



Isotopic sourcing reveals changing subsistence, cultural diversity and biological correlates with palaeodiet in fourth- to seventh-century AD Bavaria

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Abstract

Stable carbon and nitrogen isotopic ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in bone collagen of archaeological skeletal finds are indicators of the protein sources in individuals' basic diet. Isotopic sourcing allows us to quantify the biomass contribution of major dietary components and to differentiate between the source contribution of various animal species (domesticates, game). We re-evaluated previously published isotopic signatures in skeletons from three burial sites in Bavaria, dated from Late Antiquity to Early Mediaeval times (Erding-Klettham, Erding-Altenerding, Straubing-Bajuwarenstraße) by use of a mixing model. The result is a more detailed reconstruction, supported by contextual evidence, of both early subsistence economies and individual dietary preferences. We were able to confirm relationships between non-local dietary behaviour and foreign cultural influences (grave goods and artificial cranial modification) that have previously been suggested by the burial context and DNA analyses and that are plausibly explained by migration events. Moreover, we differentiated early and late immigrants from each other, requiring a re-evaluation of the earlier interpretation of exogamy. In addition, individual dietary preferences indicate even more migration events and social stratifications that could not previously be identified by the archaeological evidence alone.

Keywords Palaeodiet · Stable isotopes · Isotopic sourcing · Mixing models

Introduction

The composition of the basic diet of a prehistoric population has been reconstructed by the analysis of stable carbon and nitrogen isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in the bone collagen of archaeological skeletal finds for some decades (Ambrose 1993). Especially $\delta^{15}\text{N}$ is exclusively related to dietary protein and therefore an indicator of the trophic level of individual and collective diet. This provides important information

about dietary quality since animal protein is more bio-available to the human consumer than plant protein, due to its more similar composition (WHO 2014). In ecological terms, animal-derived protein is more costly since herbivores are already located on a higher trophic level than the primary producers, and a large amount of matter and energy is required to generate the animal organism. Researchers have used the trophic position of humans (from vegetarian to top-consumer), as defined by collagen $\delta^{15}\text{N}$, to assess social stratifications among past populations, however, with varied results. In some cases, the isotopic ratios indicate that socially privileged individuals had better access to meat and secondary products than the less privileged (e.g. Richards et al. 1998; Knipper et al. 2015). In other cases, such as the analysis of several early mediaeval skeletal series from Bavaria, there were no significant differences in dietary quality, as indicated by stable isotopes, between individuals that had been buried with rich grave goods on separated burial grounds and those that had been excavated from the corresponding ordinary row grave cemeteries (Czermak 2011). Hakenbeck et al. (2010, 2012) attempted to understand migration phenomena at Bavarian burial sites dating from

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late antique to early mediaeval times through the detection of non-local diets. In fact, they suggested that strongly differing isotopic signatures were indicative of exogamy.

The contextual information hidden in collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ shall be summarized only briefly (details, e.g. in Grupe et al. 2015: 463ff). Both carbon and nitrogen in collagen are derived from the growth metabolism. While all nitrogen stems from the protein portion of the diet, this holds only partly true for carbon. Only about 20% of all carbon atoms in collagen come from essential amino acids and therefore directly from dietary protein (Jim et al. 2006). Only under the prerequisite of a sufficient protein supply and lack of metabolic or diet-related disease (that only partly manifests itself on the skeleton), non-essential amino acids also become available for protein synthesis, and $\delta^{13}\text{C}$ is also an indicator of the dietary protein. Without exception, however, collagen $\delta^{15}\text{N}$ is shifted towards the animal protein component in the diet. Therefore, the proportion of dietary animal protein has been overestimated in conventional bivariate analysis. This is due to the fact that animal protein consists of up to five times more nitrogen than plant protein and this overprints the consumers' global $\delta^{15}\text{N}$ signature (see below).

On the level of the primary producers, C3, C4 and CAM plants discriminate differently against ^{13}C according to their photosynthetic pathway. CAM plants such as some succulents do not play any role in the temperate climates that are dominated by C3 plants; only some millet species are C4 plants and may leave isotopic traces in the consumers' collagen. In late antique/early mediaeval periods, the local vegetal diet consisted of C3 plants such as cereals, legumes, vegetables and roots (Adamson 2002). These plants discriminate strongly against ^{13}C and exhibit $\delta^{13}\text{C}$ -values around -26.5‰ with a high habitat-specific variability. The stable carbon isotopic signature of C4 plants is significantly more positive with an average of -12‰ (Richards 2015). Phytoplankton in freshwater bodies are responsible for isotopic fractionations that, to a major part, result in depleted $\delta^{13}\text{C}$ -values, while marine waters are enriched with ^{13}C because of high concentrations of solubilized bicarbonate (Peterson and Fry 1987).

Metabolic processes lead to an enrichment of consumer collagen $\delta^{15}\text{N}$ along the trophic chain, the well-known trophic level effect (Ambrose 1993). Within a circumscribed region and time frame, collagen $\delta^{15}\text{N}$ therefore permits the differentiation between herbivores, omnivores and carnivores. This trophic level effect has a magnitude of $2\text{--}6\text{‰}$ dependent on the vertebrate species but is around $+3\text{‰}$ for mammals (Caut et al. 2008). Individual variability may be due to pregnancies, growth processes or disease (D'Ortenzio et al. 2015), parameters that often cannot be identified from the skeletal find. Therefore, the majority of anthropological studies rely on the factor of $+3\text{‰}$ for an approximation (Ben-David and Flaherty 2012). Food chains in water

bodies are longer than in terrestrial habitats. Therefore, the most positive $\delta^{15}\text{N}$ -values are measured there. Milk protein is always enriched with ^{15}N because of an internal trophic level effect in lactating females (Kornexl et al. 1997).

Two factors are essentially responsible for the fact that palaeodiet reconstruction based on collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ does often not reach beyond the descriptive level and rather general statements. First, baseline isotopic ratios differ between ecosystems because they are dependent on climate, soil quality and manuring practices, among others. Especially manuring on a regular basis leads to elevated $\delta^{15}\text{N}$ -values in primary producers (Bogaard et al. 2013). As a consequence, human collagen isotopic ratios of different provenance and from different times are not readily comparable to each other. A comparison of human collagen data with those from contemporary animal bones is helpful for the necessary scaling (Czermak 2011).

The second and more important factor is the slow remodelling rate of bone collagen (Hedges et al. 2007) that is responsible for the fact that the measured global collagen $\delta^{13}\text{C}$ - and $\delta^{15}\text{N}$ -values are always an isotopic mixture made up of a variety of dietary components that is integrated over years and even decades in the adult skeleton. Such isotopic mixtures are difficult to detect or not at all detectable by the traditional bivariate analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, with the effect that isotopic ratios of fundamentally different diet components can mix in the consumers' collagen in a way that the resulting global isotopic signatures cannot be distinguished from each other. An example is the almost perfect identity of the collagen isotopic signatures (with regard to both the absolute values and their variability) in the skeletal series from Altdorf/Düren (North Rhine-Westphalia, Germany, nineteenth/twentieth century AD, Grigat 2014) and Volders (Austria, alpine environment, fifth to seventh century AD, McGlynn 2007) (see Jankauskas and Grupe 2019). To deduce similar dietary regimes and subsistence strategies from these similar isotopic ratios would be absurd for obvious reasons.

An isotopic sourcing by use of mixing models to better define the source contributions to the global collagen isotopic ratios in the human skeleton is therefore requisite. In this paper, we applied such a model to previously published bivariate analyses of collagen stable isotopes in three skeletal populations that date to a period of political and social changes. This way, much more detailed information on past subsistence strategies and population dynamics could be unravelled.

Such mixing models have long been applied successfully in ecological science, taking isotopic fractionation and mass balances into account. On the contrary, prehistoric anthropology has been rather hesitant to adopting this method, although its benefit has been proven for years (e.g. Newsome et al. 2004; Fabre et al. 2011; Le Bras-Goude et al. 2012;

Coltrain and Janetski 2013; Grupe 2014; Fernandes et al. 2015; Grupe et al. 2019; Cheung and Szpak 2021; Perutka et al. 2021). At present, several software are freely available (e.g. Phillips et al. 2005; Moore and Semmens 2008; Moreno et al. 2010; Parnell et al. 2010; Jackson et al. 2011; Newsome et al. 2012; Erhardt 2014). It is however necessary to gather requisite additional information on the major diet and especially protein components that are to a large degree deduced from accompanying animal bone remains. With regard to the archaeozoological results on the abundance of certain taxa and their usage, an isotopic mixing model permits “isotopic sourcing” by assessing all possible isotopic mixtures of major dietary components that are capable of explaining the measured global isotopic signature of the analysed collagen. This way, the animal component of the diet can be differentiated, e.g. in terms of game and domesticates and taxa (pig, cattle, poultry...). Where palaeobotanical material is available, the generation of isotopic food webs is much more reliable, but unfortunately such material is often not at hand. However, the source contribution of major dietary components that are frequently not preserved (vegetables, secondary products) can plausibly be estimated mathematically (e.g. Hagl et al. 2013). The major sources contributing to the consumer’s collagen isotopic signature therefore remain proxy data; however, it is possible to distinguish both on the individual and the collective level between farmers, animal breeders, fishers and mixed subsistence strategies and moreover to define the importance of certain animal taxa. This way, not only the subsistence strategy is unravelled. In addition, social stratifications, non-local influences and possibly certain professions can be detected (e.g. Ambrose 1993; Sebald et al. 2022).

Recently, previously published collagen $\delta^{13}\text{C}$ - and $\delta^{15}\text{N}$ -values in archaeological human finds and animal bones aiming at the reconstruction of palaeodiet from various burial sites in Neolithic Turkey and Greece (Sebald et al. 2022), from Neolithic Serbia and early to high mediaeval sites in Bavaria, have been re-evaluated by isotopic sourcing for a better quantification of the dietary quality (Sebald 2021). Among the latter were three Bavarian burial sites dating from late Antiquity and the early Middle Ages. The conventional analysis and interpretation of collagen stable isotopes was undertaken by Hakenbeck et al. (2010). This period can be understood as a time of political change. The “fall of the Roman empire” led to political decentralization and the gradual formation of new polities. Migration played an important role in this process. Political changes were accompanied by economic and structural upheaval, and both diet and subsistence economy were affected. Here we present the results obtained from these three burial sites and show how isotopic sourcing reveals many more details about diet, cultural influences, the differentiation between early and late immigrants and social stratification than archaeological

evidence and traditional bivariate interpretation of collagen stable isotopes can achieve.

Material

The three Bavarian burial sites that had been investigated isotopically by Hakenbeck et al. (2010) are the late Roman cemetery of Klettham and the two early mediaeval cemeteries Altenerding and Straubing-Bajuwarenstraße (Fig. 1). The two latter belong to the earliest row grave cemeteries in Bavaria. All three sites are located in a microregion with comparable ecological conditions.

Klettham dates from the fourth/fifth century AD (Sofes et al. 2012) and is a small site with only 13 burials, of which 11 were selected for stable isotope analysis by Hakenbeck et al. (2010). Altenerding dates from the fifth to the late seventh century AD and is located only a few kilometres to the south of Klettham. With c. 1400 burials, Altenerding is one of the largest early mediaeval cemeteries in Central Europe (Sage 1984). Non-local influence is evidenced by females with artificially modified skulls (Hakenbeck et al. 2012) and brooches that indicate relations with Scandinavia and Italy (Losert and Pleterski 2003). Seventy-three individuals from Altenerding had been selected for stable isotope analysis (Hakenbeck et al. 2010). The Straubing cemetery has the same date as Altenerding and was stratified into several phases (Geisler 1998; Hakenbeck et al. 2010, 2012). Isotopic data from 95 individuals have been published, among those also some females with artificially modified skulls. Stable isotope data from children’s skeletons were deliberately not re-evaluated in the present paper because children who died early could have lived on a diet very different from the diet of adults and are of limited use for the reconstruction of early mediaeval subsistence economies.

While there has been some debate about whether the skulls in question can really be considered to have been artificially modified (Trautmann et al. 2017, 2020; Grupe et al. 2018), we here retain the previously established anthropological diagnoses of artificial modification.

Methods

Isotope mixing models are based on the fact that the stable isotope ratios of carbon and nitrogen in the dietary components mix over the course of several years and are thus represented as isotopic mixtures in the consumer’s collagen. If, for example, the main protein sources were cereals and meat, then the measured collagen $\delta^{15}\text{N}$ in the human skeleton would be a mixture made up of $f_{\text{cereals}} \times \delta^{15}\text{N}_{\text{cereals}} + f_{\text{meat}} \times \delta^{15}\text{N}_{\text{meat}}$ with $f_{\text{cereals}} + f_{\text{meat}} = 1$ (100%). The same holds for $\delta^{13}\text{C}$. This way, the percentage source contribution of the

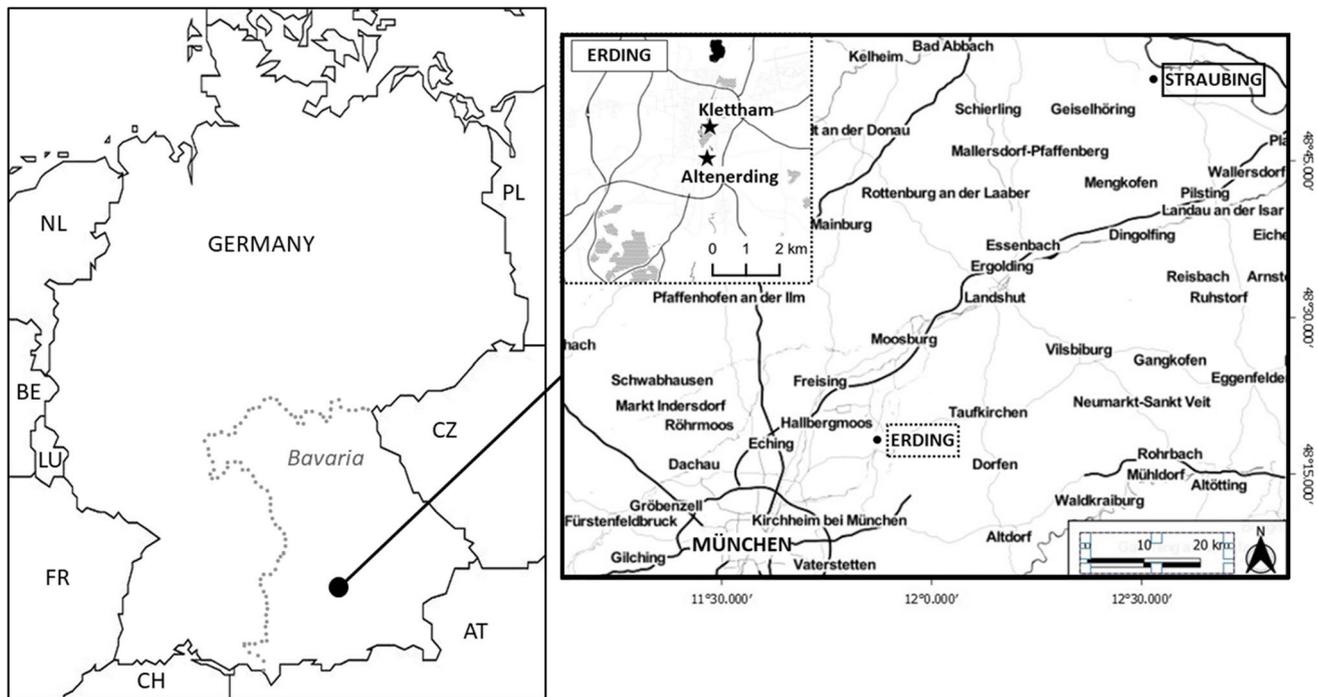


Fig. 1 Geographical location of the Klettham, Altenerding and Straubing cemeteries in Bavaria, Germany. Figure made with QGIS 2022

diet components can be assessed. As long as the available data permit, more components can be entered into the equation, e.g. to differentiate the meat component according to the sources, such as “game” or “domesticated”.

The published collagen stable isotope ratios (Hakenbeck et al. 2010; Table 1) were re-evaluated using different software for isotopic sourcing. Because of the non-linear relationship between collagen isotopic ratios and those of the basic food in omnivores (Milner et al. 2004), concentration-based mixing models need to be chosen, and the carbon and nitrogen concentrations of the dietary components need to be entered into the model as well. The FRUITS software (Fernandes et al. 2015) is frequently used in bioarchaeology. However, in our experience, FRUITS requires too many parameters (e.g. protein proportions) that are mostly not available for the reconstruction of archaeological food webs. These parameters need to be estimated, introducing even more noise into the calculations. We therefore tested IsoConc (Phillips and Koch 2002), an excel-based method generated by matrix algebra (<https://www.epa.gov/eco-research/stable-isotope-mixing-models-estimating-source-proportions>), the R-package MixSIAR Version 3.1. (Stock et al. 2018) (<https://github.com/brianstock/MixSIAR>, Stock and Semmens 2016) and the R-implemented SISUS (<https://statacumen.com/sisus/>, Erhardt 2014). All three software led to comparable results (Sebald 2021); however, SISUS proved most user-friendly for our purposes. Therefore, the results presented in this paper are generated by SISUS.

SISUS permits entering several diet components into the food web; however, the mathematical error rises with the number of end members. For the establishment of a palaeofood web, only the most important diet components should be entered, that is, as many as necessary, but at the same time as few as possible. In addition, the choice of end members requires comparison with, e.g. archaeozoological results such as the prevalence of certain taxa. SISUS uses exact data for the calculations instead of distributions. It presents results for all possible isotopic mixtures that explain the consumer’s collagen isotopic mixture from the end members without any accompanying probabilities. The smaller the difference between minimum and maximum calculated source contribution, the more accurate is the reconstructed food web (Fry 2006). For individuals that are not captured by the food web delineated by the chosen end members, no results are presented (for details see Sebald 2021). While attempts were made for these individuals with more hypothetical values, the results appeared rather arbitrary and an individual interpretation as to why these individuals plot outside the food web is more successful.

Because of metabolic processes, collagen $\delta^{13}\text{C}$ - and $\delta^{15}\text{N}$ -values differ from those of the diet components. Therefore, the data published by Hakenbeck et al. (2010, 2012) were adjusted to the isotopic ratios in the diet components according to the accepted general source-to-product isotopic spacings: $\delta^{13}\text{C}_{\text{diet}} = \delta^{13}\text{C}_{\text{collagen}} - 5\text{‰}$, and $\delta^{15}\text{N}_{\text{diet}} = \delta^{15}\text{N}_{\text{collagen}} - 3\text{‰}$ (Newsome et al. 2004).

Table 1 Raw data ($\delta^{13}\text{C}_{\text{collagen}}$, $\delta^{15}\text{N}_{\text{collagen}}$; Hakenbeck et al. 2012) and diet-adjusted global isotopic signatures of the diet ($\delta^{13}\text{C}_{\text{diet}}$, $\delta^{15}\text{N}_{\text{diet}}$). *AE* Altenerding, *KL* Klettham, *S* Straubing, *m* male, *m?* probably male, *f* female, *f?* probably female. ***mathematical outlier for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, **mathematical outlier for $\delta^{13}\text{C}$, *mathematical outlier for $\delta^{15}\text{N}$; bold, eminent outlier indicative of a non-local diet; shaded, individuals with artificial cranial deformation

burial	age	sex	C/N	%N	$\delta^{15}\text{N}_{\text{collagen}}$ [‰]	$\delta^{15}\text{N}_{\text{diet}}$ [‰]	%C	$\delta^{13}\text{C}_{\text{collagen}}$ [‰]	$\delta^{13}\text{C}_{\text{diet}}$ [‰]
AE55	adult	m	3.2	14.6	11.01	8.01	39.6	-19.4	-24.4
AE76	Infans II	indet	3.2	14.9	9.7	6.7	40.6	-19.6	-24.6
AE91	adult	f	3.1	16.9	9.1	6.1	45.5	-19.7	-24.7
AE92	adult	m	3.1	15.6	9.5	6.5	41.8	-19.5	-24.5
AE105	adult	f	3.2	15.7	9.1	6.1	43.2	-19.4	-24.4
AE106	senile	m	3.2	15.2	10.1	7.1	41.0	-19.3	-24.3
AE117	senile	f	3.1	20.6	9.7	6.7	55.0	-19.5	-24.5
AE142	senile	f	3.2	14.2	10.7	7.7	38.4	-19.7	-24.7
AE146	adult	f	3.2	15.1	10.8	7.8	41.0	-19.6	-24.6
AE151	mature	f	3.1	15.0	9.0	6.0	40.5	-19.2	-24.2
AE154	adult	m	3.2	14.0	9.1	6.1	38.9	-19.9	-24.9
AE156	adult	f?	3.2	16.3	8.6	5.6	44.6	-19.4	-24.4
AE189	juvenile	indet	3.2	12.9	9.7	6.7	35.9	-19.2	-24.2
AE192	senile	f	3.2	14.6	9.7	6.7	39.9	-19.4	-24.4
AE201	adult	f	3.2	15.1	9.0	6.0	40.7	-20.0	-24.9
AE204	senile	f	3.2	14.2	9.3	6.3	38.8	-19.4	-24.4
AE218	senile	f?	3.2	14.5	9.1	6.1	39.7	-19.6	-24.6
AE224	senile	f	3.1	16.4	9.4	6.4	43.8	-19.0	-24.0
AE256	senile	f?	3.2	14.4	9.8	6.8	39.0	-19.6	-24.6
AE272	mature	f	3.1	15.5	9.5	6.5	41.7	-19.4	-24.4
AE280	adult	f	3.2	14.3	8.3	5.3	38.7	-19.7	-24.7
AE289	adult	f	3.2	14.5	8.3	5.3	39.2	-19.4	-24.4
AE297	adult	f?	3.2	15.2	9.4	6.4	41.0	-19.2	-24.2
AE329	mature	f	3.2	16.3	9.8	6.8	44.0	-19.3	-24.3
AE343	adult	f	3.2	15.0	7.9	4.9	40.7	-19.1	-24.1
AE344	mature	m	3.2	15.2	9.6	6.6	41.1	-19.3	-24.3
AE421	mature	f	3.2	14.7	11.2	8.2	39.9	-20.0	-25.0
AE427	senile	m?	3.1	14.5	9.9	6.9	38.9	-19.6	-24.6
AE452	senile	f	3.2	16.9	10.0	7.0	45.7	-19.3	-24.3
AE469	adult	m	3.2	14.8	9.2	6.2	40.0	-19.0	-24.0
AE487	adult	m	3.2	16.3	9.7	6.7	44.5	-19.5	-24.5
AE492	adult	m	3.2	14.1	8.9	5.9	38.3	-19.5	-24.5
AE501	adult	m	3.2	15.3	9.9	6.9	41.4	-19.4	-24.4
AE513**	adult	f	3.2	14.7	9.1	6.1	39.9	-16.8	-21.8
AE516	Infans II	indet	3.1	14.9	9.0	6.0	40.1	-19.0	-24.0
AE521	adult	f	3.2	16.0	9.8	6.8	43.5	-18.8	-23.8
AE530	senile	f	3.2	14.8	9.3	6.3	40.5	-18.8	-23.8
AE554	juvenile	f?	3.1	16.1	8.6	5.6	43.2	-19.5	-24.5
AE587	mature	m	3.2	15.0	9.9	6.9	40.9	-19.3	-24.3
AE604	adult	f	3.2	16.7	9.1	6.1	45.0	-19.3	-24.3
AE607	adult	f	3.2	13.6	9.1	6.1	36.7	-19.5	-24.5
AE618	adult	f?	3.2	15.2	9.1	6.1	41.4	-19.7	-24.7
AE625	adult	f	3.1	17.6	9.1	6.1	47.2	-19.5	-24.5
AE631	mature	m	3.1	17.5	10.4	7.4	46.9	-19.3	-24.3
AE646	adult	f?	3.1	14.7	9.1	6.1	39.5	-19.6	-24.6
AE652	senile	m	3.2	15.3	10.7	7.7	41.5	-19.7	-24.7

Table 1 (continued)

AE657	adult	m	3.2	17.8	10.4	7.4	48.7	-19.9	-24.9
AE658	adult	f	3.1	15.3	9.2	6.2	41.2	-19.5	-24.5
AE674	senile	m	3.2	14.5	11.0	8.0	39.2	-19.4	-24.4
AE729	adult	m	3.2	15.4	10.0	7.0	41.9	-19.6	-24.6
AE788	adult	m?	3.1	15.7	9.6	6.6	42.3	-19.8	-24.8
AE809	nb	f	3.1	16.1	9.8	6.8	43.2	-19.8	-24.8
AE820	adult +	m	3.1	18.4	10.0	7.0	48.9	-20.0	-25.0
AE830	adult	m?	3.1	8.0	9.0	6.0	21.6	-19.8	-24.8
AE897	senile	f	3.2	18.9	9.8	6.8	51.3	-19.3	-24.3
AE902	adult	m	3.2	15.2	8.9	5.9	41.3	-19.8	-24.8
AE903	mature +	m	3.2	15.1	10.6	7.6	41.8	-19.6	-24.6
AE909	mature	f	3.2	13.2	11.1	8.1	36.0	-19.9	-24.9
AE948	mature +	m	3.2	16.0	10.5	7.5	43.2	-19.7	-24.7
AE997	senile	m?	3.1	15.9	8.5	5.5	42.7	-19.0	-24.0
AE1037	mature +	m	3.2	15.7	9.5	6.5	42.4	-19.6	-24.6
AE1083**	senile	f?	3.2	17.3	9.6	6.6	47.0	-18.2	-23.2
AE1108**	senile	f	3.2	14.7	10.4	7.4	39.8	-18.2	-23.2
AE1119	adult +	f	3.1	16.1	9.2	6.2	43.4	-19.6	-24.6
AE1125	adult +	m	3.2	14.6	9.3	6.3	39.6	-19.7	-24.7
AE1135**	adult	f	3.2	13.9	10.1	7.1	38.1	-20.3	-25.3
AE1284	mature	m	3.2	15.6	10.7	7.7	42.3	-19.5	-24.5
AE1299	adult	f	3.2	15.2	10.8	7.8	41.0	-19.5	-24.5
AE1323	mature	m	3.2	14.8	9.8	6.8	40.3	-19.7	-24.7
AE1332	senile	f	3.2	12.7	9.5	6.5	35.1	-19.7	-24.7
AE1334	juvenile	m	3.2	16.0	9.3	6.3	44.2	-19.9	-24.9
AE1343	juvenile	m	3.2	15.4	9.3	6.3	42.0	-19.0	-24.0
AE1350	mature	f	3.2	15.2	9.6	6.6	41.3	-18.9	-23.9
KL1663	adult	f	3.1	16.2	9.3	6.3	43.3	-19.8	-24.8
KL1700	senile	f	3.1	16.1	9.5	6.5	43.3	-19.3	-24.3
KL1702	adult	f	3.2	15.7	9.3	6.3	42.5	-19.8	-24.8
KL1662	mature	m	3.1	17.4	9.9	6.9	46.9	-19.9	-24.9
KL1664	mature	m	3.2	17.9	8.8	5.8	48.5	-19.5	-24.5
KL1665	adult	m	3.2	15.8	9.2	6.2	43.7	-19.4	-24.4
KL1669	adult	m	3.2	20.0	9.3	6.3	54.9	-19.5	-24.5
KL1703	adult	m?	3.2	13.0	9.4	6.4	36.1	-19.5	-24.5
KL1719	senile	m	3.2	15.5	9.0	6.0	42.9	-19.5	-24.5
KL1720*	Infans I	m?	3.2	15.4	11.7	8.7	42.0	-19.6	-24.6
KL1721***	mature	f?	3.2	13.8	10.9	7.9	37.2	-17.1	-22.1
S066**	adult	f	3.2	11.4	9.0	6.0	30.9	-20.6	-25.6
S067	adult	f	3.2	16.9	10.0	7.0	46.7	-19.7	-24.7

Table 1 (continued)

S073	mature	m	3.1	17.5	9.8	6.8	46.7	-19.3	-24.3
S077	adult	f	3.1	17.2	9.9	6.9	46.0	-20.0	-25.0
S085	mature	m	3.2	16.6	9.2	6.2	46.0	-19.9	-24.9
S093	mature	m	3.2	12.9	9.2	6.2	35.0	-19.6	-24.6
S094*	mature	f	3.2	13.0	7.8	4.8	35.2	-19.4	-24.4
S095	adult	m	3.2	16.7	9.7	6.7	45.4	-18.9	-23.9
S098	adult	f	3.2	16.6	9.1	6.1	46.0	-19.1	-24.1
S100	adult	f	3.2	15.8	9.2	6.2	43.9	-20.0	-25.0
S130	adult	m	3.1	17.8	10.0	7.0	47.9	-20.1	-25.1
S170	adult	m	3.2	15.0	9.9	6.9	40.4	-19.8	-24.8
S171	adult	m	3.1	17.6	9.8	6.8	46.9	-19.8	-24.8
S172	adult	m	3.2	17.0	10.0	7.0	46.6	-19.7	-24.7
S182	mature	m	3.2	15.1	10.7	7.7	41.7	-19.4	-24.4
S228**	adult	f	3.1	18.3	9.0	6.0	49.2	-18.7	-23.7
S233	adult	f	3.2	16.2	9.4	6.4	43.8	-19.7	-24.7
S235	mature	m	3.2	14.3	9.5	6.5	39.3	-18.7	-23.7
S236	mature	m	3.2	13.7	9.2	6.2	37.9	-19.9	-24.9
S240	adult	m	3.2	15.4	9.2	6.2	41.8	-19.3	-24.3
S241	adult	m	3.2	15.7	9.5	6.5	43.0	-19.3	-24.3
S243	senile	m	3.2	15.6	10.5	7.5	42.9	-18.9	-23.9
S246	senile	f	3.2	12.9	9.6	6.6	34.9	-19.8	-24.8
S248	adult	f	3.1	13.9	9.9	6.9	37.5	-19.9	-24.9
S262	mature	f	3.2	15.9	9.9	6.9	44.1	-19.7	-24.7
S265	adult	f	3.2	16.4	9.7	6.7	45.1	-19.9	-24.9
S299	mature	f	3.2	15.5	8.8	5.8	43.2	-19.8	-24.8
S300	adult	f	3.2	16.0	8.8	5.8	43.7	-19.9	-24.9
S305	mature	f	3.2	14.0	9.4	6.4	37.9	-20.1	-25.1
S306	adult	f	3.2	15.8	9.3	6.3	43.0	-19.9	-24.9
S308	mature	m	3.3	14.8	9.7	6.7	41.3	-20.0	-25.0
S309	mature	m	3.2	14.5	10.0	7.0	40.1	-19.7	-24.7
S310	mature	f	3.2	16.0	9.8	6.8	44.0	-19.1	-24.1
S315	adult	m	3.2	13.8	8.9	5.9	37.9	-19.6	-24.6
S316	mature	m	3.2	16.1	9.8	6.8	43.4	-19.6	-24.6
S317	adult	f	3.2	16.3	9.4	6.4	44.3	-19.4	-24.4
S320	adult	f	3.2	16.1	8.9	5.9	44.6	-19.6	-24.6
S321	senile	f	3.3	14.0	9.7	6.7	39.1	-19.9	-24.9
S326	mature	m	3.2	10.2	10.1	7.1	28.3	-19.8	-24.8
S328	adult	f	3.1	16.4	8.7	5.7	44.2	-19.6	-24.6
S329	adult	m	3.2	15.7	9.6	6.6	42.9	-19.7	-24.7
S330	adult	m	3.2	14.8	10.3	7.3	40.7	-19.7	-24.7

Table 1 (continued)

S349	mature	m	3.1	14.9	9.8	6.8	40.2	-19.2	-24.2
S354	adult	f	3.2	12.2	9.8	6.8	33.7	-19.9	-24.9
S355	adult	f	3.2	18.9	9.0	6.0	51.3	-19.5	-24.5
S356	adult	m	3.2	18.0	9.1	6.1	48.5	-19.8	-24.8
S358	mature	m	3.1	13.4	10.7	7.7	36.0	-18.7	-23.7
S360	adult	f	3.2	16.1	8.8	5.8	43.3	-19.7	-24.7
S361	adult	f	3.1	17.0	9.1	6.1	45.6	-19.6	-24.6
S369	adult	f	3.2	15.6	10.1	7.1	43.3	-20.0	-25.0
S374	adult	m	3.2	12.8	10.4	7.4	34.7	-19.8	-24.8
S377	mature	f	3.2	15.8	9.0	6.0	43.8	-20.0	-25.0
S388	mature	f	3.2	14.6	9.6	6.6	39.7	-20.0	-25.0
S399	senile	f	3.2	15.0	10.0	7.0	40.6	-19.7	-24.7
S412	mature	f	3.2	15.7	9.8	6.8	42.7	-20.0	-25.0
S428	adult	m	3.3	13.8	9.8	6.8	38.9	-19.5	-24.5
S445*	adult	m	3.2	15.6	5.0	2.0	42.5	-21.1	-26.1
S450	adult	f	3.2	15.4	9.3	6.3	42.6	-20.0	-25.0
S451	adult	f	3.3	15.7	9.9	6.9	43.8	-19.9	-24.9
S452	mature	m	3.2	14.2	10.0	7.0	39.2	-19.5	-24.5
S470	senile	f	3.2	18.4	9.9	6.9	49.8	-19.8	-24.8
S473	adult	m	3.2	14.7	9.5	6.5	39.8	-19.9	-24.9
S474	adult	f	3.2	11.7	9.6	6.6	32.4	-19.8	-24.8
S477	mature	f	3.2	13.2	9.3	6.3	35.9	-19.9	-24.9
S478	adult	m	3.3	13.9	10.4	7.4	38.8	-19.5	-24.5
S479	adult	f	3.2	15.5	10.4	7.4	42.2	-19.6	-24.6
S480	mature	f	3.3	15.4	8.9	5.9	43.1	-19.6	-24.6
S481	adult	f	3.2	12.9	9.2	6.2	35.7	-19.4	-24.4
S483	adult	f	3.3	14.0	9.9	6.9	39.2	-19.5	-24.5
S484	adult	m	3.2	10.8	9.3	6.3	30.0	-19.9	-24.9
S485	mature	m	3.2	14.3	9.5	6.5	39.5	-20.2	-25.2
S486	mature	m	3.2	14.8	9.7	6.7	41.0	-20.1	-25.1
S487	mature	f	3.2	14.2	9.6	6.6	38.7	-19.6	-24.6
S489	senile	f	3.2	12.9	10.1	7.1	35.9	-19.6	-24.6
S490	adult	m	3.2	14.2	9.4	6.4	39.4	-19.9	-24.9
S491	mature	m	3.2	14.1	9.8	6.8	39.1	-19.4	-24.4
S493	mature	m	3.3	11.7	10.3	7.3	33.1	-19.7	-24.7
S494	adult	f	3.2	15.4	9.9	6.9	42.2	-19.7	-24.7
S495	mature	f	3.3	14.2	10.1	7.1	39.7	-19.9	-24.9
S497	adult	f	3.2	17.6	10.0	7.0	48.9	-19.8	-24.8
S499	adult	f	3.2	16.0	9.6	6.6	44.5	-19.7	-24.7
S500	adult	f	3.3	12.3	9.4	6.4	34.3	-19.8	-24.8
S501	mature	m	3.2	12.2	10.1	7.1	33.6	-19.6	-24.6
S502	mature	f	3.3	10.8	9.0	6.0	30.2	-20.0	-25.0
S520	adult	f	3.2	16.1	9.3	6.3	44.6	-19.9	-24.9
S535	mature	f	3.1	15.5	9.0	6.0	41.7	-20.2	-25.2
S537	adult	f	3.2	16.2	8.5	5.5	44.5	-19.6	-24.6
S538	mature	m	3.2	14.6	10.2	7.2	40.1	-19.3	-24.3
S581	mature	m	3.2	18.2	9.6	6.6	49.9	-19.5	-24.5
S600	adult	f	3.3	14.7	9.8	6.8	41.2	-19.8	-24.8
S604	adult	f	3.2	12.4	9.8	6.8	34.5	-19.6	-24.6
S660	adult	m	3.3	11.3	10.1	7.1	31.8	-19.7	-24.7
S665	adult	m	3.3	10.0	9.5	6.5	28.4	-20.0	-25.0
S708	senile	f	3.1	16.5	9.7	6.7	44.3	-19.5	-24.5
S739	mature	m	3.2	16.0	9.5	6.5	44.0	-19.6	-24.6

Isotopic ratios of the end member “meat” are likewise calculated from collagen isotopic signatures of animal bones: $\delta^{13}\text{C}_{\text{meat}} = \delta^{13}\text{C}_{\text{collagen}} - 4\%$, and $\delta^{15}\text{N}_{\text{meat}} = \delta^{15}\text{N}_{\text{collagen}}$ (Newsome et al. 2004) (Table 1). For the Klettham cemetery, sufficient archaeozoological data were available (Hakenbeck et al. 2010), but not so for the other two sites. For Altenerding and Straubing, a data pool from comparable sites in mediaeval Bavaria was established by Sebald (2021) resulting in 62 individual animal bone isotopic signatures (Table 2). Archaeological data for the definition of the vegetal end member were lacking, as is often the case in bioarchaeology. It is not advisable to estimate the isotopic signatures of primary producers from the collagen isotopic ratios of animal bones since even strict herbivores may feed from plants that do not serve human consumption or are even not edible for humans. Therefore, we defined the vegetal end members hypothetically in a way that was both compatible with the isotopic signatures of the animal bones and especially with the baseline data published by Bakels (2019) (for details, see Sebald 2021).

Since the protein component of the basic diet is overrepresented in the consumers’ bone collagen, carbon and nitrogen concentrations in the diet need to be considered as well as the digestibility of the diet components. Therefore, we relied on the formula published by Robbins (1993, see also Phillips and Koch 2002) rather than using element concentrations measured in the archaeological bones. The proportions of the respective dry weight percentages were derived from the USDA database (USDA 2019): carbon [%] = $52 \times \text{protein} + 75 \times \text{lipid} + 45 \times (\text{carbohydrates} + \text{fibres})$; nitrogen

[%] = $16 \times \text{protein}$. Based on physiological data, digestibility for animal protein and fat was set to 100%, for vegetal components 90% for proteins (C, N), 100% for carbohydrates and 0% for fibres (Newsome et al. 2004).

The end members for the food web are chosen in a way that the envelope delineated by them captures all or at least as many of the diet-adjusted human $\delta^{13}\text{C}$ - and $\delta^{15}\text{N}$ -values as possible (Table 1, Figs. 2, 3, and 4). The spacing between minimum and maximum source contributions calculated by SISUS in this study is small or at least acceptable throughout (Table 3), e.g. the most parsimonious food web has been generated (see Fry 2006). Other dietary items may have been consumed on a more or less regular basis, but the source contribution was too small to show up in the isotopic ratios, and hence, the role in the overall subsistence economy was small. The generated food web indicates the main subsistence economy. Individual dietary preferences that need a separate discussion are readily identified by the position of the human diet-adjusted data within or outside the envelope.

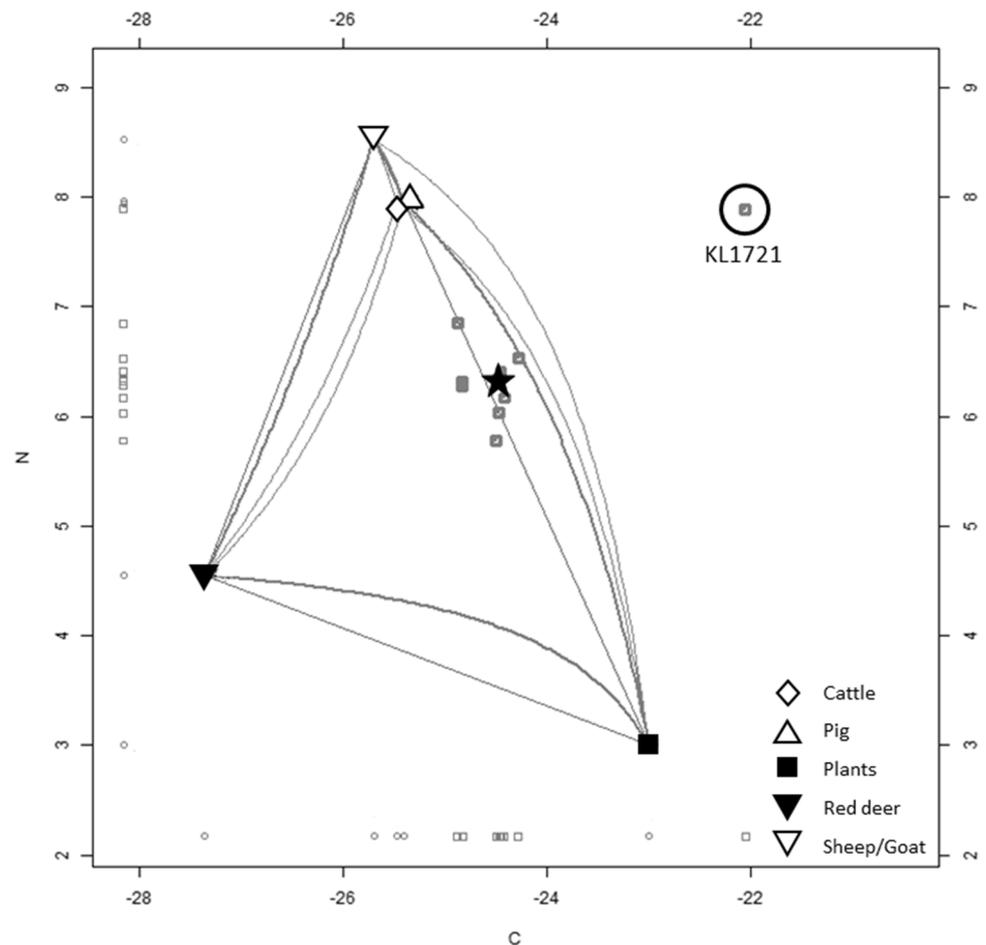
The raw data obtained from the human skeletal finds were checked for outliers by an IQR analysis to monitor possible individual dietary preferences or foreign influences. These univariate statistical outliers were however not excluded from the isotopic sourcing. As a consequence, median instead of mean values were entered into the model, since the former are more robust towards outliers. The IQR analysis is also indispensable because the animal bones that were used for the construction of the food web are suitable representatives for the species in question; however, they are certainly not the direct leftovers of the human consumers.

Table 2 Isotopic ratios of the end members for the mixing model. Animal end members: median values. *n* number of samples. *Calculated by use of data from the USDA data base. USDA-IDs: chicken (5332, 2066, 5048, 5075, 5084, 5100, 5115, 5127, 8006, 5109), plants (16,069, 16,144, 11,300, 11,304, 20,004, 20,005, 20,130, 20,070, 20,008, 20,063, 20,064, 20,065, 20,062, 0132, 45,026,702,

20,033, 20,034), cattle (13,017, 13,023, 23,459, 13,147, 13,929, 23,471), red deer (17,164, 17,343, 35,080), sheep/goat (17,168, 17,169, 17,371, 17,224), pig (10,005, 10,219, 10,001, 10,008, 10,016, 10,020, 10,060, 10,070). Raw data for the animal bones, see Strott (2007), Czermak (2011) and Hakenbeck et al. (2010). Superscripts A and B refer to the Altenerding (A) and Straubing (B) site, respectively

		Klettham					
End member	<i>n</i>	%N*	$\delta^{15}\text{N}_{\text{collagen}}$	$\delta^{15}\text{N}_{\text{meat/plant product}}$	%C*	$\delta^{13}\text{C}_{\text{collagen}}$	$\delta^{13}\text{C}_{\text{meat/plant product}}$
Cattle	2	9.6	7.9	7.9	59.6	-21.5	-25.5
Red deer	1	13.3	4.6	4.6	54.2	-23.4	-27.4
Sheep/goat	4	11.1	8.5	8.5	58.1	-21.7	-25.7
Pig	6	7.8	8.0	8.0	62.1	-21.4	-25.4
C3 plants	-	2.4	-	3	45.1	-	-23.0
		Altenerding ^A . Straubing ^B					
End member	<i>n</i>	%N*	$\delta^{15}\text{N}_{\text{collagen}}$	$\delta^{15}\text{N}_{\text{meat/plant product}}$	%C*	$\delta^{13}\text{C}_{\text{collagen}}$	$\delta^{13}\text{C}_{\text{meat/plant product}}$
Chicken ^{A,B}	3	9.2	7.4	7.4	64.0	-20.5	-24.5
cattle ^{A,B}	23	9.6	6.0	6.0	59.6	-21.3	-25.3
Sheep/goat ^{A,B}	17	11.1	7.1	7.1	58.1	-21.4	-25
Pig ^{A,B}	19	7.8	7.6	7.6	62.1	-20.8	-24.8
C3 plants ^A	-	2.4	-	4.0	45.1	-	-24.0
C3 plants ^B	-	2.4	-	4.0	45.1	-	-24.5

Fig. 2 Concentration-based mixing model for the human skeletons from Klettham. Source contributions were calculated from the population median (star). Source contributions: Red deer 8.1%, cattle 13.2%, pig 14.3%, sheep/goat 10.1%, plants 54.4%. Circle: mathematical outlier. Thin lines indicate the basic mixing model that does not take concentration into account; bold lines indicate the extended mixing model with additional information, here: concentration



Since even individual animals from the same species may exhibit individual dietary preferences, the actual isotopic variability of the end members will be underestimated. All human isotopic signatures that are not captured by the food web but plot very close to it and constitute no statistical outliers are therefore not readily indicative of a differing individual dietary habit.

Results

The average percentage source contributions of the chosen protein sources for the three populations are listed in Table 3 (individual results see Sebald 2021). With the exception of a few individuals, the vegetal part of the basic diet was made up of C3 plants, as expected. Although at all three sites, the majority of the individuals tested had diet-adjusted isotopic signatures that are grouped around the median, individual dietary preferences also become clear.

The diet-adjusted human isotopic signatures from late antique Klettham cluster rather tightly around the population median with only one exception (Fig. 2). The food web affords five end members, since the diet-adjusted

mixed isotopy of the human collagen is not explicable by the sources plants and domesticates (cattle, pig, sheep/goat) alone. At least one additional source with both lower $\delta^{13}\text{C}$ - and $\delta^{15}\text{N}$ -values is requisite. Red deer as a representative for game has a suitable isotopic signature but would have contributed least to the animal protein sources with an average of 8% only (Fig. 2). Meat was derived preferably from cattle and pig with nearly identical source contributions, followed by sheep/goat. Plant protein contributed between 51 and 59% (average 54%). The reconstructed food web is physiologically plausible. However, the conventional bivariate statistical analysis of the Klettham data by Sofeso et al. (2012) that postulated a high-quality meat-based diet needs to be revised (see the “Discussion” section).

The mathematical outlier concerns an old adult (40 years+) female (KL1721) that had consumed a diet that was completely different from that of other individuals (Table 1, Fig. 2). With a c. 2‰ more positive $\delta^{13}\text{C}$ -value, C4 plants like millet could have played a substantial role in her daily diet (Hakenbeck et al. 2010; Sofeso et al. 2012). Taking the local $\delta^{13}\text{C}$ -value of C3 plants for the individuals from Klettham (-24.6‰ ; Table 1) and assuming a $\delta^{13}\text{C}$ of -12‰ for C4-plants (see the “Introduction” section),

Fig. 3 Concentration-based isotopic mixing models for the skeletons from Altenerding. *Italics*: Individuals with artificial cranial modification. Source contributions were calculated from the population median (star). Top (without secondary products): Chicken 24.2%, cattle 6.3%, pig 13.3%, sheep/goat 7.0%, plants 49.2%. Bottom: Chicken 13.2%, cattle 8.7%, pig 10.5%, sheep/goat 7.8%, plants 50.8%, milk (calculated from domesticates excl. pig) 9.1%. Circle: mathematical outlier. Dotted circle: conspicuous individuals with artificial cranial modification. Line thickness, see Fig. 2

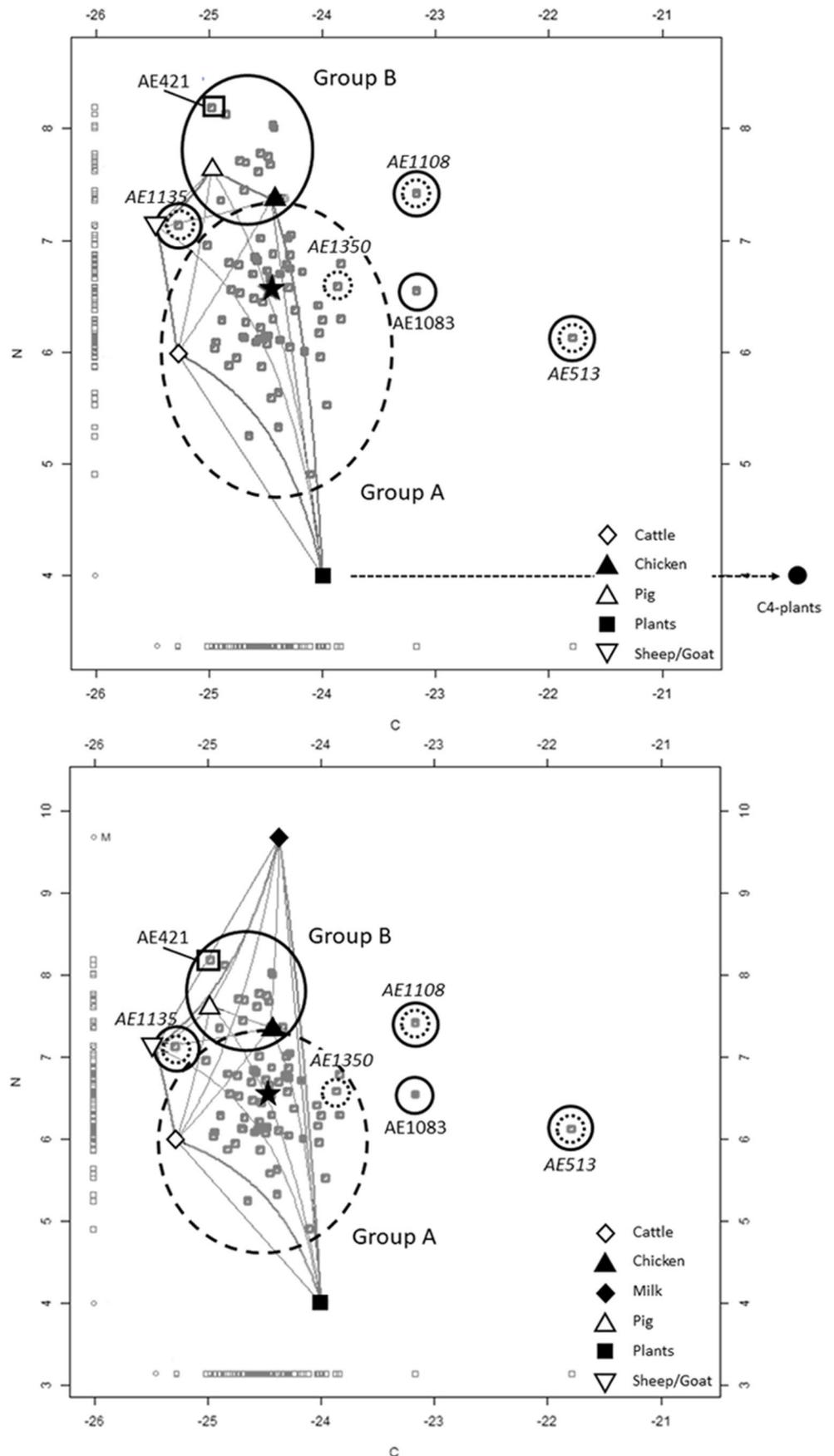


Fig. 4 Concentration-based mixing model for the Straubing population. Italics: Individuals with artificially modified skulls. Source contributions calculated based on the population median (star, calculation excl. S445). Chicken, 28.5%; cattle, 9.5%; pig, 12.1%; sheep/goat, 7.0%; plants, 42.9%. Circle: mathematical outlier. Dotted circle: conspicuous individuals with artificial cranial deformation. Line thickness, see Fig. 2

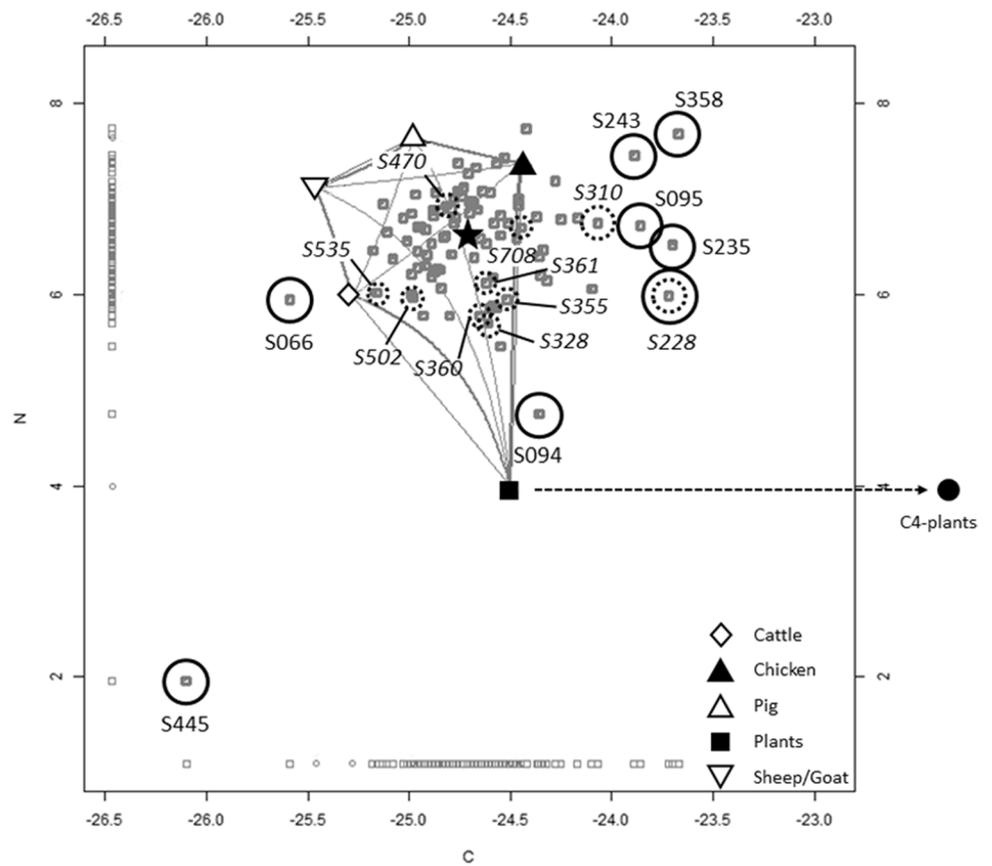


Table 3 Percentage biomass source contribution of the dietary end members calculated by SISUS. *Except KL1720 (Infans I), **except S445 (no human sample), *MIN* minimum, *sd* standard deviation, *MED* median, *MAX* maximum, *span* max–min

Site	Source	MIN	MEAN	sd	MED	MAX	Span
Erding-Altenerding	Chicken	0.022	0.242	0.085	0.246	0.44	0.418
	Plants	0.373	0.492	0.043	0.498	0.575	0.202
	Cattle	0	0.063	0.044	0.055	0.187	0.187
	Sheep/goat	0	0.07	0.05	0.062	0.21	0.21
	Pig	0	0.133	0.095	0.117	0.403	0.403
Erding-Altenerding	Chicken	0	0.132	0.09	0.119	0.44	0.44
	Plants	0.373	0.508	0.042	0.512	0.599	0.226
	Cattle	0	0.087	0.054	0.083	0.244	0.244
	Sheep/goat	0	0.077	0.054	0.067	0.244	0.244
	Pig	0	0.105	0.081	0.086	0.407	0.407
	Milk _{cattle, sheep/goat}	0	0.091	0.061	0.082	0.3	0.3
Erding-Klettham*	Red deer	0.056	0.081	0.011	0.08	0.111	0.055
	Pig	0	0.143	0.102	0.125	0.432	0.432
	Cattle	0	0.132	0.093	0.115	0.393	0.393
	Sheep/goat	0	0.101	0.072	0.088	0.302	0.302
	Plants	0.512	0.544	0.016	0.541	0.587	0.075
Straubing**	Chicken	0.088	0.286	0.08	0.288	0.473	0.386
	Plants	0.244	0.429	0.067	0.440	0.547	0.303
	Cattle	0	0.095	0.067	0.083	0.283	0.283
	Sheep/goat	0	0.07	0.05	0.060	0.208	0.208
	Pig	0	0.121	0.086	0.106	0.365	0.365

then the measured $\delta^{13}\text{C}_{\text{collagen}}$ of this female would be explainable by a 80%:20% mixture of C3 and C4 plants, since the percentage source contributions of both types of plants needs to add up to 100%. Besides millet, a dietary preference for photosynthetically inactive plant parts (roots, tubers, nuts...) could also explain the elevated $\delta^{13}\text{C}$ -value of this female (Cernusak et al. 2009; Grupe et al. 2019). The rare consumption of freshwater fish is also a possible explanation for the females' $\delta^{15}\text{N}$ -value since Erding is surrounded by tributaries of the Isar River. However, freshwater fish is mostly depleted with ^{13}C (Peterson and Fry 1987); therefore, the consumption of a different plant food is more plausible. Regardless, together with the 1.6‰ elevated $\delta^{15}\text{N}_{\text{collagen}}$ relative to the population median, this female consumed more animal protein and different plant sources than the other individuals in the same cemetery. This is consistent with the earlier interpretation that this clearly different dietary habit may be evidence of immigration (Hakenbeck et al. 2010; Sofeso et al. 2012), since the collagen isotopic signatures of this female had not been adapted to the local signatures before she died. Sofeso et al. (2012) identified the adult male KL1665 as a possibly additional immigrant according to his $^{87}\text{Sr}/^{86}\text{Sr}$ isotopic ratio, though this needs to be rejected on the basis of recent regional isotopic mapping (Toncala et al. 2017). The gross palaeodiet of this male is also not different from the others.

The Altenerding cemetery is of a later date than Klettham and is located in close vicinity, though no settlement continuity is assumed. According to the isotopic sourcing, palaeodiet was similar but not identical. The percentage source contribution of vegetal protein is still around 50% but may have varied more since mathematically, a contribution between 38 and 60% is capable of explaining the consumer's mixed isotopic ratios. Game is no longer an indispensable end member and may have played an inferior role with regard to the meat supply. In contrast, chicken as a representative of meat and also secondary products are needed as an end member for at least some individuals. The Altenerding food web therefore needs more and different end members than the one for Klettham.

Both visually and isotopically, the individuals from Altenerding can be differentiated into two groups according to their dietary behaviour (Fig. 3). The basic diet of the majority of individuals (group A) is isotopically explainable by a mixture of protein derived from plants and domesticates (cattle, sheep/goat, pig, chicken). A small number of individuals exhibit higher collagen $\delta^{15}\text{N}$ -values (group B), and here the food web requires an additional protein source. The isotopic ratio of secondary products such as milk and cheese can be estimated from the collagen values of milkable domesticates (Hagl et al. 2013) and this would constitute a meaningful end member in the Altenerding population. While we cannot exclude that members of group A consumed a minor proportion of secondary products, secondary

products are indispensable for the members of group B and make up about 9% of the protein source contribution.

Four females, namely the young adults (20–40 years old) AE513 and AE1135 and the old adults AE1108 (60+ years old) and AE1350 (40–60 years old), had artificially modified skulls and exhibit collagen isotopic ratios that are indicative of different dietary components. While AE513 and AE1108 lie outside of the food web because of their more positive $\delta^{13}\text{C}$ -values, the diet-adjusted isotopic ratio of AE1350 plots at the periphery of group A. Since this female had died at an age of 40 years or more, she may well have been primarily foreign to the site but must have immigrated several years before her death. AE1135 plots close to group A; however, her diet-adjusted isotopies are nearly identical to those of meat from sheep/goats. With regard to the distribution of the data points in Fig. 3, she must have consumed a different meat source. With regard to her low $\delta^{13}\text{C}$ -value, she had also consumed a different plant component than the majority of the other individuals including those with modified skulls. Her dietary pattern is therefore different, but this fact would have remained undetected without an isotopic sourcing. Since the mixed isotopy of the basic diet of AE1135 is barely captured by the food web, she must have immigrated to the site as a juvenile. For none of these four females, secondary products are needed for the reconstruction of a parsimonious food web, while two of them had elevated $\delta^{13}\text{C}$ -values that indicate the consumption of C4 plants (Hakenbeck et al. 2010).

Two other females exhibit a conspicuous dietary pattern, both have unaltered skulls. Considering her position in the food web, AE1083 likely also consumed a measurable proportion of C4 plants. Her $\delta^{13}\text{C}$ -value matches that of AE1108 who has been identified as a migrant because of her cranial modification. AE421 has the most positive $\delta^{15}\text{N}$ -value of all individuals and was buried with grave goods that indicate relations to Scandinavia or the Baltics. Therefore, she was identified as a possible immigrant by Hakenbeck et al. (2010). However, her collagen isotopic ratios are nearly identical with those of the female AE909 (AE421: $\delta^{15}\text{N} = 11.2\text{‰}$, $\delta^{13}\text{C} = -20.0\text{‰}$; AE909: $\delta^{15}\text{N} = 11.1\text{‰}$, $\delta^{13}\text{C} = -19.9\text{‰}$), the grave goods of which were inconspicuous. Whether marine fish had been a regular component of the basic diet as postulated by Hakenbeck et al. (2010) is a matter of debate since marine resources exhibit both elevated $\delta^{15}\text{N}$ - and $\delta^{13}\text{C}$ -values, but this is contradicted by the position of the diet-adjusted isotopies in the food web. The regular consumption of secondary products is more plausible. This is another example of the benefits of isotopic sourcing that permit us to estimate dietary components that are lacking from the archaeological record. The other extreme of the food chain is again represented by a female (AE343) that may have lived on a largely vegetarian diet according to her $\delta^{15}\text{N}$ of 4.9‰ only (Table 1).

The food web of the contemporary cemetery of Straubing is also quite complex (Fig. 4). In its parsimonious form, it requires neither game nor secondary products, but again poultry. With a median of 43% vegetal protein contribution, it is comparable to Altenerding in this respect. Two females with artificially modified skulls (S228 and S310) exhibit more positive collagen $\delta^{13}\text{C}$ -values that indicate a different vegetable dietary component with a measurable contribution of C4 plants. They share the feature of elevated $\delta^{13}\text{C}$ -values with the males S095, S235, S243, and S358. Seven additional females with deformed skulls (S328, S355, S360, S361, S470, S502, S535) consumed a basic diet that matches the diet of the total population, while the palaeodiet of the old adult female S708 is barely captured by the food web.

Especially low $\delta^{13}\text{C}$ -values were measured in the female S066 and the allegedly male S445, though the latter was already suspected by Hakenbeck et al. (2010) of being a non-human bone sample. This is confirmed by the isotopic sourcing since the data points of S445 are totally incompatible with the food web. With a $\delta^{13}\text{C}$ of -20.6‰ , S066 has an isotopic ratio that is still compatible with the normal variability in C3 plants. It is therefore a matter of debate whether this is indeed a non-local signature. If this female really was an immigrant to the site, then her dietary habits do not indicate that she came from a very different ecozone. As in Altenerding, one female (S094) had lived on a largely vegetarian diet. Just as at Altenerding, the isotopic sourcing of the skeletons from Straubing reveals a diversity of protein sources that indicate foreign cultural influences in some individuals, but this is not related to sex or artificial cranial modification throughout.

Discussion

The most parsimonious food webs have been generated for three Bavarian sites covering the late antique and early mediaeval periods. Estimating the most probable source contributions to individual basic diets by isotopic sourcing leads to much more refined, quantifiable interpretations, compared to the traditional bivariate statistical analyses.

First, Figs. 2, 3, and 4 clearly show a considerable dietary variability among those individuals that are captured by the general food web for the sites. The collagen isotope ratios of these individuals can be explained by the regular consumption of locally available protein sources. Since humans are omnivores with a particularly flexible and opportunistic dietary behaviour, this comes as no surprise; however, isotopic sourcing permits the evaluation of the causes of the observed variability. Individual dietary preferences may be simply due to individual taste, but of course also due to social or cultural reasons, or immigrant status.

Animal protein provides three to five times more nitrogen to the diet than vegetal protein (Table 2); therefore, the consumers' collagen $\delta^{15}\text{N}$ -value is always shifted towards the animal dietary component. Isotopic sourcing allows us to quantify the real animal-derived source contribution. If, as in the case of the three Bavarian sites, the protein biomass proportion of plants and animal products is about 50:50, the vegetal contribution was in reality much larger. This composition of daily diet is consistent with expectations regarding the work burden and energy supply needed for early mediaeval food production. A meat-dominated diet, as, e.g. suggested for Klettham by Sofeso et al. (2012), is not supported by the isotopic evidence at any of the sites re-evaluated by us.

Another benefit of mixing models is that even the most parsimonious food web can differentiate between the source contributions of game and domesticates as long as these end members differ isotopically. While the food webs at Altenerding and Straubing do not need a "game" end member, this was requisite for the earlier settlement at Klettham, where game contributed to about 8% to the consumers' mixed collagen isotopic ratios. Although a small contribution of meat from game cannot be excluded for the two early mediaeval populations, this dietary component does not show up isotopically, indicating that hunting was not a substantial part of the early mediaeval subsistence economy. This is also plausible with regard to the historical context since in late antiquity, hunting was not yet limited by law, and it is well imaginable that red deer had been preferably hunted for raw material and that its meat was later eaten.

The source contribution of certain domesticated taxa can be assessed both on the collective and the individual level (see skeleton AE1135). The vicinity of the diet-adjusted human isotopic data to one of the chosen end members in the food web (Figs. 2, 3, and 4) already indicates a preference for the respective species. In this way, individual dietary preferences or individual access to certain resources are revealed.

Missing end members can be estimated by the use of mixing models. It is possible to estimate the expected isotopic ratio of basic dietary components that leave few or no traces at all in the archaeological record. This holds, e.g. for small fish bones, the abundance of which is frequently underestimated when they are collected from the site by hand-picking (Becker & Grupe 2012), but especially for secondary products which can explain some elevated $\delta^{15}\text{N}$ -ratios in skeletons from Altenerding.

We want to emphasize that isotopic sourcing generates proxy data, e.g. a calculated protein contribution by a selected source of supposedly 24.4% should be translated into "about one quarter". These uncertainties are to a small part due to instrumental measurement error and to a large part however due to the mostly unknown or poorly defined

individual dietary preference of individual animals. More comprehensive stable isotope analyses of archaeozoological finds are therefore desirable (Ugan and Coltrain 2012).

Mixing models have their limits in so far as qualitative differences between animal protein sources (e.g. flesh versus entrails), or different preparation methods for meals cannot be revealed according to present knowledge. Although this will not bias the reconstruction of subsistence strategies, social stratifications may remain undetected. Since human bone collagen integrates palaeodiet over many years, seasonal dietary peculiarities or short-term food crises (e.g. crop failure) are not detectable.

A special emphasis in this study lies on possible correlates between diet and migrant status, the latter being indicated either by non-local grave goods or cultural practices such as artificial cranial modification. At Altenerding, the multifaceted basic diet of females becomes visible by those females that represent the extremes of the total variability (see AE909 and AE343 in terms of $\delta^{15}\text{N}$). Therefore, it is difficult to distinguish outside cultural influences from social stratification or simply individual dietary preferences. Despite non-local grave goods pointing to very different ecological backgrounds (Scandinavia or the Baltic versus Southern Germany), the basic diet of AE421 is no marker for possible immigration. Despite a clearly different diet, AE1083 bears no biological markers or items of material culture that could support a non-local origin. Non-local grave goods did not necessarily migrate together with their owners, but may also have been acquired through trade. With regard to biological markers such as artificial cranial modification, one should consider the possibility that not all members originating from a foreign society need to bear the same trait. This seems to be the fact at both the Altenerding and Straubing site.

At Altenerding, the females with artificially modified skulls AE513 and AE1108 have elevated $\delta^{13}\text{C}$ -values indicative of the consumption of C4 plants that were not staple foods in early mediaeval Bavaria. Artificial cranial modification is assumed to indicate cultural influence mainly from central and southeastern Europe (Veeramah et al. 2018). The palaeogenomic analysis by Veeramah et al. (2018) revealed that AE1108 had an East Asian ancestry contribution of about 20%, though there is no evidence to suggest that this woman migrated from outside Europe. However, there is a clear cluster of individuals with modified skulls in east-central Europe, and many of these have a similar isotopic signature to AE1108, with elevated $\delta^{13}\text{C}$ -values (Hakenbeck et al. 2017; Hakenbeck 2018). The evidence suggests therefore that this woman is an immigrant to the site who died before her collagen stable isotope signatures were adjusted to the local ones. Patterns of female migration are often explained with exogamy in the sense that young females of childbearing

age marry into a different society. AE1108 however was at least 60 years old when she died; therefore, exogamy cannot constitute the only or most plausible explanation. One could also think of migrating groups, possibly families comprising more than one generation. The isotopic signatures of the female AE1135 were captured by the food web; however, she had lived on a very different diet especially with regard to her meat source. She had died between 20 and 40 years of age and could therefore well be an earlier immigrant to the site with collagen isotopies that still carried some of the earlier non-local signatures. While Trautmann et al. (2017) questioned whether the skull of this woman had really been modified, the earlier interpretation of skull modification (Helmuth 1996) agrees with the different dietary preference of this woman. She may therefore also have been a migrant to the area. The diet-adjusted collagen isotopic signatures of AE1350 plot at the periphery of group A (Fig. 3). This female had died at an age of 40 years or more and could also have been foreign to the site but must have immigrated several years before her death.

At Straubing, females with artificially modified skulls also either exhibit a non-local diet with a substantial source contribution of C4 plants (S228, S310) and are barely captured by the food web (S708), or they lived on a diet that was indistinguishable from the local one (S328, S255, S360, S361, S470, S502, S535). The most probable reason is the time elapsed since immigration that permitted collagen isotopic signatures to adjust to the local ones to varying extents. Interestingly, four adult males also had a clearly C4 plant-based diet (S095, S235, S243, S358) but no artificially modified skulls. If these four individuals had been females with modified skulls, immigration and even exogamy would have readily served as an explanation.

Together with the immigrant female of advanced age from Altenerding (AE1108), the isotopic sourcing points to the necessity of a more differentiated interpretation of migration in early mediaeval Bavaria. S310 was older than 40 years when she died, but she still exhibited the non-local diet. Since she was after reproductive age, exogamy is also debatable here. The woman with an artificially modified skull S708 is barely captured by the local food web, meaning that her collagen isotopic signatures were already close to the local ones, but she also died at the advanced age of more than 60 years. The fact that adult males exhibit non-local dietary signatures similar to the ones of females with modified skulls, some of the latter migrating clearly at post-reproductive age is a strong indicator of migration not only in the course of exogamy, but also for groups of people migrating or individuals changing their place of residence for other reasons such as properties, social status and affiliations or simply personal choice. Cultural contacts to several parts of Europe at the two early mediaeval sites are certain

based on the archaeological context. Cranial modification constitutes a biological correlate, but definitely not for all immigrants.

According to the palaeogenomic profiles established by Veeramah et al. (2018), a higher genomic diversity was found in females with modified skulls. While, e.g. AE1108 had an ancestry contribution from East Asia (see above), S310 exhibits relationships to southern Europe. Different possible places of origin are reflected in the palaeodiet as well. Males exhibited a genomic affinity to northern and central Europe, but, unfortunately, the four adult males with the non-local diets from Straubing were not examined.

A more complex relationship between diet and biocultural markers for migration may also explain the fact that at Straubing, some individuals exhibit diet-adjusted collagen isotopic signatures that are no longer captured by the most parsimonious food web but plot very close to it. These individuals all exhibit slightly more positive $\delta^{13}\text{C}$ -values (Fig. 4). Since the overall variability of $\delta^{13}\text{C}$ is substantially smaller than the variability of $\delta^{15}\text{N}$, such small deviations could easily be explained by the lack of information concerning the individual dietary variability of animals (see above). Also, an individual preference for tubers or nuts could serve as an explanation. However, based on the total available information so far, one could also think of immigrants that had migrated not too long before and, therefore, exhibit mixed isotopic ratios between the local and the non-local ones. As long as no more detailed information about possible places of individual origin is available, this possibility needs to remain hypothetical as well. A traditional bivariate analysis of collagen isotopic ratios would certainly identify these individuals that plot on the periphery of the total variability, but isotopic sourcing is capable of providing hypotheses as to why this is and these can be tested individually with the archaeological context.

Finally, no statistical relevant dietary differences according to sex were evident in the three studied populations that reached beyond slight individual dietary preferences (Sebald 2021). There was no evidence of easier access to valuable food resources by males, such as might be expected in a patriarchal society.

Conclusion

The reconstruction of palaeodiet by means of collagen stable carbon and nitrogen isotopes is part of the routine toolkit in archaeological and anthropological sciences. It is relatively cheap and does not require a huge amount of labour. It is however not an end in itself. The fact that skeletal series exhibit an average life expectancy and average child mortality for the period and no unusual markers of physiological stress or malnutrition, etc. (Steckel et al. 2019) indicates

that the population broadly had access to an adequate diet. In such a case, the general subsistence strategy and possible social or gender-related access to distinct dietary components are of interest but also any hints regarding immigration from regions with different dietary habits. In-depth consideration of the archaeological context is requisite for the formulation of suitable hypotheses that can later be supported or rejected by stable isotope analyses.

The application of concentration-based isotopic mixing models permits a realistic approximation to former conditions. Beyond the evaluation of the trophic level of the human consumers, percentage source contributions of protein from different dietary components (plants, domesticates and game of different taxa, secondary products, aquatic resources) can be quantified with sufficient precision. The location of the data points in the food web further permits the formulation of hypotheses regarding the measured mixed collagen isotopic ratios, the cause of which can be deduced together with the archaeological findings (e.g. seasonality versus mobility). For the skeletal series re-evaluated in this paper, some individual dietary preferences that indicate immigration are fully compatible with palaeogenomic profiles (Veeramah et al. 2018); however, others are not. Unfortunately, we have palaeogenomic information only for a small subsample of the investigated individuals.

Any isotopic sourcing requires availability of archaeozoological and ideally also palaeobotanical finds. Therefore, it is highly desirable that also these finds are extensively archived to permit for a subsequent isotopic analysis. Only this way, isotopic sourcing will be capable of fully exploiting the contextual potential of skeletal isotopic signatures.

Author contribution SH and GG published the original stable isotope data with the conventional bivariate analysis for the first time. SVS re-evaluated the original data by application of isotopic mixing models and generated the figures. All authors wrote, read and approved the final manuscript.

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Declarations

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