intra-individual data for Mesolithic and Neolithic sites in Northern Europe, the observed collagen-to-dentine offsets for the Šventoji 23 individual no. 1 should be considered limited (Eriksson and Lidén 2013). An adult of unknown age and sex ("grave 2") showed differences between the M1 tooth and bone collagen in order of 1.6‰ and 0.9‰ for δ^{15}N and δ^{13}C, respectively. The M1 tooth δ^{15}N collagen value (16‰) is elevated compared with that of bone (14.4‰). As M1 forms between the ages of 2 and 4 years (Eriksson and Lidén 2013), this value is most likely indicative of breastfeeding. Some studies argue that for hunter-gatherers in Europe and Siberia breast milk was the major protein source until the age of 2–3 years (Howcroft et al. 2014; Waters-Rist et al. 2011). Only slightly elevated δ^{15}N (by 0.3‰) in the 7–11 year old child's ('grave 3') M1 tooth may be indicative of earlier weaning compared with individual No 2. Although we only have data from three individuals, it appears that some Subneolithic individuals at Šventoji underwent a particular change of diet during their lifetime although this change does not diminish the dominant role of lagoonal food compared with marine or terrestrial diet components.

Revised chronology of the Benaičiai cemetery

Two graves within the Benaičiai burial ground (Kretinga district) were redated from 910 − 800 cal BC (Ki-10,632, 2690 ± 70 BP) established by liquid scintillation radiocarbon dating in the Kiev lab (Merkevičius 2005) to 2620–2490 cal BC (Poz-61,591, 4040 ± 30 BP) by AMS radiocarbon dating at the Poznań lab (Table 3). Thus, site grave goods and burial customs should be classified as CWC. The new AMS radiocarbon dates for the female and infant indicate that these individuals are 1300 years older than previously assumed. A goat bone from infant's grave (no. 3) was dated at Kiev, while at Poznań a human skull was dated. Theoretically, the possibility that an animal bone entered a grave context during post-depositional processes still remains. Unfortunately, we had no way of investigating that possibility as the bone was not available and was most likely fully destroyed during the dating process. Large discrepancies between radiocarbon dates of bones measured at Vilnius/Kiev and at the Poznań/Helsinki labs, however, have been previously observed (Piličiauskas and Heron 2015).

Neolithic human protein diet at Benaičiai

There are significant differences between the diets of the Šventoji Subneolithic individuals compared with the two Neolithic Corded Ware Culture (CWC) individuals from Benaičiai (Fig. 2). The Benaičiai infant has a δ^{15}N collagen value (10.8‰) elevated by 0.9‰ compared with the female (9.9‰) due to breastfeeding (see Howcroft et al. 2014). The δ^{15}N collagen value of the Benaičiai female is lower than the mean value of Šventoji humans (15.1 ± 0.6‰) by 5.2‰. The Benaičiai adult female's dietary protein consisted primarily of terrestrial animals and probably some domesticated animals as a goat bone was found in an infant's grave (Fig. 3; Merkevičius 2005). The adult female δ^{15}N collagen value is 5‰ higher than herbivores and other terrestrial animals (4.9‰, $n = 18$). It can be hypothesized that the δ^{15}N collagen values of the Benaičiai individuals are slightly higher than the wolf's signal due to a greater dietary contribution from domestic animals (having heterogeneous diets) or from a minor input of freshwater food. On the NW Lithuanian coast the emergence of a new subsistence strategy is roughly contemporaneous with the start of the decline of the formerly highly productive lagoonal lakes at Šventoji ca. 2500 cal BC as well as with the spread of the Corded Ware Culture 2800–2500 cal BC in the Eastern Baltic. CWC people were engaged in animal husbandry, although still maintaining hunting and fishing to some extent (Piličiauskas 2016).

Baltic context of protein diet

The comparison of the protein diet of Lithuanian coastal populations with those from other Baltic contexts clearly shows that the Benaičiai data agrees well with the CWC diet type, while the Šventoji data indicates a distinct diet compared with the inland Subneolithic hunters and fishermen, as well as being distinct from the diets observed for pure marine-based economies (Fig. 5). A comparison of stable isotope data between distant regions or different periods, however, may be complicated or even misleading given potential differences in food isotopic baselines. The distribution of the isotopic data shown in Fig. 5, suggests that the diet of

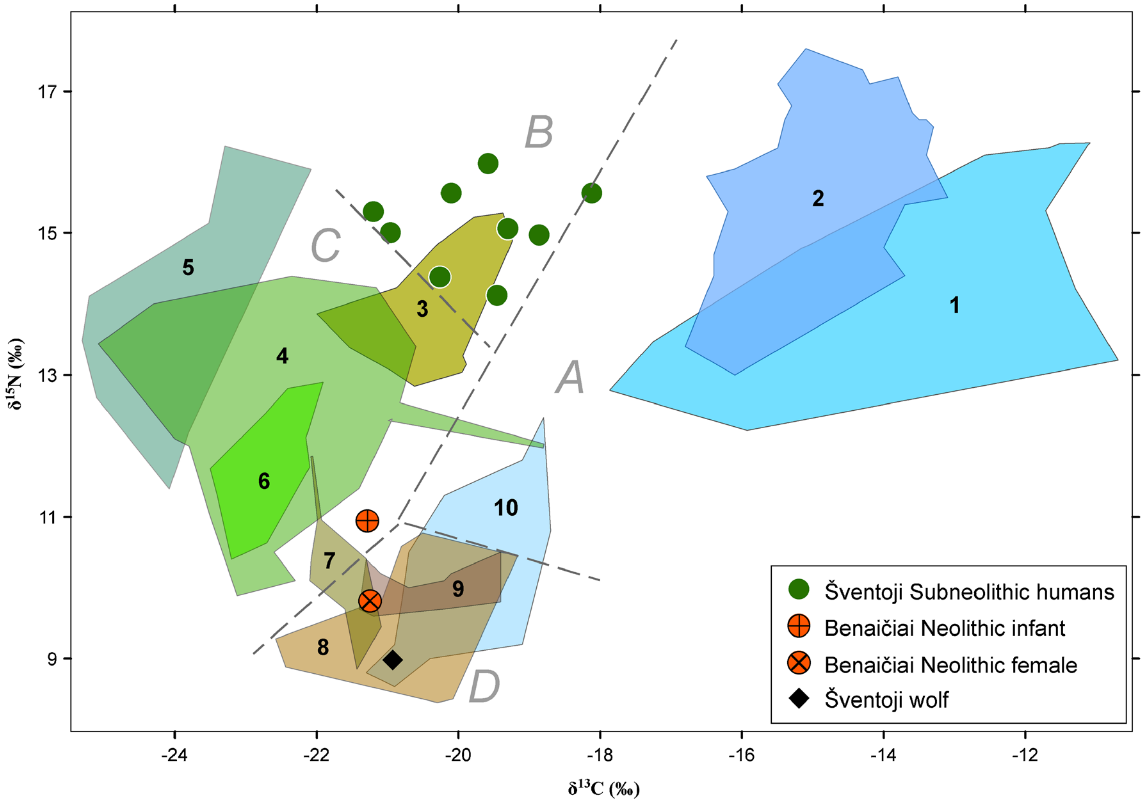

Fig. 5 Šventoji and Benaičiai human bone collagen stable isotope data combined with data from other European Mesolithic, Subneolithic, and Neolithic sites. *1*, Late Mesolithic in Denmark; *2*, Middle Neolithic (Pitted Ware Culture) in Gotland; *3*, Neolithic in Ostorf, N Germany; *4*, Mesolithic-Subneolithic in Zvejnieki, N Latvia; *5*, Mesolithic-Subneolithic in Estonia; *6*, Late Mesolithic-Subneolithic in Lithuania; *7*, Neolithic (CWC) in Latvia, Lithuania, and Poland; *8*, Neolithic in Denmark; *9*, Late Bronze Age in Estonia and Latvia; and *10*, Middle Neolithic (Battle Ax Culture) in Skania (Fischer et al. 2007; Eriksson 2004; Lübke et al. 2009; Eriksson et al. 2003; Tõrv and Meadows 2015; Antanaitis-Jacobs et al. 2009; Pospieszny et al. 2015; Laneman 2012; Laneman and Lang 2013; Fornander 2013). Children 1–4-year-old are excluded in order to avoid data distortion due to breastfeeding. Major subsistence strategies are framed by dashed gray lines and indicated by capital letters: *A* marine fishing and seal hunting, *B* lagoonal fishing, *C* inland fishing and hunting, and *D* animal husbandry and farming

the Šventoji population was similar to that of the Neolithic Ostorf cemetery in northern Germany (Lübke et al. 2009), while the diets of Šventoji/Ostorf popluations differs significantly (both $\delta^{15}N$ and $\delta^{13}C$ higher) from that of both Zvejnieki and inland Lithuanian Mesolithic-Neolithic populations. The Ostorf cemetery, however, is located on a lake island, about 30 km from the sea, and therefore marine protein would most likely not have made a significant contribution to the diet. An alternative interpretation seems more reasonable. Most likely in all three regions, i.e., Šventoji, Ostorf, and Zvejnieki the last hunter-gatherers relied heavily on freshwater fish although, of course, only the Šventoji people had easier access to marine food because of their proximity to the coast. Variation in the stable isotope values of consumed freshwater species, rather than differences in diet, may result in significantly distinct human stable isotope values. This conclusion is certainly valid for Šventoji and Zvejnieki (see Fig. 2 for freshwater fish isotopic values at Šventoji and at Riņņukalns—the Late Subneolithic site nearby Zvejnieki cemetery).

FRE/MRE correction at Šventoji

The recent paper by Piličiauskas and Heron (2015) discusses the values of FRE and MRE for the Šventoji former lagoon and the Littorina Sea. These were estimated by determining the radiocarbon dating offsets between coeval samples of seal and fish bones and terrestrial plants. Using the determined values for FRE and MRE and by reconstructing the diets of the prehistoric individuals through stable isotope analysis, it becomes possible to correct human radiocarbon dates and to evaluate how these corrected ages fit within the general site chronologies.

To obtain numeric estimates of the protein contributions from lagoonal, marine, and terrestrial food groups towards human bone collagen, a non-routed diet model with zooarchaeological priors introduced was defined using the statistical package FRUITS (Fig. 4b). Model estimates were combined with observed MRE and FRE (Table 4). Two scenarios for FRE/MRE corrections were investigated in the present study. The first assumes an MRE of 190 ± 43 years for the

Littorina Sea and the minimum FRE observed for the Šventoji paleolagoon of 320 ± 42 years. The second scenario keeps the same MRE values but takes as reference a larger FRE value of 510 ± 72 years. Estimates of human dietary radiocarbon reservoir effects are shown in Table 4 for all individuals using both FRE values. Corrected human radiocarbon dates were calibrated and plotted by contextual dates obtained mostly of terrestrial plants and animals (Fig. 6). Given that the radiocarbon dates from isolated unarticulated human bones and from terrestrial animal samples are not tightly constrained and the fact that no information is available regarding spatial relationships among dated samples, it is difficult to know whether the smaller (scenario 1) or larger (scenario 2) corrections are more likely to be valid. The corrected date values place human bone into expected ranges and confirm that the average FRE in local freshwater fish consumed by Šventoji residents may have fallen somewhere between the two previously observed FREs (320 ± 42 and 510 ± 72 years).

FRE/MRE corrected AMS radiocarbon dates imply that a calendar age of ca. 3000 cal BC is highly probable for the single human bones at the Šventoji 23 and 6 sites, although individual no. 1 from the Šventoji 23 site had lived 100 or a few hundred years later. The chronology of the Šventoji 4 human skull, however, is much more complicated, due to the large uncertainties in order of 80–120 years before and after the FRE/MRE corrections are applied (Table 4; Fig. 6). Following calibration of corrected radiocarbon date, it cannot be clearly stated whether the skull still belongs to the Subneolithic or to the Neolithic periods given that a change in ceramics from the Late Subneolithic porous ware to Neolithic GAC ware has been dated to 2720/2650 cal BC according to an age-depth model compiled for the Šventoji 4

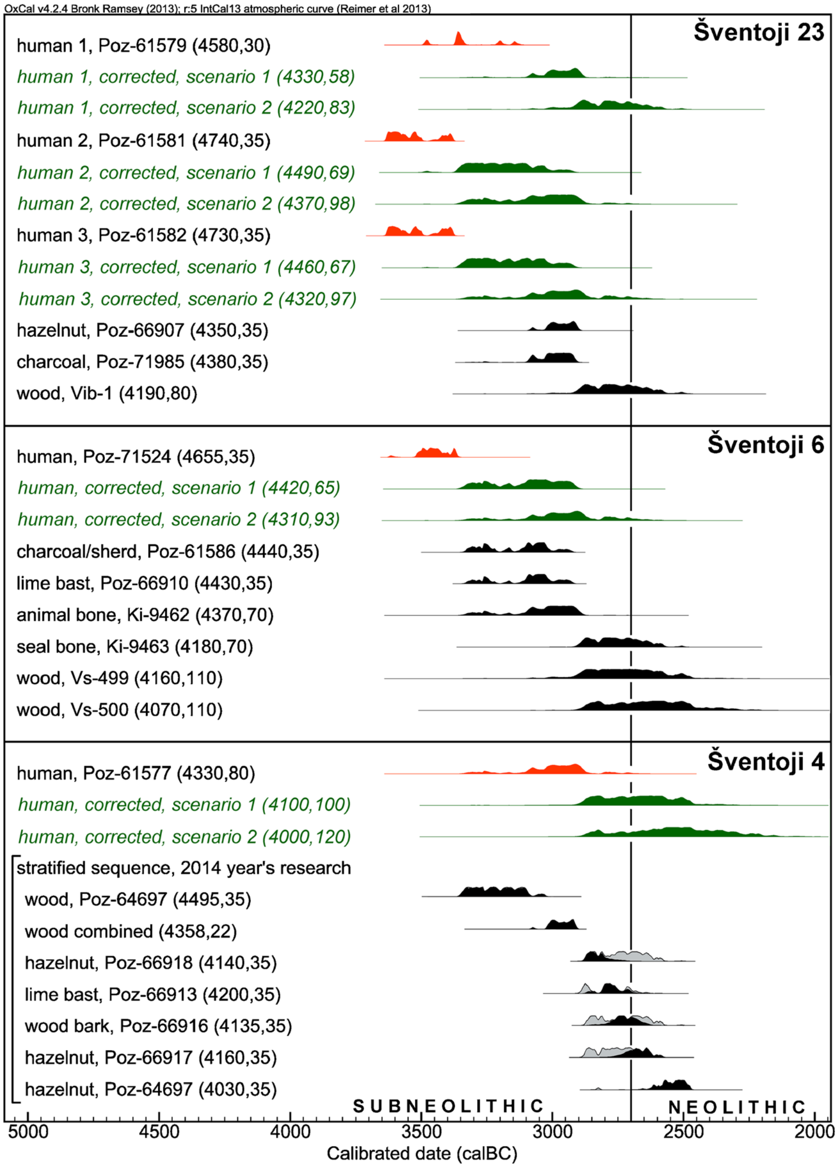

Fig. 6 FRE/MRE corrected and calibrated human bone dates (under two scenarios) plotted by contextual dates from the same sites

site. Assuming that the male from Šventoji 4 belongs to the Neolithic instead to Subneolithic period, his stable isotope values may indicate that there was no dietary change at the beginning of the Neolithic, i.e., prior to the CWC arrival. This would not be surprising as no domestic animal bones have yet been ascribed to GAC sites and the settlement pattern during the GAC is the same as during the Subneolithic, the same fishing stations were in use during both periods (Piličiauskas et al. 2012).

Isolated human bones

Stable isotope data of isolated human bones found at Subneolithic coastal sites indicate that they belong to lagoonal populations, probably local, or at least to non-inland populations, given characteristic marine or lagoonal isotopic signatures. Inland hunter-gatherers, even those with similar subsistence strategies, involving an important reliance on aquatic resources, typically show lower δ^{15}N and more negative δ^{13}C bone collagen values in Lithuania as well as in neighboring Latvia (Fig. 5). This may be evidence that the human bones, mostly skull fragments found during excavations, belonged to ancestral or relatives' skulls used for demonstration or/and sacrifices in the water rather than to enemies' skulls used as trophies. It seems that some human bodies or only particular parts (e.g., skulls) would have played an important symbolic role in the life of the living people. It should be admitted, however, that in the SE Baltic area disarticulated human remains, including skulls or their fragments, are not found only at the Baltic coast but are also present at inland lakeshore sites used by the last hunters-gatherers (e.g., Daktariškė 1, Kretuonas 1C, and Dudka) (Butrimas 1982; Girininkas 1994; Gumiński 2003). A phenomenon of isolated or loose human bones from various Mesolithic contexts is widely known all over Europe (e.g., Schulting 2015; Brinch Petersen 2015). Perhaps the most spectacular finding of this nature in Northern Europe Mesolithic is from Motala in Central Sweden, where selected human bones, mostly skulls, from a dozen individuals were deposited on the stone packing within a shallow lake, and two of the skulls were found mounted on wooden stakes still embedded in the cranium (Hallgren 2011).

Conclusions

Single human bones found at Subneolithic fishing stations and refuse layers of dwelling zones were previously thought to be useless for research. However, after direct AMS radiocarbon dating, these appear to be an important source of information on coastal diets during the time period between 3100 and 2700/2600 cal BC. Carbon and nitrogen stable isotope analysis of bone collagen revealed new and strong evidence for a very specific subsistence strategy on the coastline of the SE Baltic—reliance on freshwater fish species from lagoons and seals. It seems that seals and forest animals contributed to the protein portion of the diet of coastal people to a lesser extent than lagoonal fish. Significantly different inland stable isotope data of isolated human bones found at Subneolithic coastal sites indicate that these individuals likely belonged to local lagoonal populations.

A simple non-routed FRUITS dietary model which ignores a possible minor protein contribution from terrestrial plants appeared to provide reliable correction to human radiocarbon dates exhibiting FRE and MRE dietary radiocarbon reservoir effect. The FRE/MRE correction to AMS radiocarbon dates of single human bones found at the Šventoji sites provides a reference chronology of 3100–2600 cal BC.

The Benaičiai cemetery lying only 10 km from the sea has been AMS radiocarbon redated from the Late Bronze Age to the Neolithic, i.e., 2600/2500 cal BC. Stable isotope analysis of two Corded Ware Culture individuals from the Benaičiai cemetery indicate a sharp dietary shift towards terrestrial protein that occurred only between 2700 and 2500 cal BC in the Šventoji River basin. This is contemporaneous with both the Corded Ware Culture arrival (2600/2500 cal BC) and with the beginning of natural decay of the lagoons and lagoonal lakes (ca. 2500 cal BC) (Piličiauskas 2016). Both may have had a great impact on traditional Subneolithic strategies of food procurement.

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