Changing diet in a changing world

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Abstract

One of the most fundamental interactions between people and landscape is through food. How food is obtained, which kinds of food are eaten, and the way food is prepared are important parts of human identity. The transition from foraging to farming (from the Mesolithic to the Neolithic in the case of Danish prehistory) can thus be regarded as one of the most profound changes in human history.

The problem of change or continuity of diet during the Mesolithic-Neolithic transition has been debated vigorously over the past decades, with a focus on the question of whether aquatic resources continued to be exploited in the Neolithic. Different methods from archaeology and the natural sciences have come to different conclusions, based on different data and sample materials, which reflect different aspects and time scales of the prehistoric economy.

In this study, I will show how analyses of bones and pottery can add to our understanding of the complex dietary situation during the Neolithisation, when hunting, fishing and gathering was practised at the same time as dairy husbandry and cereal agriculture. I will place the results of the Femern project into their south Scandinavian context and discuss how cultural identity may be reflected in the foods produced and eaten by different groups at the time around 4000 BCE.

Femern project; diet; food; Neolithisation; pottery

Introduction

One of the most fundamental interactions between people and landscape is through food. People depend on the resources that are provided by their environment. At the same time, people influence the environment by their actions, through hunting, fishing, gathering and of course more fundamentally through agriculture. How food is obtained, what kinds of food are eaten, and the way food is prepared are important parts of human identity. The transition from foraging to farming can thus be regarded as one of the most profound changes in human history. This is the case for all societies where such transitions occur, regardless of when or where in the world this happens. In the case of Danish prehistory, the introduction of agriculture is the most important aspect of the shift from the Mesolithic to the Neolithic.

The problem of change or continuity of diet at the Mesolithic-Neolithic transition in northwest Europe, especially Britain and Denmark, has been debated vigorously during the past decades, with a focus on the question of whether aquatic resources continued to be exploited in the Neolithic (Barberena and Borrero 2004; Blankholm 2008; Fischer 2007; Fischer *et al.* 2007; Hedges 2004; Lubell *et al.* 1994; Milner *et al.* 2004; 2006; 2007; Richards and Schulting 2006; Richards and Hedges 1999; Richards *et al.* 2003; Schulting and Richards 2002; Tauber 1981b; 1981a; 1983; Villotte *et al.* 2014). Different archaeological and bioarchaeological methods have exposed the various aspects of the economy, diet and cuisine. Each specialized discipline can only analyse certain datasets and can come to different conclusions than other methodologies that focus on different sample materials, datasets, geographical areas or timescales. Therefore, the apparently contradictory conclusions of different studies actually show the overall variability of diet during the Neolithisation.

In this study, I will show how analyses of bones and pottery can add to our understanding of the complex dietary situation during the Neolithisation and explore the relationship between hunting, fishing and gathering with dairy husbandry and cereal agriculture. I will put the results of the Femern project into their south Scandinavian context and discuss how cultural identity may be reflected in the foods produced and eaten by different groups in the time around 4000 BCE.

This study focuses on two groups of finds. Firstly, I will present stable isotope measurements on animal bones and on wood, as they can be regarded as proxies for the stable isotope values of the food that was prepared and consumed at these sites. Secondly, I will summarize isotopic and biomolecular analyses of ceramic sherds. This includes analyses of food crusts on the sherds, which most probably are dominated by the last cooking event, as well as analyses of the ceramic matrix, which contains biomolecules absorbed during earlier cooking events.

Lipid analysis can pick out individual compounds that are indicative of individual ingredients, which might be overlooked by bulk stable isotope analysis. On the other hand, bulk stable isotope analysis identifies the ingredients that contributed most to the food crust. An additional advantage is that bulk stable isotope analysis uses the same sample material as radiocarbon dating, so this method is ideal for predicting reservoir effects in food crusts.

Stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$)

Ideally, we would measure isotope ratios of all the ingredients that were available in prehistory in order to reconstruct the meals prepared in the analysed pottery. This is impossible for several reasons: In the case of plant foods, the only materials available for analysis are wood and hazelnut shells – and not the edible parts of the plants. In the case of animal food, only the bones are preserved. Therefore, we have to use the available material, informed by analyses on modern reference samples, as proxies for the Stone Age food resources.

Modern reference samples are only useful to a limited extent because of anthropogenic effects that distort the δ^{13} C and δ^{15} N values, such as the Suess effect (decreasing δ^{13} C values due to combustion of fossil fuels) or modern agriculture with intense manuring, either with animal manure (increasing δ^{15} N values) or with chemical fertilizers (decreasing δ^{15} N values), as well as heated greenhouses (decreasing δ^{13} C values). Modern land-use practices can also have altered the environment to such a degree that plants growing "wild" and unmanaged today will have different isotope values than their Stone Age counterparts. This can also be the case for wild animals, *e.g.* a wild boar that, although shot in a forest, had fed mainly on maize, a C4 plant (Philippsen 2012, 123).

δ^{13} C values of plants and wood samples

The δ^{13} C values of wood (trunk, branches and roots) are consistently more enriched than those of the leaves (Li and Zhu 2011), which would have been used *e.g.* as leaf fodder for cattle. Therefore, we cannot use wood δ^{13} C values directly to reconstruct the δ^{13} C values of the plant food. In addition, there are no preserved remains of the plant food that was actually consumed by people, such as leafy vegetables, fruits, berries, nuts, roots and tubers. Mushrooms, although more closely related to animals than to plants, can be included here as well: we only have some samples of tinder fungus, but no finds of edible mushrooms.

The wood δ^{13} C values, however, can be used to explore the variability one has to expect at the base of the food chain (Philippsen *et al.* 2019). While the absolute values might not be directly comparable, the broad ranges found in the wood samples can also be expected in other parts of the plants.

 $δ^{13}$ C values in dense forests are generally lower than in more open landscapes. The CO₂ from decaying organic material has $δ^{13}$ C ratios comparable to that of the organic material. As about 99% of the organic matter produced in a forest is returned to the atmosphere as CO₂, the air in a dense forest is enriched by CO₂ from decaying plants, which has $δ^{13}$ C values close to those of the plants (around -25‰), and thus lower than the atmosphere's -7‰. This so-called canopy effect is most pronounced in leaves growing closer to the ground. It can shift $δ^{13}$ C ratios by *c*. 3‰ to 5‰ (Medina and Minchin 1980; Vogel 1978), which means that about 15% of the carbon in leaves growing close to the ground is derived from decaying organic matter (Vogel 1978). Other physiological causes have been suggested, such as altered fractionation due to photosynthesis in low light or nutrient deficiency.

This can also lead to lower δ^{13} C values along the food chain to forest and even aquatic fauna (Francey and Farquhar 1982; van der Merwe and Medina 1991), for example in the bones of herbivores that mainly browsed in forests. Thus, the canopy effect has been suggested as an explanation for the fact that aurochs in Denmark tend to have lower δ^{13} C values than contemporaneous domesticated cattle (Noe-Nygård and Hede 2006). However, the forests have to be very dense in order to result in a measurable canopy effect (Drucker *et al.* 2008). In the case of ¹⁴C concentrations, the canopy effect is less important for prehistoric samples, as most of the carbon is recycled shortly after the formation of the primary plant matter. However, it can be an issue in modern reference samples, as *e.g.* leaves growing next to a motorway were found to have ¹⁴C-concentrations up to 9% lower than the atmosphere (Münnich 1961).

δ^{13} C and δ^{15} N values of animal bones

In addition to the above-mentioned canopy effect, other aspects can influence the δ^{13} C values of animal bones. The main factor in Danish Stone Age research is the proportion of marine versus terrestrial resources. The difference between C3 and C4 photosynthetic pathways is irrelevant, as C4 plants do not occur naturally in relevant numbers and domesticates such as millet are only introduced later. Only few edible C4 plants are native to northern Europe, such as purslane (*Portulaca oleracea*). The C3 cycle is particularly suited to wet and mesophytic environments (Browman 1981) and C3 plants are preferred by herbivores because they are easier to digest.

There is a δ^{13} C fractionation of about 5‰ from plant food to animal bone collagen and generally less than 1‰ per subsequent trophic level (Katzenberg *et al.* 2000; Lanting and van der Plicht 1998; Schoeninger and DeNiro 1984). The δ^{13} C values in bone collagen reflect the δ^{13} C values of the protein component of the diet, especially in the case of protein-rich diets, but depend also on the amount of protein in the diet and on the difference in the δ^{13} C values of protein and non-protein fractions (van Strydonck *et al.* 2009).

δ¹⁵N values mainly reflect the animal's trophic level (Ambrose 2001; Schoeninger and DeNiro 1984; Schoeninger *et al.* 1983) but can also be influenced by physiological and environmental factors (Knowles and Blackburn 1993). For example, it has been observed that horses from Neolithic contexts had lower δ¹⁵N values than other contemporary herbivores (Klassen *et al.* 2023; Stevens *et al.* 2010). This could be caused by differences in habitat/diet (*e.g.* horses browsing on trees), or physiology (non-ruminant vs. ruminant). A similar effect, horses having lower δ¹⁵N values than other animals, has already been observed for a Middle Pleistocene context (Kuitems *et al.* 2015, Table 3), so it could be a general characteristic of the physiology or diet of Equidae.

Some factors, such as those caused by aridity, are not relevant for Denmark and will not be discussed further here. Fertilizing grassland or crops with animal manure can result in δ^{15} N increases by about one trophic level, or *c*. 3.5‰ (Bogaard *et al.* 2013; Fraser *et al.* 2011). This increase will be transferred to increased δ^{15} N values in herbivore bone collagen. When under the control of humans, increased δ^{15} N values can be caused by a different mechanism. The animals can have more "omnivorous" feeding patterns, including *e.g.* pondweed or human food refuse (Bonsall *et al.* 1997; Schwarcz 1991).

$\delta^{\scriptscriptstyle 13}C$ and $\delta^{\scriptscriptstyle 15}N$ values of food crusts on pottery

There are large differences between the δ^{13} C values of bone collagen and of the other edible parts of the animal, with differences of 1.5 to 4‰ between fish flesh and bone collagen (Katzenberg *et al.* 1995; Lanting and van der Plicht 1998), or of more than 7‰ between bone collagen and body fat in an ungulate (Browman 1981). Fat is generally depleted in δ^{13} C when compared to lean meat (Bonsall *et al.* 1997; DeNiro and Epstein 1976; Parker 1964). Therefore, isotope values between bone collagen and food crusts are not directly comparable.

Fully terrestrial samples have isotope ratios of $\delta^{\rm 13}C$ =-29 to -26‰ and $\delta^{\rm 15}N$ =2.5 to 6‰.

Fully marine samples have δ^{13} C=-18 to -15‰ and δ^{15} N around 10‰ or higher (Philippsen 2012, and references therein). Most food crust samples would be expected to lie on a mixing line between fully terrestrial and fully marine. Values outside of the

mixing line are most probably caused by mixtures of ingredients with different carbon and nitrogen concentrations. For example, a mixture of protein-rich terrestrial food with lipid-rich marine food would result in a value below the mixing line.

The effect of heating (such as boiling or roasting) or fermentation on the isotope values is small and no systematic fractionation effects have been observed (Abonyi 1993; Bonsall *et al.* 1997; Boudin *et al.* 2009; DeNiro and Hastorf 1985; Hastorf and DeNiro 1985; Katzenberg *et al.* 2000; Marino and DeNiro 1987; Privat *et al.* 2005).

Lipid analysis

Lipids absorbed in the ceramic matrix are protected from degradation and contamination and are thus regarded as an ideal sample material (Heron *et al.* 1991). There is a long tradition for fatty acid analysis of prehistoric samples (Chapman and Plenderleith 1926; Charters *et al.* 1993; Condamin *et al.* 1976; Evershed 2008; Evershed *et al.* 2001; Formenti and Condamin 1978; Isaksson 1997; Olsson 2003; Olsson and Isaksson 2008; Mathiassen 1935; Mottram *et al.* 1999; Plant 1879; Rottländer 1985; 1990; Rottländer and Blume 1980; Rottländer and Schlichtherle 1980; 1983; Van Diest 1981). Certain fatty acids are indicative of heated fish oil (Hansel *et al.* 2004) and are thus direct evidence for the preparation of marine food.

In the early 2000's, preparative capillary gas chromatography (PCGC) was used to isolate individual fatty acids from absorbed lipid residues (Copley *et al.* 2003; Stott *et al.* 2001; 2003). The C_{16.0} and C_{18.0} fatty acids are targeted here, as they are the most abundant fatty acids (Berstan *et al.* 2008). In addition to radiocarbon dating, these fatty acids can also be used for δ^{13} C analysis. The δ^{13} C values of the C_{16.0} and C_{18.0} fatty acids, and especially the difference between the two, termed Δ^{13} C, indicate the presence of dairy fat and groups the lipid residues into marine, non-ruminant adipose, ruminant adipose and ruminant dairy (Copley *et al.* 2003; Dudd and Evershed 1998; Mukherjee *et al.* 2005). The above-mentioned canopy effect would also lead to lower δ^{13} C values of the fatty acids, but the Δ^{13} C values would be unaffected (Mukherjee *et al.* 2005).

Integrated pottery analysis

The most comprehensive cuisine reconstructions are obtained when the different methods are combined. Lipid analysis can pick out individual compounds that are indicative of individual ingredients, which might be overlooked by bulk stable isotope analysis. On the other hand, bulk stable isotope analysis identifies the ingredients that contributed most to the food crust. An additional advantage is that bulk stable isotope analysis uses the same sample material as radiocarbon dating, so this method is ideal for predicting reservoir effects in food crusts (because the carbon used for radiocarbon dating is the same, and thus from the same source(s), as the carbon used for bulk stable isotope analysis).

Food crusts are biased towards the final cooking events, while lipids absorbed in the clay matrix are only slowly replaced and show no strong signal of the final cooking (Miller *et al.* 2020).

Study site

An overview of the Femern project and descriptions of the individual sites is provided by Måge et al. (this volume). Here, I will summarize the main aspects of the sites considered in this study.

Surveys and rescue excavations prior to the construction of the Femern Belt Tunnel resulted in the discovery of numerous archaeological sites from the past 10000 years. This study focuses on sites discovered in an area of former sea floor, which had been diked after a storm surge in 1872. Culturally, these sites can be assigned to the Danish Mesolithic Ertebølle Culture (EBC) and the Neolithic Funnel Beaker Culture (TRB). They date to around 4000 BCE, a period that has traditionally been termed the Neolithisation of Denmark. The Stone Age coastal landscape changed continually, with ephemeral barrier islands forming temporary lagoons and shallow fjords. The sediments in the study area reflect the postglacial sea-level rise: glacial till with soil formation horizons is overlain by freshwater peat, then marine gyttja and finally marine-deposited sand (Bennike et al. 2022; Groß et al. 2018). The sites covered in this study comprise depositions and refuse areas in the shallow water, but no dry-land settlement remains or burial sites. While the preservation of organic remains is excellent, the dynamic coastal environment has caused those sites to be palimpsests of mixed and redeposited artefacts and ecofacts. There is no stratigraphical relation between the finds. Due to the continuous sea level rise, the same type of layer (e.g. freshwater peat or marine gyttja) formed at different times, depending on the site's elevation and distance from the shore. Only a few finds were still in situ, including fish weirs, stakes and artefacts stuck into the sea floor, while the sediments around them may have been eroded and re-deposited. It is therefore impossible to assign individual artefacts to a specific time period just by measuring their geographical position and elevation. A minor proportion of the ceramic sherds can be assigned to the EBC or one of the phases of the TRB. Apart from these, only directly dated samples can be considered when investigating changes of economy and diet over time. Radiocarbon dates of the different artefact groups are provided by Måge *et al.* (this volume). For example, the radiocarbon dates show that domesticated animals had already appeared before 4000 BCE, while fish weirs only gained in importance during the Middle Neolithic.

Here, I will present an overview of the isotopic and biomolecular data from the Femern project. A full analysis, including comparisons to data from other sites, will be published later (Philippsen et al. in prep.).

Materials

I include 130 radiocarbon dates of bones from the entire Femern project. These samples were selected because of their archaeological interest, not for palaeodietary reconstructions. All bones and bone artefacts had been deposited in the former sea floor. Some were food refuse thrown into the shallow water, others were placed deliberately at certain locations, such as a concentration of mandibles found within a circular structure of wooden stakes (e.g. Sørensen this volume).

As no burials were found, only four stray finds of human bones are available for the entire project. None of these dates to the Mesolithic. Therefore, we use stable isotope and lipid analyses of food crusts on pottery and ceramic sherds to reconstruct the cuisine rather than the long-term diet that would be reflected in the human bones.

Stable isotope values were obtained from 52 food crusts on pottery sherds from the sites of Syltholm II (MLF00906-I, MLF00906-II) and Syltholm XIII (MLF00939-I; cf. Måge *et al.* this volume). Food crusts adhering to two stone slabs thought to have a food preparation function (finds: X5486 and X9077) were analysed by GC-MS, as well as the food crusts on potsherds and sediment samples from putative cooking pits. Based on the results of the GC-MS analysis, six samples were selected for GC-C-IRMS analysis. These include one Ertebølle and five Funnel Beaker vessels. These data were published in Courel *et al.* (2020) and Cubas *et al.* (2020), respectively. In addition, Vasiliki Papakosta (Stockholm University) conducted lipid residue analysis on food crusts on nine Ertebølle potsherds (Papakosta *et al.* 2019).

Methods

Radiocarbon dating and stable isotope analysis of animal bones and food crusts

Collagen was extracted from bone samples according to the protocol by Longin (1971), with modifications by Brown *et al.* (1988) and Jørkov *et al.* (2007). All age determinations were performed by AMS by measuring the ratio of ¹⁴C to ¹³C atoms at the Aarhus AMS Centre, Department of Physics and Astronomy, Aarhus University. The ages are stated in conventional radiocarbon years BP and corrected for isotope fractionation by normalising to δ^{13} C=-25‰ VPDB (Stuiver and Polach 1977). The radiocarbon ages are calibrated to calendar years before present (cal BP) using the IntCal20 calibration curve (Reimer *et al.* 2020). Marine samples are subject to a reservoir age, which can be estimated to be around 250 ¹⁴C years for the study area and period (Philippsen 2018). This value is similar to the reservoir age of 273 ± 18 ¹⁴C years reported for southern Kattegat in the Neolithisation period (Fischer and Olsen 2021). However, the reservoir age may have varied somewhat over the Holocene, and the ages of marine material are therefore more uncertain than the ages of terrestrial material (Olsen *et al.* 2009).

The δ^{13} C and δ^{15} N values of the bones were measured by isotope radio mass spectrometry (IRMS) at the Aarhus AMS Centre. The reported measurement uncertainties are 0.05 to 0.71‰ for δ^{13} C and 0.1 to 0.36‰ for δ^{15} N. δ^{13} C and δ^{15} N values of food crusts were measured at the University of Bradford and the University of York.

Lipid analysis (GC-MS and GC-C-IRMS)

Food crusts and dried sediment samples were ground and extracted with a dichloromethane/methanol mixture (2:1 v/v). A measured amount of an internal standard was added to each sample before analysis to allow quantification and the samples were derivatised before analysis. Gas chromatography (GC) was used to check the lipid preservation and presence of contaminants. Based on the GC results, samples were selected for gas chromatography – mass spectrometry (GC-MS) analysis. GC-MS analysis was carried out on an Agilent 7890A series GC attached to an Agilent 5975C Inert XL mass selective detector. Based on the GC-MS results, samples were selected for isotopic analysis (GC-C-IRMS) of the $C_{16:0}$ and $C_{18:0}$ fatty acids (gas chromatography – combustion – isotope ratio mass spectrometry).

Results and discussion

Radiocarbon dating and stable isotope analysis of animal bones and bone artefacts

In total, 130 radiocarbon dated bone samples were analysed in this study. Not all dated samples were large enough to allow for stable isotope (especially $\delta^{15}N$) measurements. For 129 of these samples, $\delta^{13}C$ values are available. 115 samples yielded $\delta^{15}N$ values. Error bars are excluded from the graphs for clarity and because in many cases the size of the symbol exceeds the size of the error bars. Due to space limitations, all radiocarbon dates and stable isotope measurements are available as supplementary material.

The stable isotope results (δ^{13} C, δ^{15} N) of human and animal bones from the Femern project are shown in fig. 1. This figure includes data from all archaeological periods examined in this project. Most samples belong to herbivores and have corresponding isotope ratios; δ^{13} C between -24 and -21‰, δ^{15} N between 3 and 9‰. Most of the herbivores lie in a narrow δ^{15} N range, though: Apart from one wild horse with δ^{15} N=3.2‰, a red deer with δ^{15} N=4.1‰ and two sheep/goats with δ^{15} N>8‰, the range is 4.7 to 7.8‰. Measurements on terrestrial herbivores are shown in a separate diagram together with the δ^{13} C values of wood samples as a proxy for vegetation δ^{13} C values (fig. 2).

The two sheep/goats with $\delta^{15}N>8\%$ are in the same area of the diagram as three humans, three wild cats and a dog; their diet can be regarded as terrestrial on a higher trophic level and/or a terrestrial diet with the admixture of some marine resources. The bone with $\delta^{15}N=9.9\%$ is a humerus from a sheep with a lot of cut marks; the osteological report does not mention that it is from a young individual. The bone with $\delta^{15}N=8.4\%$ is the left shoulder blade of a sheep, also with cut marks and also not classified as a young individual. A nursing effect can thus be excluded and the high $\delta^{15}N$ values must be a result of the diet. In the case of sheep, marine plants or macroalgae could have supplemented the fodder, whether provided by humans or sought out by the animals themselves. Goats, dogs and cats could have fed on food remains left by humans.

As described in the introduction, a very dense forest can cause a depletion in the δ^{13} C values of the vegetation, and in the δ^{13} C values measured throughout the food web based on this vegetation. There are only a few specimens where a canopy effect is probable: The only terrestrial herbivores that have δ^{13} C values below -23‰ are sheep/ goat, roe deer and red deer (fig. 2). The sheep/goat (the species could not be determined) with δ^{13} C=-24.2‰ is the oldest domesticated animal from the site (fig. 3; 5313 ± 32 BP, 4310–4304 (0.7%) and 4249–4046 (94.8%) cal BC, calibrated with IntCal20). It could have been browsing in the forest or have been fed leaf fodder. The red deer and roe deer bones span the whole range of *c*. 24 to 21‰, while the cattle/aurochs only have δ^{13} C values between *c*. 22.5‰ and 21‰.

The two sheep bones with the highest $\delta^{15}N$ values have been discussed above. Apart from these, there is also a group of five cattle bones with $\delta^{15}N>7\%$, while all other herbivores have $\delta^{15}N$ values below 7‰. Further studies will show whether there really are two isotopically distinct groups of cattle. Interestingly, some of the cattle and sheep/ goat have higher $\delta^{15}N$ values than all of the pig samples, although pigs are omnivores and sheep/goat and cattle are herbivores. The pigs were thus most probably not fed with food refuse, as this would have caused a higher trophic level and more marine $\delta^{13}C$ values.





Figure 1. Stable isotope values of bones from the Femern project.

Such an effect has been observed with wild boar from an Ertebølle kitchen midden site in Jutland (Maring and Riede 2019).

The horse bone has the lowest δ^{15} N value (3.2‰) of the dataset, which agrees with previous studies of prehistoric horse bones (Klassen *et al.* 2023; Kuitems *et al.* 2015; Stevens *et al.* 2010). This specimen of *Equus ferus* is dated to 2812 ± 29 BP (1051–897 (94.7%) and 867–857 (0.8%) cal BC, calibrated with IntCal20) and is thus too young to be relevant for a discussion of the Neolithisation process.

There are some apparent trends in fig. 2. For example, there seems to be a linear relation between the $\delta^{15}N$ and $\delta^{13}C$ values of *Bos taurus* with a correlation coefficient of R²=0.61. However, generally the sample numbers are too small to allow for meaningful statistical analyses.

Figure 3 displays the δ^{13} C values of the aforementioned taxa over time. It is difficult to discern any trends, as many animal species are only found from within short time periods. For example, the group of animals with the highest δ^{13} C values includes two harbour porpoises (*Phocoena phocoena*), two Eurasian otters (*Lutra lutra*) and two dogs (*Canis lupus* fam.) from a very narrow timespan. While the δ^{13} C values of around -10%



δ^{13} C, δ^{15} N of terrestrial herbivores bones

Figure 2. Upper part of the diagram: δ^{13} C and δ^{15} N values of terrestrial herbivores. Lower part: δ^{13} C values of wood from the Femern project (Philippsen *et al.* 2019), average $\pm 1\sigma$, as proxy for plant δ^{13} C values. The values in the diagram are in the same order as the species names in the legend.

are not unusual for porpoises, they are an interesting case for the dogs – these clearly had a largely marine diet, unlike the slightly later humans from this site. The marine diet of the otters indicates that they had lived at the coast and consumed marine fish, which is not unusual for the Eurasian otter (Kruuk 2006), and that they had not been caught in an inland lake or stream. However, the otter needs regular access to freshwater to clean its fur (Ozkazanc *et al.* 2019). Therefore, its presence indicates that there must have been access to a lake or stream nearby. The extended use of the sites by humans would, of course, not have been possible without access to freshwater either. However, for human use, a small freshwater spring would have sufficed.

Some trends can be observed in the δ^{13} C values over time. The *Ovis* δ^{13} C values increase with time (R²=0.72), while there is also a slight increase in *Cervus elaphus* δ^{13} C values (R²=0.35). This might indicate that the forest was being cleared and the sheep/goats were grazing in a more open landscape. Furthermore, they could consume larger amounts of seaweed and/or human refuse. This is supported by the increase in δ^{15} N values by 4500 cal BP (supplementary material). The δ^{13} C increase in red deer is



Figure 3. δ^{13} C values compared to the radiocarbon age of bones from the Femern project. This plot includes more data points than fig. 1, as not all samples were large enough to allow for a δ^{15} N measurement.

not accompanied by an increase in δ^{15} N. Therefore, their increasing δ^{13} C values can best be explained by a change in landscape, which became more open. In contrast, there is a decrease in *Sus* δ^{13} C values (R²=0.76). This would indicate that the pigs had a slightly more marine diet during the Ertebølle period and a more terrestrial diet later. However, there is no trend in the δ^{15} N values that could support this interpretation (supplementary material).

The four human bones, which unfortunately were all stray finds, show no trend over time. $\delta^{15}N$ values are only available for three of the human bones. They decrease from 9.6‰ in 4875 cal BP to 7.7 ‰ in 3738 cal BP – a decrease of less than one trophic level.

Food crust stable isotopes (δ^{13} C, δ^{15} N)

The stable isotope values of food crusts from the Femern project have been and will be published elsewhere (see introduction for details and references). A synthesis paper of all results including data tables is under preparation. Therefore, this section will only summarize the main results in figures (all data is available in the supplementary material).



Figure 4. Stable isotope results (δ^{13} C, δ^{15} N) of food crusts on sherds from one vessel, pot 22 from MLF00903-I. Left: full range diagram for comparability with the other isotope diagrams in this paper; right: detail.



Figure 5. Stable isotope values of food crusts on Funnel Beaker and Ertebølle sherds as well as lamp fragments. δ^{13} C in & VPDB; δ^{15} N in & AIR. The pottery type is indicated by the shape of the symbol: funnel beakers for Funnel Beaker pottery, pointed-based vessels for Ertebølle pottery, and shallow bowls for lamps. Crusts on the outer surface of the vessels are indicated by a lighter symbol.

The variability of the stable isotope values has been tested by analysing nine interior and two exterior samples from sherds of the same vessel, "Pot 22", from MLF00939-I. Although the results span a range of about 1‰ for δ^{13} C and 1 to 1.5‰ for δ^{15} N, depending on whether the exterior crusts are included, all values would indicate the same interpretation of terrestrial, low to middle trophic level food. I thus suggest regarding

EBC interior (n=9)	δ13C (‰ VPDB)	δ15N (‰ AIR)
Min	-26.69	2.99
Max	-18.32	9.70
Lamp interior (n=4)	δ13C (‰ VPDB)	δ15N (‰ AIR)
Min	-26.19	5.45
Max	-18.27	9.23
Lamp exterior (n=2)	δ13C (‰ VPDB)	δ15N (‰ AIR)
Min	-20.67	3.78
Max	-19.16	6.89
TRB interior (n=31)	δ13C (‰ VPDB)	δ15N (‰ AIR)
Min	-28.70	2.76
Max	-15.36	10.04
TRB exterior (n=6)	δ13C (‰ VPDB)	δ15N (‰ AIR)
Min	-26.21	6.08
Max	-20.88	10.17

Table 1. Minimum and maximum values of all analysed food crusts.

measurements on individual sherds as representative of the entire vessel, even though experimental studies have shown that some variation has to be expected when cooking mixed foods (Philippsen 2012).

The δ^{13} C values of all analysed food crusts are in the interval between -29 and -15‰. δ^{15} N values range from *c*. 2.5 to 10.5‰. Most values follow a mixing line between fully terrestrial (δ^{13} C=-29 to -26‰, δ^{15} N=2.5 to 6‰) and fully marine (δ^{13} C=-18 to -15‰, δ^{15} N around 10‰, fig. 5).

As shown in fig. 5, Ertebølle and Funnel Beaker pottery have the same range of isotope values and both pottery types were used for both terrestrial and marine resources. The funnel beaker δ^{13} C values span a larger range than those of the Ertebølle vessels. This could be caused by a diversification of food resources during the Funnel Beaker period, or could just be an effect of the larger sample size. The minimum and maximum values of all analysed food crusts are given in Table 1.

Lipid analysis (GC-MS and GC-C-IRMS)

Based on the GC-MS results, seven samples were selected as being suitable for isotopic analysis (GC-C-IRMS) of the $C_{16:0}$ and $C_{18:0}$ fatty acids: P145 X57, P251 X3363, P252 X3495, P253 X8352, P254 X9243, P256 X10588 and P257 X11841 (P=sample number, X=find ID).

Lipids were extracted both from food crusts and from the ceramic matrix of sherds. Fig. 6 displays the δ^{13} C values of the C_{16:0} and C_{18:0} fatty acids. The measurements on the Funnel Beaker sherds were made on five food crust samples, while the Ertebølle pottery includes one food crust sample and nine samples of the ceramic matrix. The funnel beaker samples display either purely marine or purely terrestrial (dairy) fats, while the values of the Ertebølle sherds vary between ruminant adipose fat, where an admixture of dairy cannot be excluded, and marine fat.



Figure 6. δ^{13} C values of the C_{16:0} and C_{18:0} fatty acids, measured in ‰ VPDB (Courel *et al.* 2020; Cubas *et al.* 2020; Papakosta *et al.* 2019). The pottery type is indicated by the shape of the symbol: funnel beakers for Funnel Beaker pottery (additionally coloured pink), pointed-based vessels for Ertebølle pottery. Ellipses indicate the typical isotopic ranges of modern reference fats. Left: all Funnel Beaker and Ertebølle sherds. Right: only Funnel Beaker sherds. Numbers indicate the Funnel Beaker type in those cases where it could be assessed (typological analysis of the pottery by A. Glykou, unpublished report).



Figure 7. Stable isotope values of food crusts on Funnel Beaker sherds. δ^{13} C in ‰ VPDB; δ^{15} N in ‰ AIR. Coloured numbers indicate the Funnel Beaker type, blue numbers for samples of the vessel's interior surface, red numbers for exterior samples. Text indicates the assignment based on lipid analysis (GC-MS, GC-C-IRMS) of the same food crusts (Cubas *et al.* 2020).

Comparison stable isotopes – lipids

In six cases, bulk stable isotope and lipid analyses were performed on the same food crusts. Five of these were funnel beakers and are shown in fig. 7, one was an Ertebølle sherd and is displayed in fig. 8.

Additionally, lipids were extracted from the ceramic matrix of nine Ertebølle sherds. Food crusts on five of these sherds were also sampled for stable isotope measurements. Three of the isotope values are excluded from the plots because of too low nitrogen or carbon contents. However, fig. 8 shows a plot of the stable isotope values of food crusts on Ertebølle sherds, which are included for better comparability with the lipid results. Marine biomarkers and/or marine lipid δ^{13} C values were found in all five cases, irrespective of the bulk stable isotope results. This indicates that both techniques are necessary to understand the full range of foodstuffs prepared or stored in the vessels. Food crusts are biased towards the final cooking events, while lipids absorbed in the clay matrix are only slowly replaced and show no strong signal of the final cooking (Miller *et al.* 2020). For example, we analysed one Ertebølle sherd with terrestrial food crust (fig. 8). In this case, the pot was probably used once or several times for the preparation of marine food, while the last cooking event only contained terrestrial ingredients.



Figure 8. Stable isotope measurements of food crusts on Ertebølle pottery. δ^{13} C in ‰ VPDB; δ^{15} N in ‰ AIR. Text indicates the assignment based on lipid analysis (GC-MS and GC-C-IRMS) of the ceramic matrix by Papakosta *et al.* (2019).

Conclusion

Stable isotope analyses of the animal bones and food crusts and lipid analysis of the pottery show that the inhabitants of the Syltholm Fjord area used a broad variety of resources. This did not change during the Neolithisation process, although new pottery forms were introduced. New agricultural products, such as dairy, were integrated into the cuisine, while marine resources continued to be important. Although the stable isotope values of human bones indicate a predominantly terrestrial diet throughout the Neolithic, pottery food crusts and lipids, as well as finds of fishing fences, underline the importance of marine resources. This indicates that the Neolithisation process in this part of Denmark was not a simple replacement of a hunter-gatherer lifestyle by agriculture, or a persistence of a Mesolithic culture surrounded by Neolithic groups, but a complex interplay of traditions and innovations.

Supplementary material

Basic data for the figures is available under 10.5281/zenodo.7598004 and 10.5281/ zenodo.7597900. More detailed information on the isotope measurements and radiocarbon data are available from the author on request.

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