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Stable isotope sourcing in physical anthropology: application of mixing models

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Food components derived from plants and animals contain different amounts of carbon and nitrogen and are not assimilated equivalently. In omnivorous feeders such as humans, concentration-weighted isotopic mixing models are suitable for the assessment of the gross contribution of different dietary end members and give clues to past subsistence economies.
Keywords: palaeodiet, carbon, nitrogen, stable isotopes, mixing models

I cibi derivanti da piante e animali contengono differenti quantità di carbonio e azoto e non sono assimilati in modo equivalente. Negli onnivori, come l'uomo, modelli che mescolano differenti concentrazioni isotopiche sono adatti a individuare le diverse componenti della dieta, oltre a dare indizi sull'economia di sussistenza antica.
Parole chiave*: paleodieta, carbonio, azoto, isotopi stabili, combinazione di modelli*

1. Introduction

Today, stable isotope analysis aiming at the reconstruction of palaeodiet and place of origin is an indispensable archaeometric tool in modern prehistoric anthropology and bioarchaeology in general (see Vohberger, this volume). The interpretation of isotopic data, however, is far from trivial. Mass spectrometers produce figures and numbers which seem to be intriguingly exact, but these figures are frequently neither self-explaining, nor will they create hypotheses *per se*. Scientific methods are applied to answer scientific questions, and it is crucial to formulate adequat questions which can be solved, or hypotheses which can ei-

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ther be supported or rejected by stable isotopic data. To avoid mis- and overinterpretation of these data, it is crucial to focus on the information which is hidden in the figures generated by the laboratory. First, this requires an in-depth knowledge of the thermodynamic, biochemical, and physiological processes which lead to a distinct isotopic ratio in the consumers' tissue. Second, when applied to bioarchaeological finds such as bones and teeth, diagenesis has to be taken into account. It is important to stress that stable isotopic data derived from archaeological skeletons are indeed exact figures, but are only proxy data on the interpretive level.

The use of stable isotopes as tracers for the flow of matter through modern ecosystems is straight forward, and any interpretation based on the data can be verified experimentally – this is however not possible for past ecosystems. Stable isotope analyses of collagen, for instance, will therefore not give clues to the exact composition of daily diet, but rather serves as an approximation to the basic economy of food provisioning by permitting a differentiation between farming, dairying, fishing, and foraging economies. Since this is exactly what physical anthropology is aiming at, stable isotopic analysis is a powerful tool as long as it is applied properly. The very first aspect to be kept in mind is that the palaeodiet is usually reconstructed from collagen stable isotopic ratios. Given the slow turnover of bone tissue during life, bulk collagen analysis from adults results in an average $\delta^{15}N$ and $\delta^{13}C$ accumulated in the course of years and decades. Compact bone is usually preferred over trabecular bone because of its lesser porosity, but most frequently bone parts without diagnostic value such as rib fragments are sacrificed for collagen extraction. While remodeling is slowest in skull bones, it is highest in the iliac crest. Collagen turnover lasts between 20 and 30 years in the adult (Ubelaker, Buchholz, Stewart 2006; Wild *et alii* 2000). Any seasonality in dietary behaviour will therefore be hidden and results in a mixed isotopic signal. Consider a seasonal migration from coast to inland, and the seasonal consumption of marine and terrestrial food. Stable isotopic ratios in bone collagen will indicate a mixed diet consisting of both marine and terrestrial food – a diet which had never been consumed at any time in life.

It has been accepted since long that the reconstruction of human palaeodiet is difficult because humans are omnivorous, opportunistic and very flexible feeders. Also, baseline isotopic ratios of potential dietary components (plants, animal products) can be variable in time and space. The trophic level effect inherent to collagen $\delta^{15}N$ (on average 3.4‰; Minagawa, Wada 1984) is usually used for an estimation of the human trophic level in the local food web. While it holds true that low ratios such as +7‰ indicate a largely vegetarian diet and high figures such as +12‰

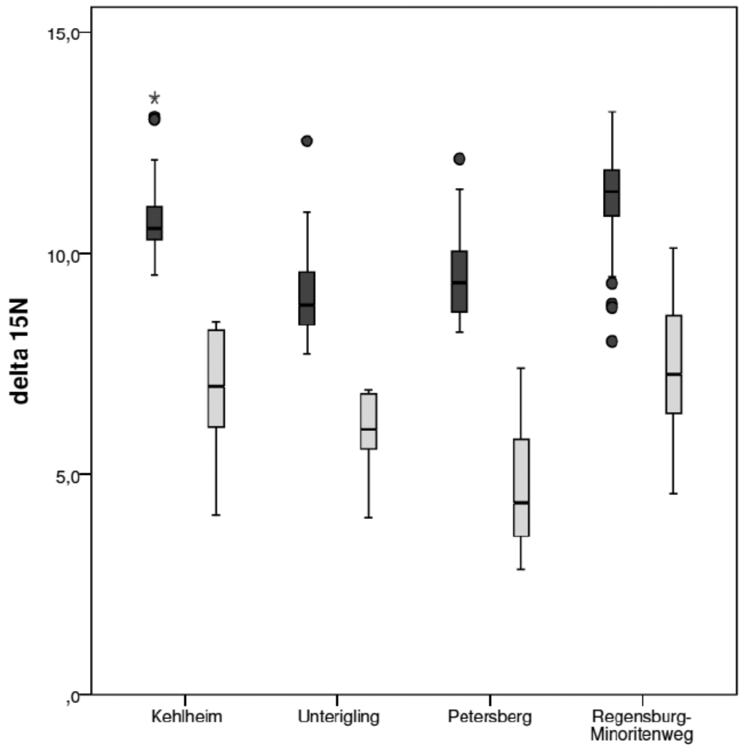

Fig. 1. Comparison of collagen δ15N values in humans (dark grey bars) and cattle (light grey bars) from four medieval sites in Upper Bavaria. Baseline herbivore δ15N varies across sites, which is reflected in the human collagen isotopic ratios (Harbeck, von Heyking, in press).

are produced by a regular consumption of animal protein, same ratios in different populations do not indicate that these people lived on same diets. For the determination of the local herbivore baseline δ15N value, bones from strict herbivores (cattle, horse) from the same site should be analyzed together with the human samples, which is widely practiced. The importance of accompanying animal bone analyses is illustrated by fig. 1, which shows the variability of collagen δ15N in cattle and humans from four medieval burial sites in Upper Bavaria, Germany (Harbeck, von Heyking in press). This study reviews isotopic analyses of human skeletal finds for the reconstruction of dietary behaviour during late antiquity and medieval times. Although all finds come from roughly comparable ecological settings, they do differ in terms of date and context. Kelheim and Unterigling are early medieval sites dating between the 6th and 10th century

AD, and in both cases, the settlement and the related graveyard have been excavated. The human skeletal remains had been investigated in a comparative palaeodemographic study focusing on the human population development in early medieval Bavaria (Strott 2006). At the Petersberg site, the majority of human skeletal finds were dated into the 10^{th} to 14^{th} century, and is associated with a monastery (Lösch 2009). Regensburg-Minoritenweg finally is a site representing the graveyard of a former poor-house dated into the 12^{th} to 16^{th} century (Dallmeier, Condreanu-Windauer, Haebler 2009). A mere look at the isotopic data presented in fig. 1 could suggest that the individuals buried at the four sites had different access to animal protein according to the variability of human $\delta^{15}N$-values. The reasons for these apparent differences could rather easily be explained by the different socio-ecological backgrounds at first glance. However, when human $\delta^{15}N$-values are compared with those of herbivorous cattle, it becomes clear that the baseline data are site specific and have primarily nothing to do with the living conditions of humans. In fact, differences in the proportion of animal protein in the human diet differs to a much smaller extent, if at all. The considerable site specific variability of cattle $\delta^{15}N$ can be due to several reasons, one important factor is the manure of arable land (Bogaard *et alii* 2007; Fraser *et alii* 2011). Mere comparison of human isotopic ratios without considering the local ecological herbivore baseline would lead to the false assumption that the two populations from the Unterigling and Petersberg site (fig. 1) had less access to animal protein than the other two populations.

While collagen $\delta^{15}N$ gives clues to the overall dietary quality in terms of bioavailable protein, it does not readily quantify the overall percentage of animal protein in the daily diet. That a full trophic level effect averages +3‰ is commonly agreed upon and has frequently proven to be a reasonable figure, however, this trophic level effect may vary because of metabolic and physiological parameters (Sponheimer, Robinson, Ayliffe 2003). Especially the choice of the herbivore taxon for the establishment of the baseline herbivore $\delta^{15}N$ is crucial because of the species specific drinking behaviour. Water conserving animals have much higher meat $\delta^{15}N$ ratios because they excrete a highly concentrated urine containing the metabolic end product urea, which is considerably depleted in the light isotope ^{14}N (Ambrose 1991). This is but one aspect which supports the claim that stable isotopic data are proxy data. A look at fig. 1 clearly shows that e.g. an interindividual difference in $\delta^{15}N$ of 1‰ does not imply that the one with the higher ratio consumed more animal protein equivalent to one third of a trophic level effect, no such simple linear relationship exists.

The linear relationship applies to the δ-values and the abundance of the heavy isotope (^{15}N, ^{13}C) in the food (Fry 2006). Therefore, $\delta^{15}N$ is a function of the abundance of ^{15}N in the food, which in turn is a function of the concentration of nitrogen as such in the food. While animal protein contains about 16% nitrogen, plants such as cereals will contribute as little as 3% nitrogen. In terms of carbon, the difference between plants (about 46%) and animal protein (about 43%) is by far less pronounced (Araus *et alii* 1997, 1999; van Klinken 1999; Fraser *et alii* 2011; Heaton *et alii* 2009). As a consequence, the animal part of the daily diet is always overrepresented by the collagen $\delta^{15}N$ value in the tissues of omnivorous feeders such as humans due to the composition and digestibility of this food component (DelRio, Wolff 2005). Only as long as a δ-value in the consumer's collagen is the product of a mixture of dietary components which contribute equivalent amounts of carbon and nitrogen and are assimilated in the same way – e.g. a mixture made up of C_3 and C_4 plants -, then the δ-values of these dietary components will mix in a linear way. If the dietary components differ in terms of element content and digestibility, they will no longer mix linearly in the consumer's tissue.

2. Mixing models

In modern ecological science, stable isotopes serve as a tracer for the reconstruction of food webs by sourcing the dietary contributions and routing of amino acids (Fry 2006). Convenient computer programs such as IsoSource (Phillips, Gregg 2003), Isoconc (Phillips, Koch 2002, Phillips, Newsome, Gregg 2005), or SISUS (Ehrhardt 2010) are available which are very useful especially in complex ecosystems. By the measurement of one isotopic ratio, two dietary components can be differentiated, measurement of two isotopic ratios permits the estimation of the contribution of three dietary components, and so on.

Consider a herbivore or strict vegetarian with a collagen $\delta^{13}C$ value of -17‰, which consumes both C_3 and C_4 plants with average $\delta^{13}C$ values of -26‰ and -13‰, respectively. In this case, linear isotopic mixing is appropriate. The mixture of the C_3 (x) and C_4 (y) plant contribution is assessed by $\delta^{13}C_{consumer} = f_x\delta^{13}C_x + f_y\delta^{13}C_y$, with f_x (=proportion of C_3 plants) + f_y (=proportion of C_4 plants) = 1. The consumer's diet had an average $\delta^{13}C$ of -22‰ after adjusting the collagen value by the ca. +5‰ fractionation factor from diet to the consumer's protein (Ambrose 1993). In this example, f_x is 0.69, and f_y is 0.31, indicating an approximately 30% contribution of C_4 plants.

Usually, both $\delta^{13}C$ and $\delta^{15}N$ are measured together in bone collagen, therefore, it is possible to identify three main dietary components x, y, and z by use of the formula for linear mixing: $\delta^{13}C_{consumer} = f_x\delta^{13}C_x + f_y\delta^{13}C_y + f_z\delta^{13}C_z$, and $\delta^{15}N_{consumer} = f_x\delta^{15}N_x + f_y\delta^{15}N_y + f_z\delta^{15}N_z$, with $f_x + f_y + f_z = 1$. Since a major part of human food is always made up of plants (with very few exceptions of dietary specialists such as traditional Inuit populations), the isotopic mixture in the consumer's collagen can no longer be linear, because of the different element contributions and digestibility of the food components. Hence, a concentration-weighted mixing model has to be established (Phillips, Koch 2002), which takes the assimilated biomass and the carbon and nitrogen content of the food sources x, y, and z into account.

Next, the dietary end members of the food web have to be defined which can only be based on archaeofaunal assemblages and archaeobotanical remains. The use of modern reference material is not recommended because it is highly probable that ecological isotopic baselines have changed. Again, one has to rely on accompanying isotopic analyses of animal bone finds associated with the site, whereby the gross dietary preferences and the physiology of the animal taxa must be known. As has been shown by fig. 1, even strict herbivores such as cattle will exhibit a certain interindividual isotopic variability. It is therefore recommended to analyze more than just one individual per taxon. If no accompanying skeletal remains from animals are available, dietary end members may be defined by animal bone analyses from other – hopefully largely contemporary – sites in the vicinity, although one must be aware of the fact that this will introduce a higher uncertainty into the final data interpretation. But sometimes, this will be unavoidable. Moreover, botanical remains are frequently also not available, although stable isotope analyses have successfully been performed on archaeobotanical finds since long (e.g. DeNiro, Hastorf 1985; Marino, DeNiro 1987). Most frequently, the average isotopic values of the plant cover at the site has to estimated by herbivore collagen isotopic data minus fractionation factor (see above).

Possible dietary end members could be for instance "domestic herbivores" and "freshwater fish". In case that the isotopic signals of cattle, sheep, goat etc. are similar, several species may be lumped together to form one gross end member with an average isotopic composition ("*a priori* aggregation" according to Phillips *et alii* 2005). Next, stable isotopic data of the food sources have to be calculated by adjusting the measurement data according to the fractionation factors commonly agreed upon (Newsome *et alii* 2004; Doppler *et alii* 2010): The average isotopic signature of the consumer's diet can be assessed by $\delta^{13}C_{consumer\ collagen}$ -5‰

and $\delta^{15}N_{consumer\ collagen}$ -3‰, the average isotopic composition of animal derived food can be assessed by $\delta^{13}C_{meat} = \delta^{13}C_{animal\ collagen}$ -4‰ and $\delta^{15}N_{meat} = \delta^{15}N_{animal\ collagen}$, and finally the average composition of vegetal food by $\delta^{13}C_{herbivore\ collagen}$ -5‰ and $\delta^{15}N_{herbivore\ collagen}$ -3‰.

In a recent study, a palaeofood web was established for Neolithic human populations from Bavaria (Hagl, Grupe in prep.). Collagen isotopic data from 92 individuals from 32 burial sites dating from 5,500 until 2,000 BC, which had been published previously (Asam, Grupe, Peters 2006), were compared with isotopic data of 120 animal bone finds representing 32 taxa from about 3,500 BC (Bösl, Grupe, Peters 2006). At this point, the claim of putting the data from human and animal bones from the same site into one and the same food web is violated, and the assessment of dietary preferences will be more biased to a certain extent. However, the faunal assemblage used in this study was excavated at the Neolithic Pestenacker site in Bavaria, where the whole material had been wet-sieved. As a result, also the tiny bones of e.g. freshwater fish were recovered, and the isotopic vertebrate food web from this site is one of the most comprehensive ones in Bavaria (Bösl, Grupe, Peters 2006).

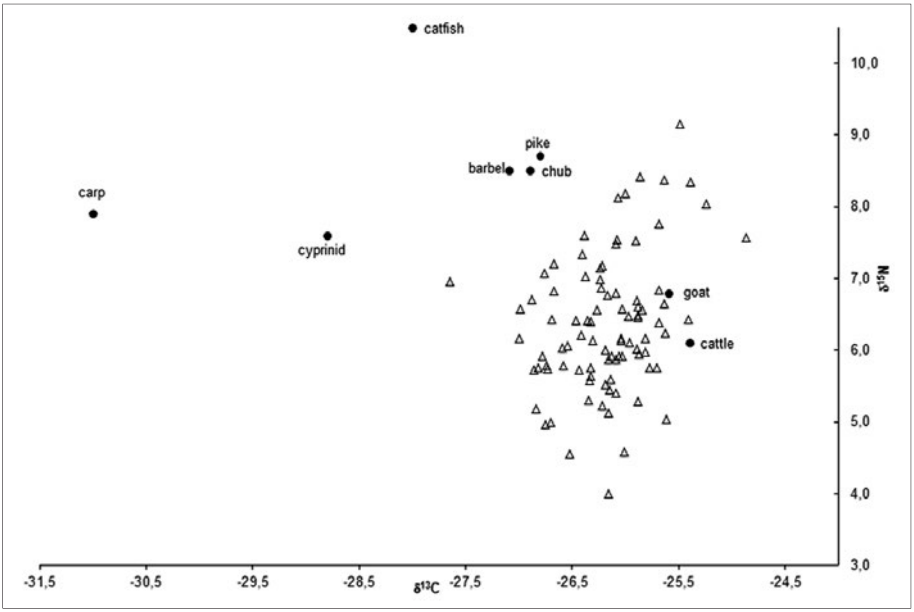

Fig. 2a. Isotopic composition of individual human diets (triangles), and a selection of the most plausible dietary end members for a gross palaeofood web in Neolithic Bavaria (Hagl, Grupe, in prep.). Isotopic data published by Asam, Grupe, Peters (2006), and Bösl, Grupe, Peters (2006).

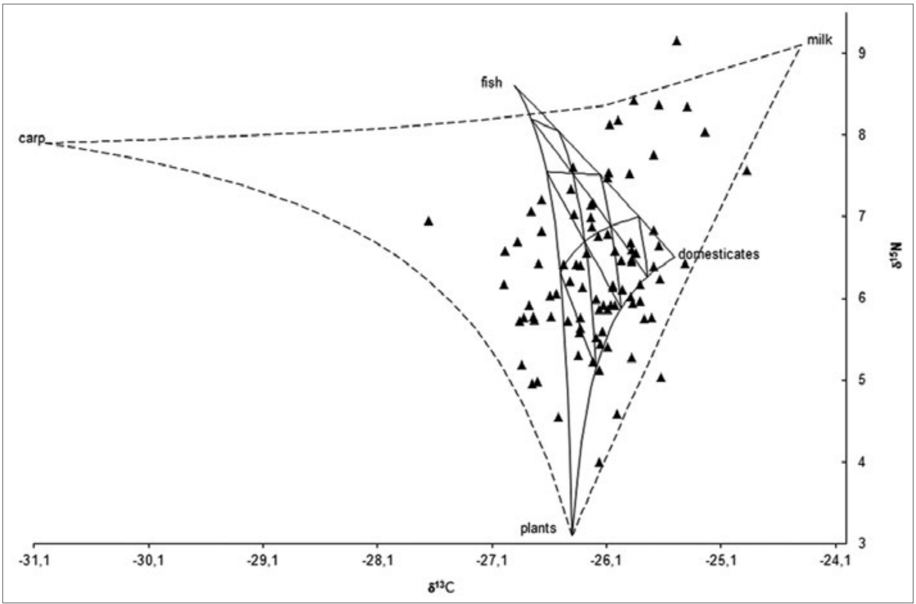

Fig. 2b. Concentration-weighted Neolithic food webs based on plants, meat from domesticates, and freshwater fish (chub, barbel, pike) (solid lines), and alternative food web based on plants, carp, and milk (dotted lines) (Hagl, Grupe, in prep.). Calculation with isoconc1_01.

The first information which is depicted from the gross food web in fig. 2a is that individual human dietary preferences were highly variable in the course of the Neolithic. Three taxa of freshwater fish had very similar isotopic signatures (chub, barbel, pike) and could be lumped into one category of freshwater fish, while e.g. the carp exhibits a conspicuously negative stable carbon isotopic signature. Taking the mean value of cattle and goat as the end member for "meat from domesticates", calculating the average isotopic signature of plant food from the collagen of these herbivores, and using the isotopically similar fish finds as third end member results in a food web which includes only about 50% of all human diets (fig. 2b). Individuals who combine more positive $\delta^{13}C$ and $\delta^{15}N$ values which are no longer compatible with the consumption of freshwater fish, and individuals with more negative $\delta^{13}C$ values fall outside the food web delineated by these three end members. The latter group fits into the food web when the carp is chosen as a representative of freshwater fish. The other group however, the $\delta^{15}N$ values of which indicate a diet higher in animal protein, necessitates the choice of a hypothetical end member, because no animal bone finds were available in the archaeofaunal assemblage which exhibit the appropriate isotopic signatures. Based on the internal trophic level effect of lactating mammals (e.g. Schurr 1997; Nitsch, Humphrey, Hedges 2011), this missing end member could have been milk (or milk products). All but a few human individuals now fit into a food web with end members plants, carp, and milk (fig. 2b).

There is an ongoing debate on at what time a Neolithic farming community was capable of being based on dairy produce, or at least when milk and milk products were plentiful available for the early farmers. It holds at least for the Bavarian Neolithic individuals tested in this study that milk and milk products were not a regular part of the daily diet before the later Neolithic phases, whereas in the early and middle Neolithic, several individuals had even lived on a largely vegetarian diet (fig. 2c).

The application of mixing models for the reconstruction of human palaeodiet requires additional measurements of a considerable number of animal bone finds, but this effort is worthwhile. Keeping in mind that isotopic mixing models will hardly provide exact estimates of diet but are rather helpful in the assessment of overall gross contributions of potential food sources (Becker, Grupe 2012), then valuable information about for-

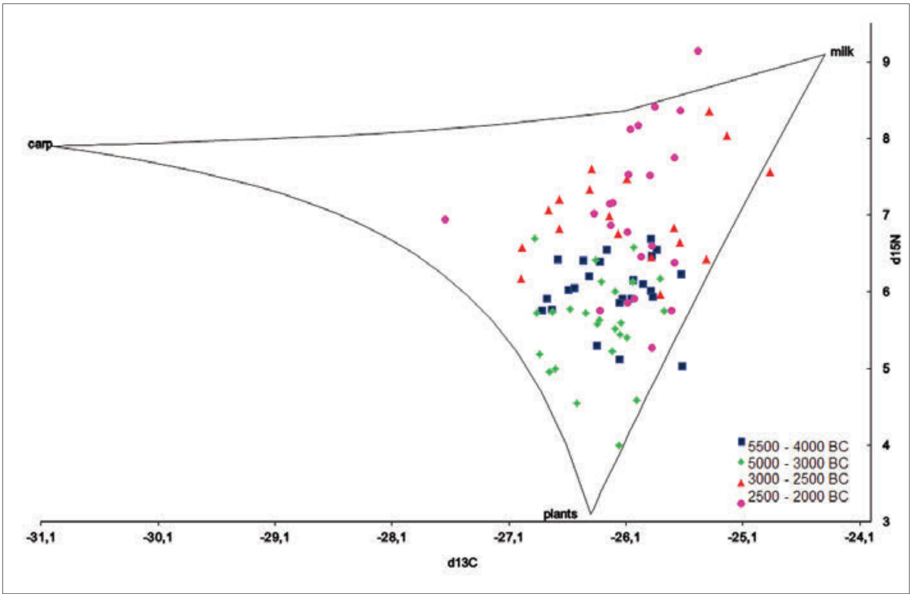

Fig. 2c. Conspicuously, all individuals who should have lived on a high protein diet (see fig. 2b) are dated into the later Neolithic phases and fit into a food web with the hypothetical end member "milk" (Hagl, Grupe, in prep.). Calculation with isoconc1_01.

mer subsistence economies will be obtained. Mixing models are without a doubt more informative than the common bivariate plot of collagen $\delta^{13}C$ and $\delta^{15}N$ values of humans and animals, and they permit the estimation of "missing end members", that is a potential dietary source which has not survived or was not recovered among the archaeofaunal assemblage.

3. Mixing muddles

Sometimes, mixing models do not provide unique solutions but rather produce a "mixing muddle" (Fry 2006). This may happen when too many dietary sources are involved, or when isotopic ratios of the sources can mix in different ways to produce the same isotopic ratio in the consumers' tissue. This may especially happen when coastal populations are studied. Such a classical mixing muddle occurred in the attempt of reconstructing the dietary economies at Viking Haithabu and its successor, the medieval town of Schleswig (Becker, Grupe 2012; Grupe, von Carnap-Bornheim, Becker 2013). Both settlements are located on opposing banks of the Schlei Fjord on the Jutland peninsula and had direct access to the Baltic Sea, terrestrial, and freshwater sources. Due to a considerably large data set consisting of isotopic analyses of 440 animal bone finds from both sites, representing 67 vertebrate species (Doppler *et alii* 2010), and ca 350 human skeletal individuals from both sites (Grupe, von Carnap-Bornheim, Becker 2013), a rather detailed vertebrate food web could be reconstructed. The trophic level effect of $\delta^{15}N$ is maintained, terrestrial herbivores, omnivores, and carnivores are separated as expected, and so are aquatic (freshwater fish and birds) and marine vertebrates (fish, birds, and mammals). It can be depicted from fig. 3 that despite overall high $\delta^{15}N$ values, human $\delta^{13}C$ is in agreement with respective data measured in terrestrial mammals, but, at the same time, falls right in between $\delta^{13}C$ measured in aquatic and marine vertebrates from the same sites. Stable carbon and nitrogen isotope values from bone collagen are thus underdetermined and therefore open to several interpretations with respect to diet. The majority of humans either lived on a high protein terrestrial diet (one should also consider eggs, milk and cheese), or they subsisted on a 50:50 freshwater and marine diet, or a 25:50:25 freshwater:terrestrial:marine diet, or any other diet made up from the available endmembers.

The human skeletal finds span a period of approximately 400 years and represent the bodily relics of the former inhabitants who witnessed the rise and fall of these two trade centres. The skeletons from Viking

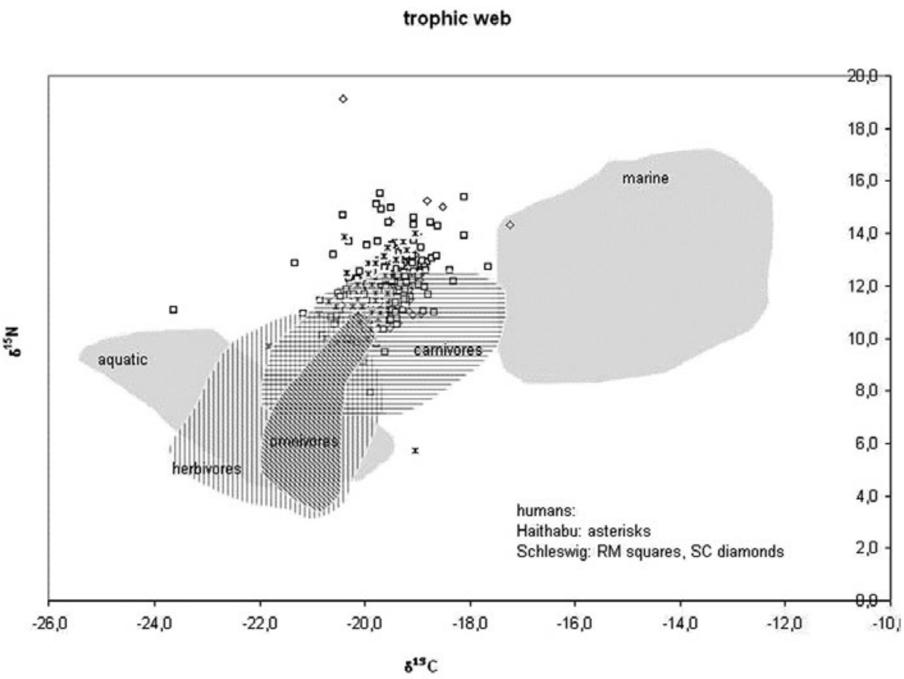

Fig. 3. Vertebrate isotopic food web and human stable isotopic data from Haithabu and the Schleswig Rathausmarkt (RM) and St. Clements (SC) sites (see text). The food web is based on mammals, birds, and fish (Doppler *et alii* 2010) (see Grupe, von Carnap-Bornheim, Becker 2013).

Haithabu originate mainly from the large graveyard encircled by the ring wall. Excellently preserved human skeletons from the Schleswig Rathausmarkt site could be grouped into two phases dendrochronologically: 1070 until 1140 AD, that is the time directly following the destruction of Haithabu, and 1140 until 1210 AD. The skeletons belonged to individuals that had lived within the confines of the medieval town, and the two phases coincide with the foundation of the settlement and its later rise. Finally, additional skeletons from the Schleswig St. Clements church graveyard (1250 until 1350 AD) are the relics of individuals stemming from a time when Schleswig was already undergoing changes in its political structure, these people were already excluded from far-distance trade. The scientific question was as to whether rise and decline of the trade centres were accompanied by an economic change which had manifested itself in changing dietary habits (Grupe, von Carnap-Bornheim, Becker 2013). Therefore, the mixing muddle had to be solved.

Because of the overall elevated $\delta^{15}N$ ratios in human bone collagen, and the assumption that plant food must have contributed to the daily diet, the question could be reduced on the possible detection of a fishing, farming, or mixed economy. Therefore, animal food sources were considered only, and a linear mixing model could be applied. Domestic mammals, freshwater fish, marine fish, and sea mammals were chosen as possible end members. As an example, the adjusted stable isotopic ratios of end members and adults from Viking Haithabu are plotted in fig. 4. Only one individual which should have largely lived on vegetarian food did not fall within the frame delineated by the chosen end members. It is also conspicuous that individual dietary preferences were highly variable, and that the "average human diet" deduced from collagen isotopic ratios is a meaningless figure.

To solve the mixing muddle, linear mixing models were calculated with the IsoSource software individual by individual for all adults from both sites (Grupe, von Carnap-Bornheim, Becker 2013). It is depictable from fig. 5 that marine food was preferred by the majority of individuals investigated

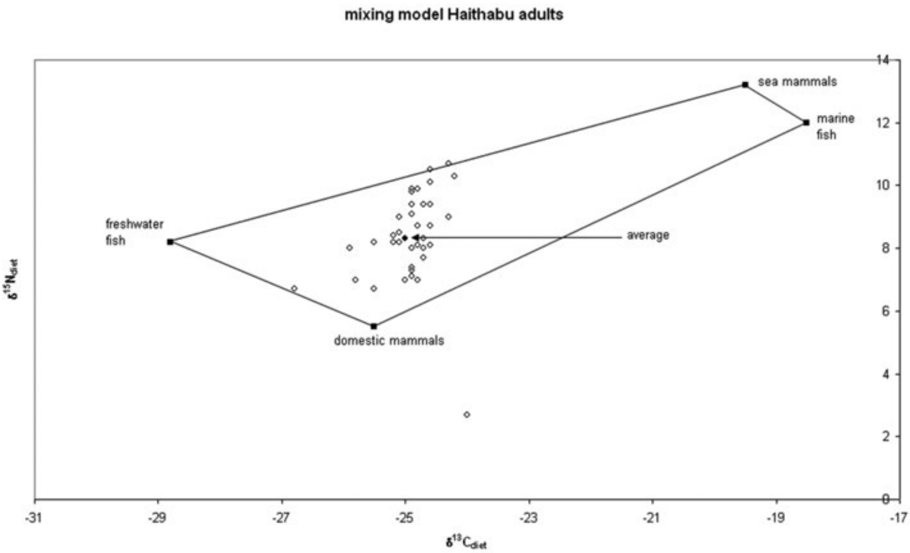

Fig. 4. Linear mixing model with four high protein dietary end-members for adult individuals from the Haithabu site. Note that the average adjusted collagen $\delta^{13}C$ and $\delta^{15}N$ values of all adults is a meaningless figure with regard to the overall individual dietary diversity. (see Grupe, von Carnap-Bornheim, Becker 2013).

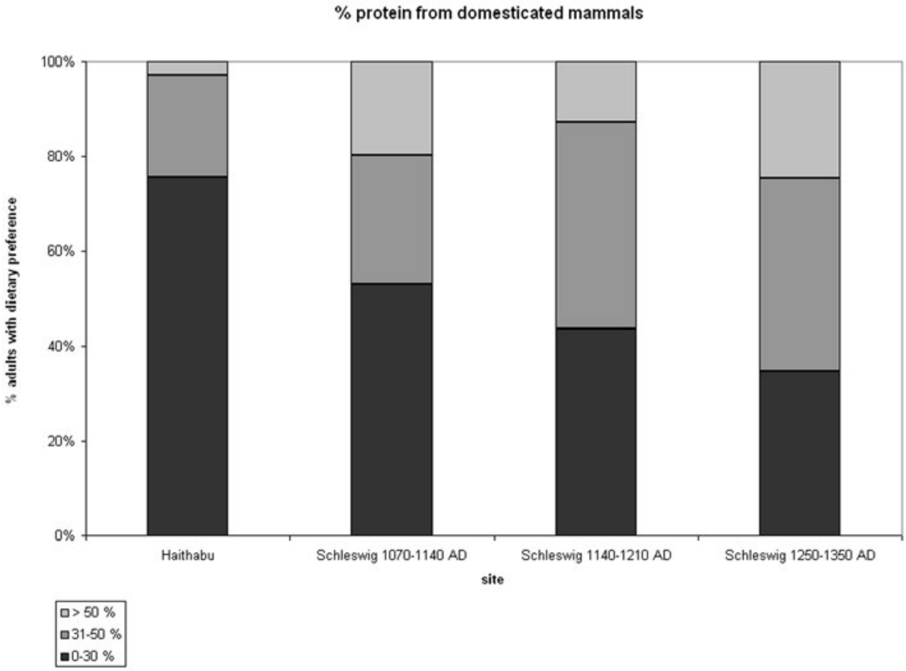

Fig. 5. From Viking Haithabu to 14th century Schleswig, the percentage of adults who obtained protein from domestic mammals rises, indicating a shift from fishing to farming.

from the prosperous trading sites (Viking Haithabu and the early phase of medieval Schleswig Rathausmarkt), but that a much higher number of individuals relied on protein acquired from domestic mammals when Schleswig lost its importance (late phase of medieval Schleswig Rathausmarkt and St. Clements site). The Vikings from Haithabu and the people buried on the St. Clements graveyard, which had already been excluded from long distance trade according the the archaeological record, represent the endpoints of this dietary range. This way, a change in subsistence economy could be reconstructed that accompanied the rise and decline of an early trade centre, whereby the change in major protein source did not impair overall protein supply. Certainly, such an application of mixing models on an individual basis is time consuming. However, a considerable variability in individual dietary preferences is expected in complex environments which permit for different subsistence strategies, and the preferred dietary economy may be totally obscured by population averages.

4. Conclusion and prospects

Stable carbon and nitrogen isotopic analysis from archaeological skeletons aiming at the reconstruction of palaeodiet has become routine in bioarchaeology since many years. It must be emphasized, however, that they will provide proxy data rather than hard evidence in terms of quantitative biomass contributions of the various food end members to the consumer. Research progress has shown meanwhile that ecological isotope baseline values may vary considerably in time and space, capable of introducing a considerable bias into any direct comparison between archaeological skeletons which have been excavated from different sites. The accompanying investigation of animal bone finds is very helpful for the assessment of the herbivore $\delta^{13}C$ and $\delta^{15}N$ baselines. The application of linear and concentration-weighted mixing models which have been developed in the ecological sciences are very suitable for a further refinement of different source contributions to human diet and are requisite for the reconstruction of subsistence economies. Further progress may be expected from elaborated isotopic routing methods and compound specific isotopic analysis (see overview by Boecklen *et alii* 2011). In contrast to modern trophic ecology, some uncertainties will always pertain while working with bioarchaeological remains, and an adequate research design is indispensable to avoid overinterpretation of collagen stable isotope ratios. Mixing models are superior over traditional comparative stable isotope interpretation because they help to better define the trophic relationship of humans, to solve mixing muddles, and to hypothesize (and test for) probable missing end members which are not preserved within the archaeological record.

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