Carbon and nitrogen stable isotope values in freshwater, brackish and marine fish bone collagen from Mesolithic and Neolithic sites in central and northern Europe

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Abstract

The aim of this research is the isotopic characterization of archaeological fish species to freshwater, brackish, and marine environments, trophic level, and migration patterns, and to determine intra-species variation within and between fish populations differing in location within central and northern Europe. Thus carbon and nitrogen stable isotope analysis was undertaken on collagen extracted from 72 fish bone samples from eight Mesolithic and Neolithic archaeological sites in central and northern Europe. Thirty-six (50%) of the specimens analysed produced results with acceptable carbon to nitrogen atomic ratios (2.9-3.6). The fish remains encompass a wide spectrum of freshwater, brackish, and marine taxa (n = 12), and this is reflected in the $\delta^{13}C$ results (-24.5‰ to -7.8‰). The freshwater/brackish fish (pike, *Esox lucius*; perch, *Perca fluviatilis*; zander, *Sander lucioperca*) had $\delta^{13}C$ values that ranged from -24.2‰ to -19.3‰, while the brackish/marine fish (spurdog, *Squalus acanthias*; flatfish, Pleuronectidae; codfish, Gadidae; garfish, *Belone belone*; mackerel, *Scomber scombrus*) ranged from -14.9‰ to -9.4‰. Salmonidae, an anadromous taxon, and the eel (*Anguilla anguilla*), a catadromous species, had carbon isotope values consistent with marine origin, and no evidence of freshwater residency (-12.7‰ to -11.7‰). The $\delta^{15}N$ values had a range of 6.2‰ (6.5‰ to 12.7‰) indicating that these fish were on average feeding at 1.7 trophic levels higher than their producers in these diverse aquatic environments. These results serve as an important ecological baseline for the future isotopic reconstruction of the diet of human populations dating to the late Mesolithic and early Neolithic of the region.

Introduction

The use of stable carbon and nitrogen isotopic analyses in archaeological human bone collagen has increasingly become an important source of information for the determination of diet, health, status and mobility of an individual, particularly for the prehistory of central and northern Europe (Fischer 2003; Fischer *et al*. 2007; Richards *et al*. 2003a; Tauber 1981). The majority of research has focused on the reconstruction of past subsistence patterns by comparatively assessing human bone collagen isotopic data against putative food resources, particularly from the same region and period. Furthermore, domesticated and wild, and terrestrial and marine faunal remains are analysed in order to establish certain aspects of the animals' life history, the local environments in which the animals lived and were hunted, and as baselines to assess human diet (Noe-Nygaard 1995; Noe-Nygaard *et al*. 2005). With increasing regularity

the application of stable isotopic analyses to fish bone collagen has demonstrated that an essential and sometimes significant proportion of the human palaeodiet consisted of freshwater (for example Dufour *et al*. 1998; Katzenberg and Weber 1999; Nehlich *et al*. 2010; Privat *et al*. 2007; Richards *et al*. 2001) and marine fish (for example Fischer *et al*. 2007; Richards and Mellars 1998). In addition, the comprehensive fish faunal assemblages from central and northern Europe attest to the importance of fish to the diets of these human populations (see Cardell 2004; Enghoff 1994, 1994-1995, 2011; Enghoff *et al*. 2007; Larsen 2005; Olson 2008; Ritchie 2010; Zabilska 2013a). Notwithstanding the large corpus of stable carbon and nitrogen, and more recently sulphur, isotope data from archaeological fish bone collagen (for example Barrett *et al*. 2008; Barrett *et al*. 2011; Bösl *et al*. 2006; Fuller *et al*. 2012; Grupe *et al*. 2009; Nehlich *et al*. 2013; Orton *et al*. 2011), relatively few isotope studies have been undertaken on fish remains dating to the Mesolithic and Neolithic from central and northern Europe (see Fischer *et al*. 2007; Robson *et al*. 2012).

Given the significant importance of fishing during the Mesolithic and Neolithic of central and northern Europe (Enghoff 2011; Enghoff *et al*. 2007; Fischer *et al*. 2007; Ritchie 2010) this paper aimed to determine intra-species variations within and between populations differing spatially and temporally in order to ascertain reproducibility over time, to improve our understanding of the palaeoecology of the region, and to inform both archaeologists and ecologists.

Freshwater, brackish, and marine fish bones from eight Stone Age archaeological sites in central and northern Europe were sampled (Figure 1), and their collagen carbon and nitrogen stable isotope values were measured. The selected specimens encompassed a wide spectrum of species routinely recovered during excavations in the region. These include, eel, gadids (primarily cod), and flatfish (*Pleuronectes platessa*/plaice, *Platichthys flesus*/flounder, *Limanda limanda*/dab), and as such reflect the most important species for reconstructing past human subsistence (Enghoff 2011; Enghoff *et al*. 2007; Ritchie 2010; Ritchie *et al*. 2013).

Since, human populations along the coastlines of central and northern Europe could feed on a mixture of available sources of fish, including freshwater, marine and diadromous taxa, the results from this study serve to provide guidance for those working on past human consumption practices. More specifically this study provides a palaeoecological baseline for future isotopic reconstruction in central and northern Europe.

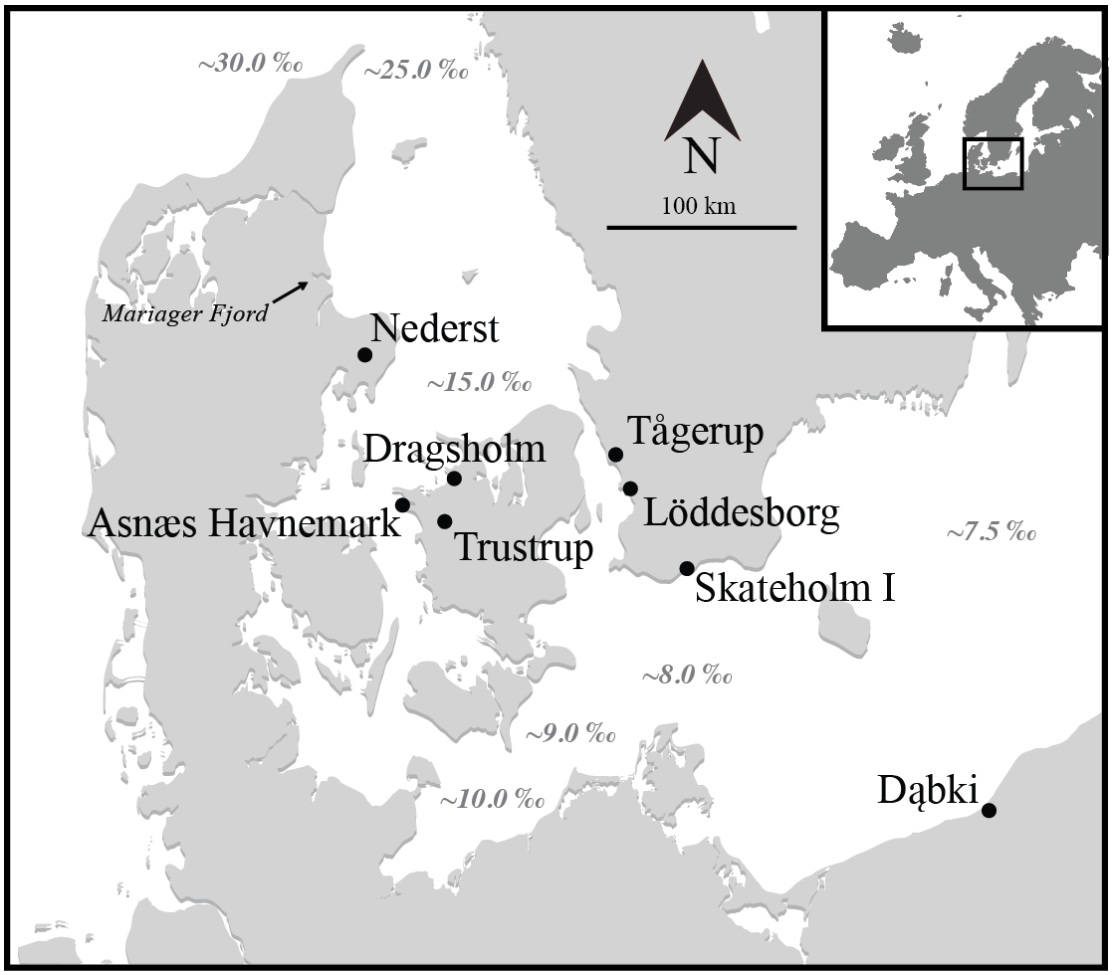

Figure 1: Distribution map of central and northern Europe showing the site locations used in this study and the present day average surface water salinity values. Salinity is an important factor that effects the structuring of fish communities in the present Baltic Sea (Lappalaien et al. 2000; Ojaveer et al. 1981).

Materials and methods

Archaeological samples

A total of 72 archaeological fish bones from eight central and northern European archaeological sites were selected for carbon and nitrogen stable isotope analysis (see Figure 1 and Table 1). The sites were selected to expand the geographical range of the sites reported in Robson *et al*. (2012) and derived from a number of archaeological sites mainly of middle Mesolithic Kongemose (*ca*. 6400-5400 cal. B. C.), late Mesolithic Ertebølle (*ca*. 5400-3950 cal. B. C.), and early Neolithic Funnel Beaker (*ca*. 3950-3300 cal. B. C.) date.

Sites with relatively large (NISP >100) fish bone assemblages were included so as to not significantly affect the integrity of the assemblages should any additional analyses

be undertaken on them. The majority of the samples were recovered along a similar salinity gradient with the exceptions of Dąbki, located in West Pomeranian, Poland and Trustrup that is situated in the Lille Åmose, northwest Zealand, Denmark. The skeletal elements analysed included: abdominal (precaudal) vertebrae (n = 7), articular (n = 1), basioccipital (n = 1), ceratohyals (n = 4), caudal vertebrae (n = 10), dentaries (n =3), first vertebrae (n = 5), interopercular (n = 1), opercular (n =1), quadrates (n = 2), thoracic vertebrae (n = 12), unspecified vertebrae (n = 24), and vomer (n = 1).

The fish bones were identified by side-by-side comparison with modern reference skeletons of known taxon. Total fish length (TL) was estimated from the majority of the fish bones according to established methods (Enghoff 1986; Enghoff 1994; Morales and Rosenlund 1979; Zabilska 2013a) utilizing regression equations (Enghoff 1994; Thom 1990; Zabilska 2013a) (see Figure 2). The spurdog and garfish TL were established by direct comparison with modern reference skeletons of known body length. The distance from the tip of the snout to the termination of the caudal fin was measured for TL.

The fish remains encompassed a wide spectrum of freshwater, brackish, and marine taxa (n = 12), selected for their variable life histories and habitat use. They include one species from each of the Siluridae and Esocidae families: wels catfish (*Siluris glanis*) and pike (*Esox lucius*) respectively. In addition, two species from the Percidae family are present: perch (*Perca fluviatilis*) and zander (*Sander lucioperca*). The marine environment is represented by five stenohaline taxa including one species from each of the Squalidae, Gadidae, Belonidae and Scombridae families: spurdog (*Squalus acanthias*), unidentified Gadidae, garfish (*Belone belone*) and mackerel (*Scomber scombrus*) respectively. To add, one euryhaline taxon is represented by the Pleuronectidae family that was not identified to species. Diadromous fishes (those that migrate between salinity gradients) are present in the sample set, including eel (*Anguilla anguilla*), unidentified Salmonidae, as well as unidentified Clupeidae.

Figure 2: Zander interopercular (TL = ca. 65-70 cm) from the site 9 at Dąbki prior to analysis.

Modern samples and correction for oceanic Suess

Five modern fish were made available from Denmark; three eels and two flounders caught in the Mariager Fjord were procured from the fish market at Hadsund, north central Jutland. In order to account for the release of higher proportions of carbon-13 into the atmosphere from the burning of fossil fuels (Suess Effect), all of the modern fish caught in the estuarine waters of the Mariager Fjord were corrected by adding 1.14‰ (Friedli *et al*. 1986) to each of the $\delta^{13}C$ values for consistency with the data reported by Robson *et al*. (2012). The present day salinity gradient along the Mariager Fjord is between 12‰ and 25‰ indicative of a brackish carbon pool.

Collagen extraction and IRMS

Archaeological and modern sample preparation was carried out at the BioArCh laboratories of The University of York (UK), whilst the isotopic measurements were undertaken at the Division of Archaeological, Geographical and Environmental Sciences, University of Bradford. Since the majority of the fish bones were small, delicate and fragile they were not cleaned of surface contamination, as this would have required power abrasion that would have damaged the samples. Each specimen was demineralised at ca. 4°C in 8 ml of either 0.1 or 0.6 M HCl depending upon the size of the individual specimen in question. Once demineralised, the samples were rinsed three times in de-ionised water, and the pH measured. The samples were then placed in an oven at ca. 80°C in pH3 HCl for 48 hours to gelatinise. The samples were centrifuged and the supernatant was ultrafiltered to isolate the >30 kDa fraction (Brown *et al*. 1988). Finally, samples were freeze-dried. For the modern specimens, bone samples were removed, boiled, and rinsed with water (2 x 15 min in an ultrasonic bath at 25°C). While boiling can mirror diagenetic processes, this requires rather long-term heating, and the

samples were boiled for less than one hour, to minimize the effect on the collagen (Roberts *et al*. 2002). Lipid was removed from a portion of each in a dissolving sequence of hexane, acetone and ethanol and rinsed in an ultrasonic bath at 25°C for 15 min, and the collagen was extracted from the samples are described above (Szpak 2011). To determine the $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios, duplicates between 0.8 and 1.2 mg of the extracted collagen was weighed into tin capsules for analysis in a Roboprep Combustion Device coupled to a Europa 20-20 Mass Spectrometer (PDZ-Europa, Crew UK). Following standard procedure the samples were measured relative to the international V-PDB standard (for $\delta^{13}C$) and the international AIR standard (for $\delta^{15}N$) using a number of laboratory standards traceable to international isotope reference standards that were analysed simultaneously with each sample group to ensure instrument integrity (Richards and Hedges 1999). Analytical error, calculated from the repeated measurements of each sample and measurements of a bovine liver standard from multiple extracts, was <0.2‰ (1σ). The statistical analyses were undertaken using the IBM Statistics Software SPSS 21.0.

Site name	Approximate dates (based on)	Based on	Period represented (cultural epoch)	Site description	Taxon	Number of fish bone sampled (acceptable collagen extracted)	Approximated salinity of the water body closest to the site	Reference (fish bone analysis)
Asnæs Havnemark, north western Zealand, Denmark	ca. 4300-4100 cal. B. C.	C-14	Terminal Mesolithic (Ertebølle)/Early Neolithic (Funnel Beaker)	Coastal site	Eel Alosa spp. Salmonidae Gadidae Mackerel Pleuronectidae	4 (2) 2 (-) 4 (1) 2 (2) 2 (2) 2 (1)	15.0‰	Ritchie 2010; Ritchie *et al*. 2013
Dąbki, site 9, West Pomeranian, Poland	ca. 5100-3600 cal. B. C.	C-14	Terminal Mesolithic (Ertebølle, Narva/Zedmar)/Early Neolithic (Funnel Beaker)	Lakeshore settlement	Eel Pike European perch Zander	8 (-) 3 (3) 3 (2) 3 (3)	7.5‰	Zabilska 2013a, 2013b; Zabilska-Kunek *et al*. (submitted)
Dragsholm, north western Zealand, Denmark	ca. 5000-3500 cal. B. C.	C-14	Terminal Mesolithic (Ertebølle)/Early Neolithic (Funnel Beaker)	Coastal site with shell bearing deposits	Spurdog Eel Gadidae Garfish Mackerel	2 (2) 4 (2) 2 (-) 2 (2) 2 (2)	15.0‰	Ritchie 2010

					Pleuronectidae	2 (2)		
Löddesborg, south western Scania, Sweden	3260 ± 80 cal. B. C.	C-14	Early Neolithic (Funnel Beaker)	Coastal site	Eel	2 (-)	9.0‰	Hallström 1984
Nederst (Skaldynge I), north central Jutland, Denmark	ca. 5400-3950 B. C.	Diagnostic artefacts	Terminal Mesolithic (Ertebølle)	Kitchen midden	Eel Gadidae Pleuronectidae	5 (4) 2 (2) 2 (2)	20.0‰	Ritchie 2010
Skateholm I, Scania, Sweden	ca. 6000-4000 cal. B. C.	C-14	Terminal Mesolithic (Ertebølle)	Coastal site	Eel	5 (-)	8.0‰	Jonsson 1988
Trustrup, Lille Åmose, Zealand, Denmark	ca. 4800-4000 B. C.	C-14	Terminal Mesolithic (Ertebølle)	Lakeshore settlement	Wels catfish	1 (-)	n/a	Ritchie unpublished data
Tågerup, south western Scania, Sweden	ca. 6700-6000 and 5500-4900 cal. B. C.	C-14	Middle Mesolithic (Kongemose)/Terminal Mesolithic (Ertebølle)	Coastal site	Eel	8 (2)	9.0‰	Eriksson and Magnell 2001

Table 1: Summary data of archaeological sites from which fish bone was sampled.

Results

Archaeological fish bone samples

Although 72 samples were prepared for analysis, only 36 produced sufficiently well preserved collagen for reliable measurement and possessed C:N ratios that were within the acceptable range of 2.9-3.6 (DeNiro 1985). The unsuccessful samples are excluded from any further analysis due to the possibility of diagenesis (see van Klinken 1999 and Szpak 2011). Of the 36 unsuccessful samples, seven had C:N ratios which were outside the acceptable range, whilst 29 samples produced insufficient amounts of collagen for analysis.

Tables 2 and 3 summarize the isotope data. The fish bone isotope data are plotted by archaeological site in Figure 3, by taxon in Figure 4, and by life histories and habitat use in Figure 5. The archaeological and modern fish bone isotope data are compared with previously published values obtained on collagen extracted from freshwater/brackish (tench/*Tinca tinca*, pike and perch), brackish/marine (cod and flounder), and catadromous (eel) fish recovered from coeval archaeological sites in central and northern Europe (data reported in Fischer *et al*. 2007; Robson *et al*. 2012). These data are plotted in Figure 6. The data reproduced from Fischer *et al*. (2007) comprise $\delta^{13}C$ and $\delta^{15}N$ values in collagen extracted from freshwater (pike and tench; $n = 20$), brackish/marine (cod and flounder; $n = 17$), and catadromous (eel; $n = 1$) fish bone from the Danish sites at Åkonge, Argus Bank, Bjørnsholm, Bøgebjerg, Krabbesholm II, Nivågård, Storelyng VI, and Vængesø III. The data reproduced from Robson *et al*. (2012) comprise $\delta^{13}C$ and $\delta^{15}N$ values in collagen extracted from catadromous fish bone (eel; $n = 36$) from the Danish and German sites of Grube-Rosenhof, Havnø, Jäckelgrund-Orth, Neustadt, Timmendorf-Nordmole and Hüde I. In addition, Figure 6 also includes the carbon isotope ranges that were obtained on eel muscle tissue that were corrected to collagen as reported in Harrod *et al*. (2005; although see Robson *et al*. 2012). Despite the fact that the data reported in Harrod *et al*. (2005) is from an Atlantic coastal catchment that will have differences in the oceanographic and limnological characteristics compared to the Baltic Sea, data from the latter study area on modern eel bone or tissue are not yet available.

Carbon isotopes

The ten taxa analysed in this study that yielded reliable data had a broad range of $\delta^{13}C$ values (-24.5‰ to -7.8‰) (Figure 7). The freshwater and marine species had values

ranging from -24.5‰ to -17.9‰, and -16.6‰ to -7.8‰ respectively. With the exception of the data obtained for perch, the data (Figure 4) show a clear difference in the $\delta^{13}C$ values between the freshwater species, pike and zander, and the brackish/marine, anadromous and catadromous species of fish recovered from the archaeological sites in Denmark, Poland, and Sweden. The one successful anadromous Salmonidae, recovered from Asnæs Havnemark had a carbon isotope ratio of -15.5‰ that is consistent with marine origin. Similarly the catadromous eel plots between -8.4‰ to -13.6‰, consistent with no evidence of freshwater residency, and comparable with the data obtained by Robson *et al*. (2012). However, the difference between the $\delta^{13}C$ values of the archaeological fish (n = 36) and the approximated modern salinity values for the water bodies closest to the archaeological sites is significant (Pearson Correlation; r = 0.829, n = 41, $p<0.0005$). The data suggest that the $\delta^{13}C$ values of the archaeological fish are positively correlated with salinity, however this interpretation is based on the assumption that a gradient existed at the time of sample preservation and that the salinity values have not markedly altered since prehistory (Figure 8). Unfortunately the eight eel specimens from Dąbki, and the two anadromous Clupeids from Asnæs Havnemark had no collagen preserved. Finally, it is worth mentioning that a single specimen of wels catfish recovered from Trustup was analysed but this yielded results indicating diagenesis.

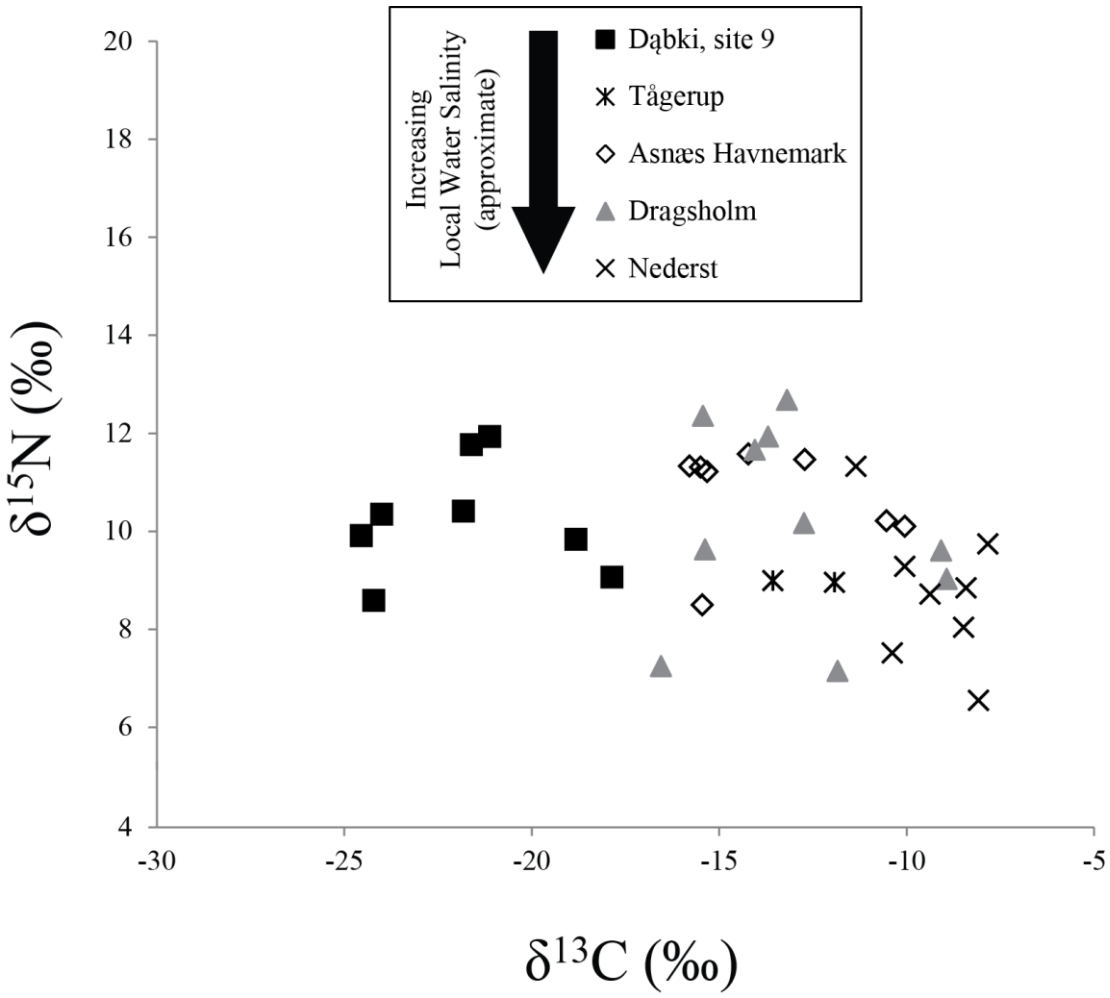

Figure 3: Carbon and nitrogen isotope data obtained from fish bone collagen from five of the eight archaeological sites in central and northern Europe.

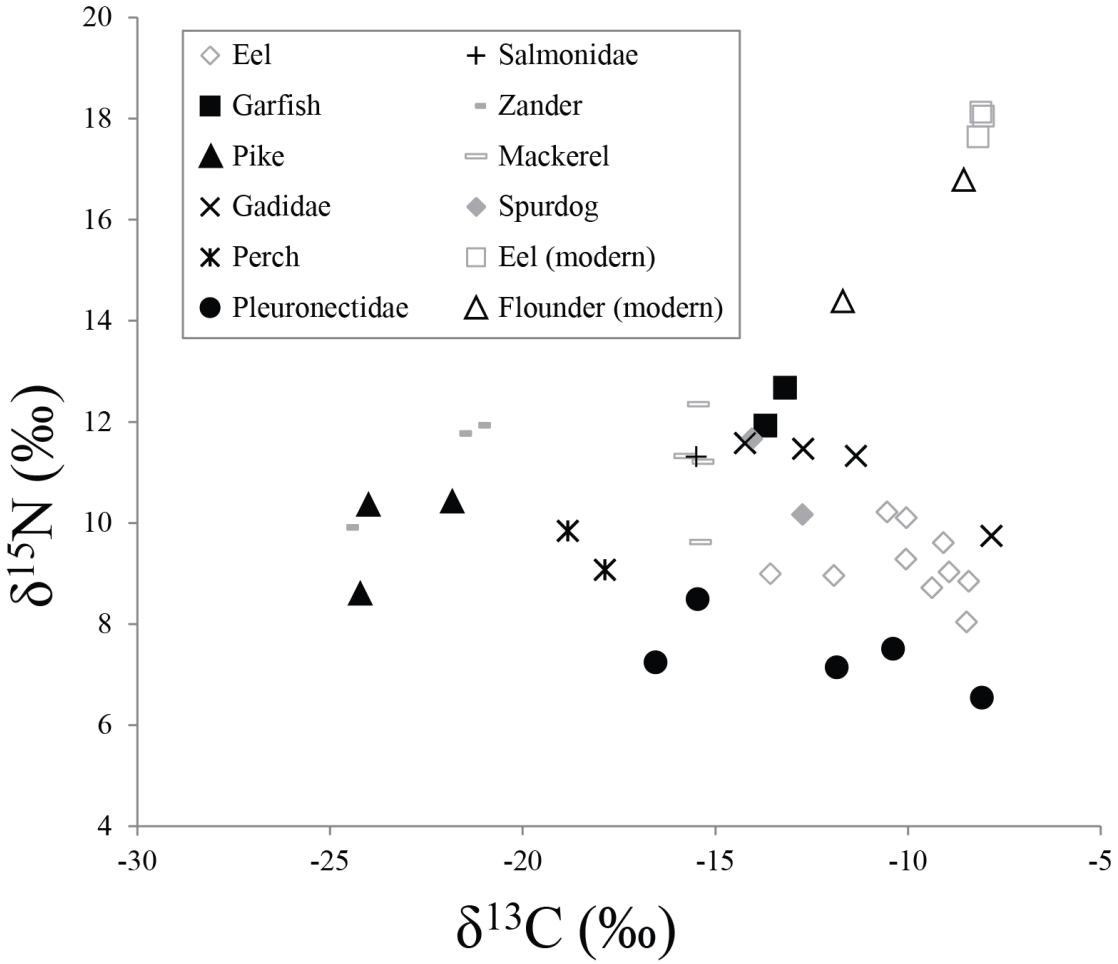

Figure 4: Carbon and nitrogen isotope data obtained from archaeological fish bone collagen from 10 taxa compared with modern eel and flounder from the Mariager Fjord, Denmark.

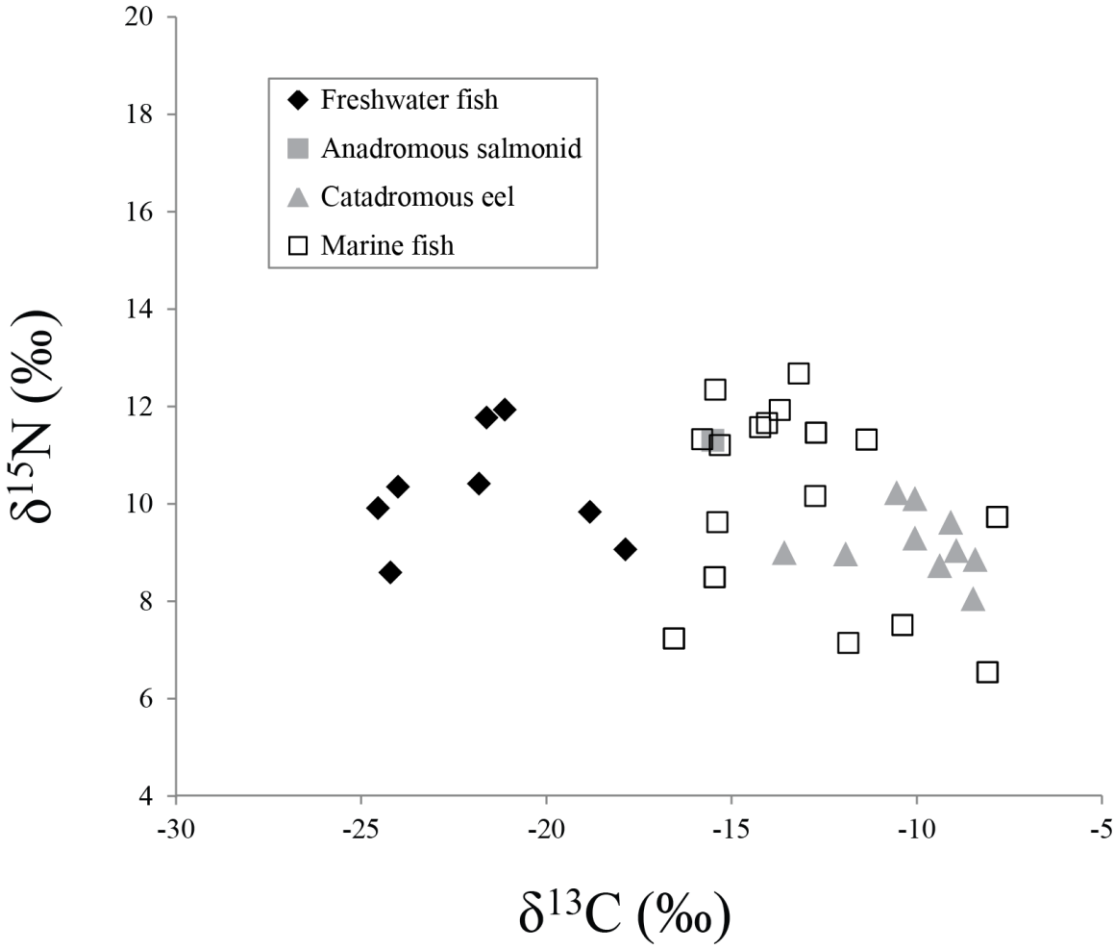

Figure 5: Carbon and nitrogen isotope data obtained from bone collagen classified by life histories and habitat use.

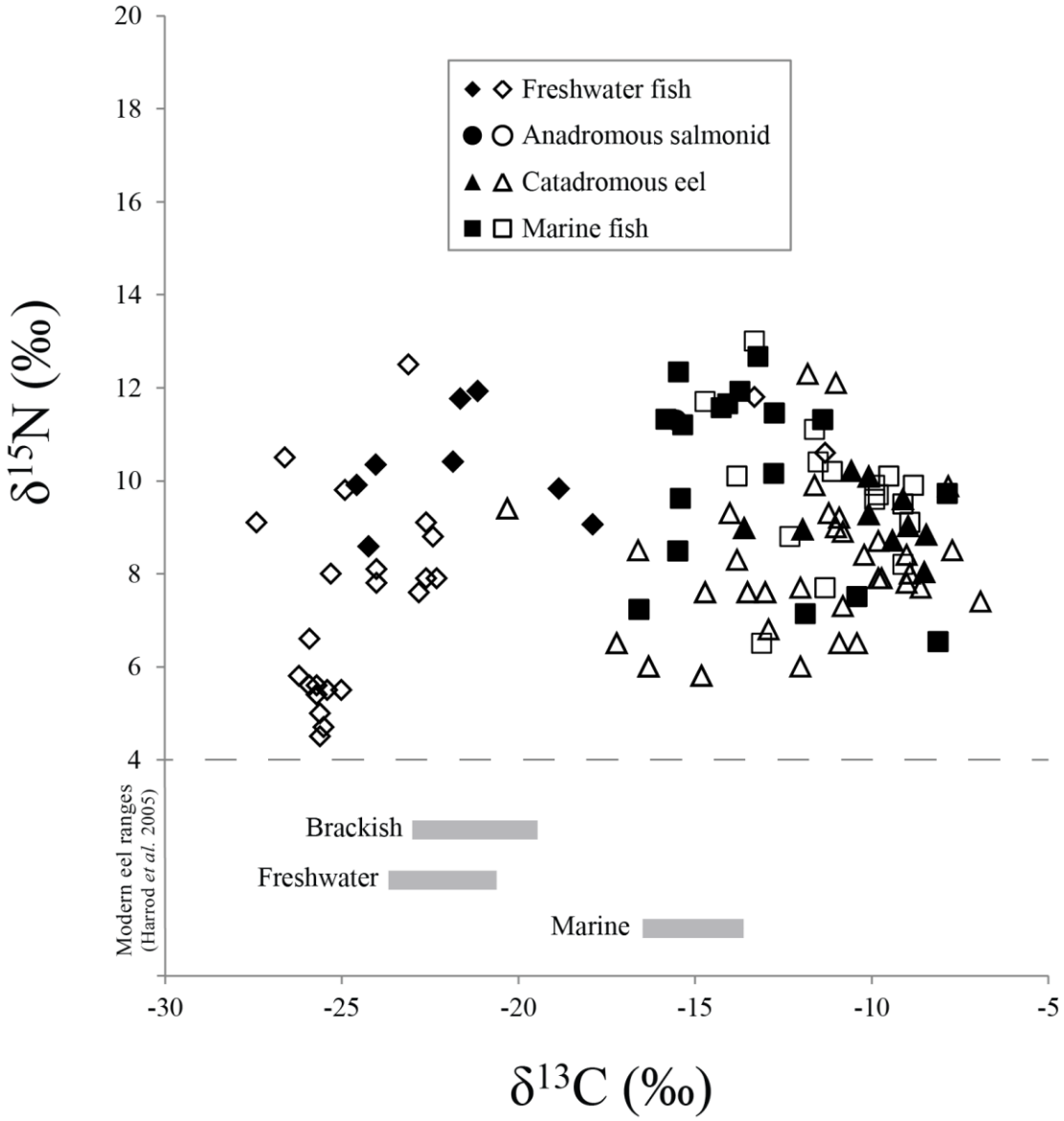

Figure 6: Carbon and nitrogen isotope data obtained from fish bone collagen from the five archaeological sites (symbols with a black fill) plotted alongside freshwater/brackish (tench, pike and perch), brackish/marine (cod and flounder), and catadromous (eel) fish (symbols with no fill) from coeval sites in central and northern Europe. The freshwater, brackish and marine carbon isotope ranges are calculated from a modern study (see Harrod et al. 2005). Note that corrections were applied to compare these data with the bone collagen values (see Robson et al. 2012).

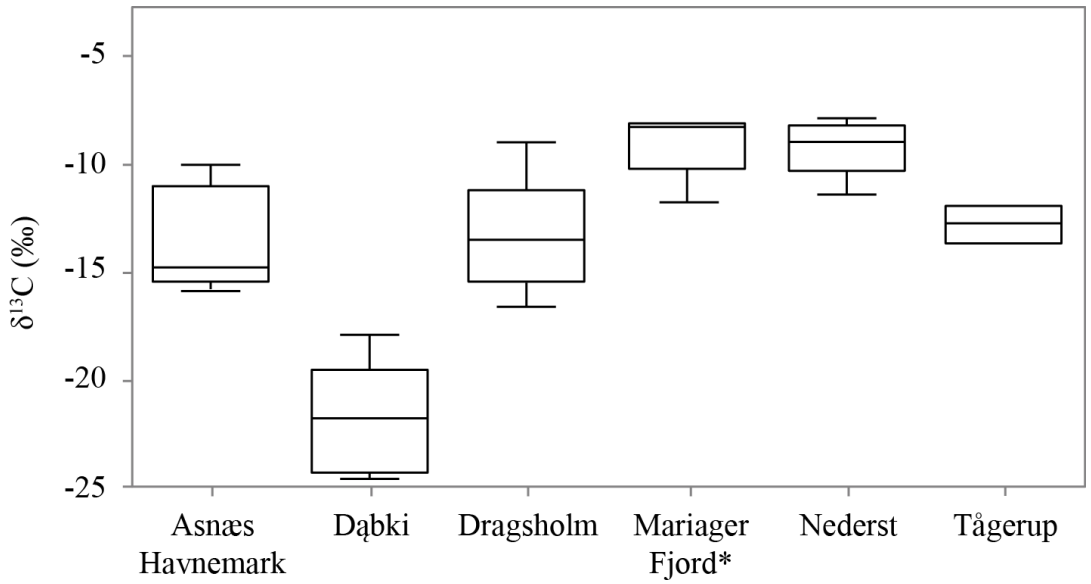

Figure 7: Box and whisker plot representing the mean and standard deviations for the $\delta^{13}C$ values from the fish bone collagen samples from the five archaeological sites with the exception of the modern specimens from the Mariager Fjord (starred).

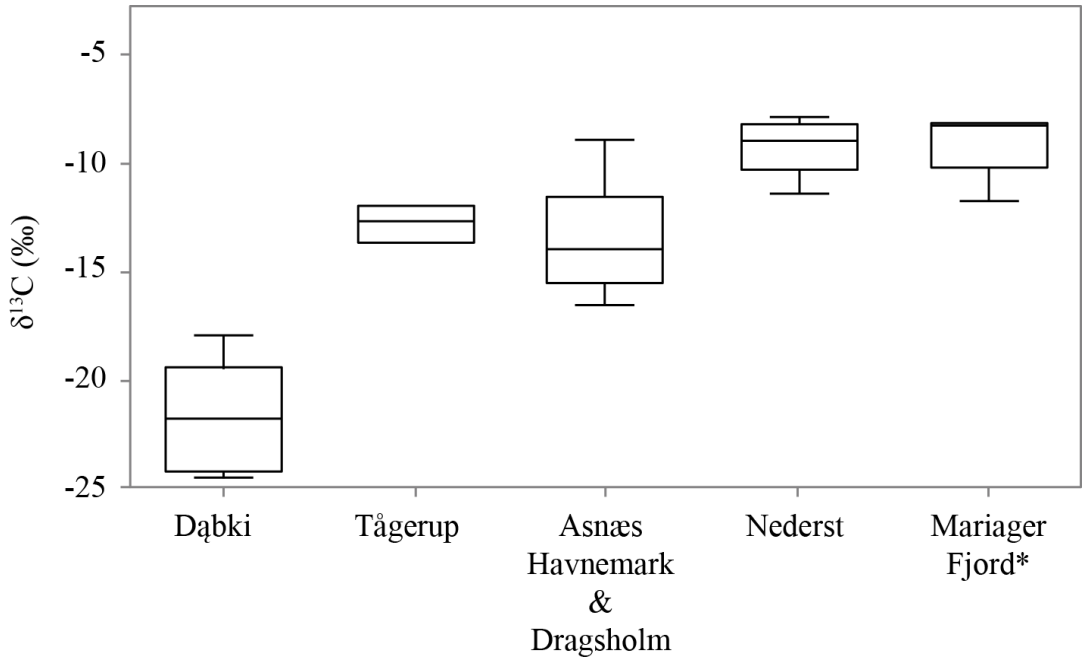

Figure 8: Box and whisker plot representing the mean and standard deviations for the $\delta^{13}C$ values from the fish bone collagen samples against the approximated salinity of the water bodies closest to the archaeological sites and the modern specimens from the Mariager Fjord (starred). On the x-axis the sites are ranked in order of increasing salinity from left to right.

In comparison with archaeological fish bone isotope data from Lithuania (see Antanaitis-Jacobs *et al*. 2009), a clear difference in the $\delta^{13}C$ values between the East and West regions of the Baltic is clear reflecting the Baltic Sea's salinity gradient

(Figure 8). Salinity levels do not vary considerably due to a combination of factors: (i) a shallow entrance exists between the Baltic and the North Sea restricting the inflow of seawater, (ii) it takes approximately 25-35 years to replenish the whole Baltic, (iii) more than 250 rivers flow into the Baltic which dilute the water retained in the sea, (iv) a large proportion of the Baltic is frozen every winter, and (v) the Baltic is essentially tideless (Kaiser *et al*. 2005). However, it is the fish bones from the kitchen midden at Nederst that are the most enriched in $\delta^{13}C$. Given the site's situation in the northern Kolindsund we would have expected more brackish water signatures. However, the numerous remains of mackerel identified in the fish bone assemblage support the above (Ritchie 2010). In comparison, Craig *et al*. (2006) similarly report more depleted $\delta^{13}C$ values for a number of dogs and seals analysed from the kitchen midden at Bjørnsholm, which is situated in the Limfjord, northern Jutland, Denmark and closest to the North Sea.

The modern estuarine eels and flounder from the Mariager Fjord, following the Suess correction, had mean carbon isotope values of -8.1‰ ± 0.1‰ and -10.1‰ ± 2.2‰ respectively (Figure 4), that are similar when compared to the archaeological eel from Asnæs Havnemark, Dragsholm, Nederst and Tågerup (-10.0‰ ± 1.6‰).

Nitrogen isotopes

The $\delta^{15}N$ data also exhibited considerable variation (6.5‰ to 12.7‰). In Table 4, the summary statistics for each species of fish included in this study are shown in relation to their habitat use and life histories as reported by Schmölcke and Ritchie (2010). There is no significant difference between the $\delta^{15}N$ values of the archaeological eel (n = 46; this study combined with the data reported by Robson *et al*. 2012), and the total length (Pearson Correlation; r = -0.213, n = 29, p = 0.267). These data show a negative correlation suggesting that, at least in the present study, longer eels had lower nitrogen isotope values, representing differences in the trophic position of the eels throughout central and northern Europe.

Figure 9 plots the $\delta^{15}N$ ratio against total fish length determined for eel, pike, gadids, perch and zander (n = 19) from each of the archaeological sites. While these data show a very weak positive correlation, the correlation is not statistically significant (Pearson correlation; r = 0.074, n = 19, p = 0.765), which is contrary to the data reported by Robson *et al*. (2012). This is not surprising since in the present study comparison is made between several different taxa from a number of archaeological sites where the

local baselines are likely to be different. The high $\delta^{15}N$ values of the modern eels and flounders from the Mariager Fjord have almost certainly been raised by eutrophication from modern pollution of the estuarine waters regardless of the level of intra-species variability in fish diet. Nevertheless, in the study by Harrod *et al*. (2005), variations in the nitrogen isotope values are likely to represent the wide range of feeding strategies.

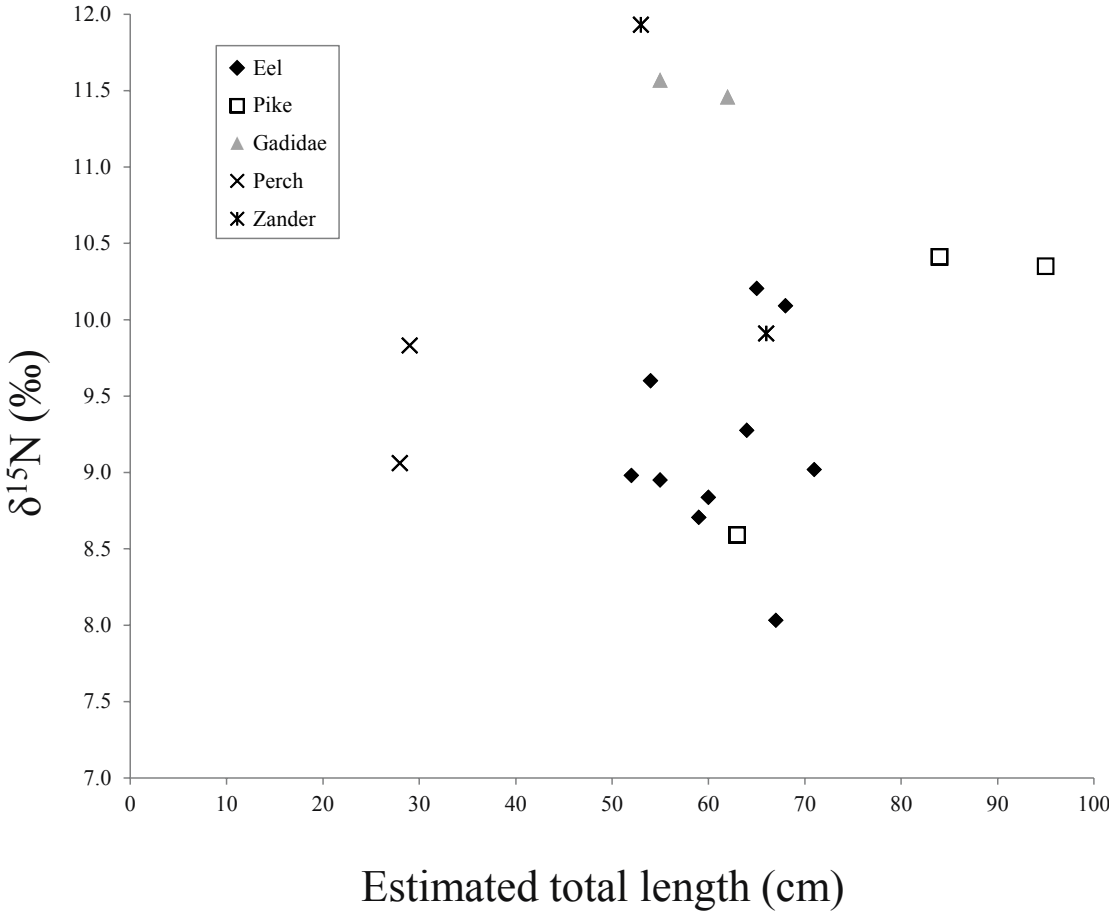

Figure 9: Plot of nitrogen isotope values against estimated total fish length calculated according to the regression equations as produced by Enghoff (1994), Thom (1990) and Zabilska (2013a). Note that the modern fish has not been included since the $\delta^{15}N$ values have been significantly elevated by modern eutrophication.

Site name	Lab no.	Taxon	Skeletal element	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	%C
Asnæs Havnemark	AHE2a+b	*Anguilla anguilla*	Ceratohyal (ca. 68 cm)	-10.0	10.1	30.1
Asnæs Havnemark	AHE6a	*Anguilla anguilla*	Ceratohyal (ca. 65 cm)	-10.5	10.2	28.9
Asnæs Havnemark	AHST3a	Salmonidae	Vertebra	-15.5	11.3	42.3
Asnæs Havnemark	AHC3a+b	Gadidae	1st vertebra (ca. 62 cm)	-12.7	11.5	30.0
Asnæs Havnemark	AHC6a+b	Gadidae	1st vertebra (ca. 55 cm)	-14.2	11.6	31.1
Asnæs Havnemark	AHM1a+b	*Scomber scombrus*	Vertebra	-15.8	11.3	35.6
Asnæs Havnemark	AHM2a+b	*Scomber scombrus*	Vertebra	-15.3	11.2	36.1
Asnæs Havnemark	AHP2a+b	Pleuronectidae	Vertebra	-15.5	8.5	27.4
Dragsholm	DE1	*Anguilla anguilla*	cf. thoracic vertebra (ca. 71 cm)	-8.9	9.0	25.7
Dragsholm	DE3a	*Anguilla anguilla*	Thoracic vertebra (ca. 54 cm)	-9.1	9.6	35.8
Dragsholm	DG1a+b	*Belone belone*	Vertebra (>70 cm)	-13.7	11.9	31.3
Dragsholm	DG3a+b	*Belone belone*	Vertebra (>70 cm)	-13.2	12.7	29.8
Dragsholm	DS3a+b	*Squalus acanthias*	Vertebra (55-65 cm)	-12.7	10.2	
Dragsholm	DS6a+b	*Squalus acanthias*	Vertebra (60-70 cm)	-14.0	11.7	
Dragsholm	DM1a+b	*Scomber scombrus*	Vertebra	-15.4	12.3	
Dragsholm	DM2a+b	*Scomber scombrus*	Vertebra	-15.4	9.6	
Dragsholm	DP3a+b	Pleuronectidae	Vertebra	-11.8	7.1	
Dragsholm	DP5a+b	Pleuronectidae	Vertebra	-16.6	7.2	
Dąbki, site 9	D9P.2a+b	*Esox lucius*	Left dentary (ca. 95 cm)	-24.0	10.4	34.1
Dąbki, site 9	D9P.4a+b	*Esox lucius*	Quadrate (ca. 84 cm)	-21.8	10.4	37.2
Dąbki, site 9	D9P.5a, b+c	*Esox lucius*	Left dentary (ca. 63 cm)	-24.2	8.6	39.3
Dąbki, site 9	D9PF.4a	*Perca fluviatilis*	First vertebra (ca. 29 cm)	-18.8	9.8	38.5
Dąbki, site 9	D9PF.6a+b	*Perca fluviatilis*	Articular (ca. 28 cm)	-17.9	9.1	39.6
Dąbki, site 9	D9Z.1a+b	*Sander lucioperca*	Basioccipital (ca. 66 cm)	-24.5	9.9	52.0
Dąbki, site 9	D9Z.2a+b	*Sander lucioperca*	Interopercular (ca. 65-70 cm)	-21.6	11.8	40.8

Dąbki, site 9	D9Z.6a+b	*Sander lucioperca*	Quadrate (ca. 53 cm)	-21.1	11.9	31.3
Nederst	NSIE3a	*Anguilla anguilla*	Caudal vertebra (ca. 59 cm)	-9.4	8.7	43.1
Nederst	NSIE5a+b	*Anguilla anguilla*	Thoracic vertebra (ca. 67 cm)	-8.5	8.0	40.6
Nederst	NSIE6a	*Anguilla anguilla*	Caudal vertebra (ca. 64 cm)	-10.1	9.3	41.6
Nederst	NSIE12a+b	*Anguilla anguilla*	Caudal vertebra (ca. 60 cm)	-8.4	8.8	46.9
Nederst	NSIG3a+b	Gadidae	Vertebra	-11.4	11.3	28.5
Nederst	NSIG5a+b	Gadidae	Vertebra	-7.8	9.7	43.2
Nederst	NSIP4	Pleuronectidae	Vertebra	-8.1	6.5	44.3
Nederst	NSIP5a+b	Pleuronectidae	Vertebra	-10.4	7.5	42.3
Tågerup	TA1.6a+b	*Anguilla anguilla*	Thoracic vertebra (ca. 55 cm)	-11.9	9.0	64.3
Tågerup	TA1.9a	*Anguilla anguilla*	Thoracic vertebra (ca. 52 cm)	-13.6	9.0	40.8
Discarded samples						
Asnæs Havnemark	AHE1	*Anguilla anguilla*	Ceratohyal (ca. 53 cm)	No collagen preserved		
Asnæs Havnemark	AHE9	*Anguilla anguilla*	Ceratohyal (ca. 53 cm)	No collagen preserved		
Asnæs Havnemark	AHS1	*Alosa* sp.	Vertebra	No collagen preserved		
Asnæs Havnemark	AHS3	*Alosa* sp.	Vertebra	No collagen preserved		
Asnæs Havnemark	AHST1	Salmonidae	Vertebra	No collagen preserved		
Asnæs Havnemark	AHST2	Salmonidae	Vertebra	No collagen preserved		
Asnæs Havnemark	AHST4	Salmonidae	Vertebra	No collagen preserved		
Asnæs Havnemark	AHP5a	Pleuronectidae	Vertebra	-14.1	8.5	30.9
Dragsholm	DE6a	*Anguilla anguilla*	Thoracic vertebra (ca. 60 cm)	-24.2	9.2	33.2
Dragsholm	DE10	*Anguilla anguilla*	Abdominal vertebra (40-50 cm)	No collagen preserved		
Dragsholm	DC1a+b	Gadidae	1st Vertebra (ca. 70 cm)	-11.5	10.3	35.6
Dragsholm	DC4a+b	Gadidae	1st Vertebra (ca. 61 cm)	-11.8	10.2	35.1
Dąbki, site 9	D9.1	*Anguilla anguilla*	Abdominal vertebra	No collagen preserved		

Dąbki, site 9	D9.2	*Anguilla anguilla*	Left dentary (ca. 54 cm)	No collagen preserved		
Dąbki, site 9	D9.3	*Anguilla anguilla*	Abdominal vertebra	No collagen preserved		
Dąbki, site 9	D9.4	*Anguilla anguilla*	Abdominal vertebra	No collagen preserved		
Dąbki, site 9	D9.5	*Anguilla anguilla*	Abdominal vertebra	No collagen preserved		
Dąbki, site 9	D9.6	*Anguilla anguilla*	Abdominal vertebra	No collagen preserved		
Dąbki, site 9	D9.7	*Anguilla anguilla*	Caudal vertebra (ca. 60 cm)	No collagen preserved		
Dąbki, site 9	D9.8	*Anguilla anguilla*	Caudal vertebra (ca. 47 cm)	No collagen preserved		
Dąbki, site 9	D9PF.5a+b	*Perca fluviatilis*	Opercular (ca. 32 cm)	-19.4	9.4	40.8
Löddesborg	LÖ2.4	*Anguilla anguilla*	Caudal vertebra (ca. 44 cm)	No collagen preserved		
Löddesborg	LÖ2.5	*Anguilla anguilla*	Thoracic vertebra (ca. 58 cm)	No collagen preserved		
Nederst	NSIE8a	*Anguilla anguilla*	Caudal vertebra (ca. 55 cm)	-10.8	8.4	40.4
Skateholm I	SKE1	*Anguilla anguilla*	Vomer (> 50 cm)	No collagen preserved		
Skateholm I	SKE5	*Anguilla anguilla*	Thoracic vertebra (ca. 67 cm)	No collagen preserved		
Skateholm I	SKE9	*Anguilla anguilla*	Thoracic vertebra (ca. 63 cm)	No collagen preserved		
Skateholm I	SKE10	*Anguilla anguilla*	Vertebra (50-60 cm)	No collagen preserved		
Skateholm I	SKE12	*Anguilla anguilla*	Thoracic vertebra (ca. 65 cm)	No collagen preserved		
Trustrup	TCV2a	*Siluris glanis*	Vertebra	-26.7	4.1	9.3
Tågerup	TA1.4	*Anguilla anguilla*	Caudal vertebra (35-45 cm)	No collagen preserved		
Tågerup	TÅ5.1	*Anguilla anguilla*	cf. caudal vertebra (35-45 cm)	No collagen preserved		
Tågerup	TÅ5.2	*Anguilla anguilla*	Thoracic vertebra (ca. 56 cm)	No collagen preserved		
Tågerup	TÅ5.3	*Anguilla anguilla*	Abdominal vertebra (30-45 cm)	No collagen preserved		
Tågerup	TA6.1	*Anguilla anguilla*	cf. thoracic vertebra (ca. 55 cm)	No collagen preserved		
Tågerup	TA6.2	*Anguilla anguilla*	Caudal vertebra (ca. 52 cm)	No collagen preserved		

Table 2: Fish bone samples and isotope data. Samples for which no stable isotope data are presented had no collagen preserved. Samples listed as discarded did not meet the range of 2.9-3.6 (C:N) as described by DeNiro (1985).

Site name	Period	Lab no.	Species (TL)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N atomic ratio
Brackish/marine samples						
Mariager Fjord	Modern	MFE1	Eel (40.0 cm)	-8.2	17.6	3.2
Mariager Fjord	Modern	MFE2	Eel (45.4 cm)	-8.1	18.1	3.1
Mariager Fjord	Modern	MFE3	Eel (46.5 cm)	-8.0	18.0	3.1
Mariager Fjord	Modern	MFF1	Flounder (24.5 cm)	-11.7	14.4	3.1
Mariager Fjord	Modern	MFF2	Flounder (29.5 cm)	-8.6	16.8	3.2

Table 3: Modern eel and flounder data. All carbon isotope data has been corrected for the oceanic Suess Effect (see text and Robson et al. 2012).

Assumed habitats	**Species or taxon**	**Common name**	**Sample size**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**
Marine	*Squalus acanthias*	Spurdog	2	-13.4 ± 0.9	10.9 ± 1.1
Freshwater; brackish; marine	*Anguilla anguilla*	European eel	46	-11.3 ± 2.7	8.4 ± 1.4
Brackish; marine	*Clupea harengus*	Herring	5	-14.7 ± 0.7	9.5 ± 0.6
Freshwater; brackish	*Tinca tinca*	Tench	8	-25.6 ± 0.4	5.4 ± 0.4
Freshwater; brackish	*Esox lucius*	Northern pike	28	-17.9 ± 6.0	9.9 ± 1.7
Freshwater; brackish; marine	Salmonidae	Salmons, trouts, charrs	1	-15.5	11.3
Brackish; marine	Gadidae	Codfishes	29	-12.2 ± 2.4	10.7 ± 1.3
Freshwater; brackish	*Perca fluviatilis*	Perch	3	-16.9 ± 2.5	9.5 ± 0.4
Freshwater; brackish	*Sander lucioperca*	Zander	3	-22.4 ± 1.9	11.2 ± 1.1
Brackish; marine	*Belone belone*	Garfish	3	-13.7 ± 0.5	11.5 ± 1.5
Brackish; marine	*Scomber scombrus*	Mackerel	4	-15.5 ± 0.2	11.1 ± 1.1
Freshwater; brackish; marine	Pleuronectidae	Right eye flounders	8	-12.7 ± 2.8	7.9 ± 1.7

Table 4: Summary statistics for the various species (or taxon) of fish sampled in this study and in the studies Eriksson (2004), Eriksson et al. (2008), Fornander et al. (2008), Fischer et al. (2007) and Robson et al. (2012) (standard deviations have only been calculated for n > 2).

Discussion

Collagen preservation

From a chemical standpoint, the fish bones were, in general, poorly preserved. The low overall success rate (50%) is likely to be the result of the diagenetic alteration of collagen (for example samples low in %C and %N producing high C:N ratios) during burial and is variable between site types. The kitchen midden at Nederst and the shell bearing deposits at Dragsholm had the greatest success rates (89% and 71% respectively). In comparison, Fisher *et al*. (2007) analysed three fish bones from Dragsholm, however, all yielded C:N atomic ratios outside the acceptable range (DeNiro 1985). It seems that this is related to the predominantly shell matrix of the kitchen middens. For comparison, Robson *et al*. (2012) analysed 12 eel bones from the Havnø kitchen midden, of which 11 produced collagen with acceptable C:N ratios, a rate of 92%, and Gron (2013) reported similarly 100% for 13 mammal samples from the kitchen midden at Fårevejle. The coastal site at Asnæs Havnemark, and the lakeshore settlement at Dąbki had success rates of 50% and 47% respectively. These were followed by Tågerup at 25%. Fish bones from neither the open coastal site at Löddesborg or the coastal burial site at Skateholm I possessed any preserved collagen, whilst the one sample from Trustrup, a caudal vertebra identified as deriving from wels catfish, yielded collagen that was either contaminated or severely diagenetically altered, as evidenced by a C:N ratio of 14.8. In comparison, in the study by Eriksson (2006), a wels catfish vertebra was sampled from Zvejnieki II, Latvia which also yielded similar data, a $\delta^{13}C$ value of -26.7‰, a $\delta^{15}N$ value of 6.4‰ but with a C:N ratio of 14.2.

In a previous study of the faunal remains from the burial sites at Skateholm I and II, Eriksson and Liden (2002) likewise reported a very poor success rate. Out of a sample set of 45 bones from both sites, only five produced well-preserved collagen, as indicated by the C:N ratio (DeNiro 1985). Unfortunately neither the five pike, nor the one Salmonidae bone samples selected for analysis produced any collagen. Although only one specimen was analysed from Trustrup, it is worth mentioning that Gron (2013) submitted 13 mammalian samples from the site for carbon and nitrogen stable isotope analysis. In his study, all samples were unsuccessful and either fell outside the acceptable ranges of atomic carbon to nitrogen or impossible values were measured. Seemingly diagenesis at the site is a major problem, possibly due to a combination of factors including, but not limited to, near-shore lake dynamics, seasonal temperature shifts, nearby springs, and travertine precipitation (Ford and Pedley 1996).

Taking the above into consideration, our data and previously published data suggest that bone collagen is better preserved within kitchen midden contexts when compared to the other site types. In all likelihood this owes to the calcium carbonate ($CaCO_3$) content of the shells buffering against acid hydrolysis of the soluble bone collagen (see Noe-Nygaard 1987; Schulting 2011). In comparison, it is worth noting that the fish bones from Dąbki were dark brown (almost black) in colour (see Figure 2), and were recovered from a depositional context rich in organic material. Similarly, the faunal material recovered at Trustrup was a light brown colour and was recovered from dynamic contexts rich in organic material. These burial contexts represent aggressive environments in terms of the chemical diagenesis of bone collagen (see Fuller *et al*. 2012; Szpak 2011), since the acid dissolution of the mineral component of the bone as well as the exchange with the water table cannot be prevented (Noe-Nygaard 1987).

Freshwater/brackish fish (northern pike; perch; zander)

The eight reliable specimens of pike, perch and zander analysed from Dąbki had mean $\delta^{13}C$ values of -23.3‰ ± 1.3‰, -18.3‰ ± 0.7‰, and -22.4‰ ± 1.9‰, and $\delta^{15}N$ values of 9.8‰ ± 1.0‰, 9.5‰ ± 0.5‰ and 11.2‰ ± 1.1‰ respectively (based on both repeated measurements of each sample and between individuals). Among the freshwater/brackish fish, the pike had the most ^{13}C-depleted mean values, while zander had the most ^{15}N-enriched mean values. The data suggest that the pike and zander deposited at Dąbki have carbon isotope values consistent with freshwater residency, whilst the two perch samples with values of -17.9‰ and -18.8‰, although outside the range of the archaeological freshwater species, are consistent with a brackish source or that they fed in the littoral zone of a lake (see Robson *et al*. 2012) and comparable with the values for freshwater pike and zander previously reported (Antanaitis-Jacobs *et al*. 2009; Eriksson2006; Fischer *et al*. 2007). The sample of fish bone from Dąbki is small but indicated carbon isotope values consistent with both freshwater and brackish residency. The variation in $\delta^{15}N$ values is likely to represent the different feeding strategies, and thus reflect multiple trophic positions occupied by the different species of fish. Zander prey primarily on other fish species, normally patrolling in open water where they actively hunt and pursue prey as solitary individuals, although they can often be found in shoals. Pike tend to lie in ambush preying on smaller species of fish, crustaceans or insects (Davies *et al*. 2004), although they are known to have cannibalistic tendencies. Since zander had the highest $\delta^{15}N$ values regardless of total

fish length, this could be a reflection of baseline differences between littoral and pelagic habitats (Harrod *et al*. 2010). An alternative explanation however could be that pike and zander had different diet-tissue fractionation values.

Brackish/marine fish (spurdog; pleuronectidae; gadidae; garfish; mackerel)

Although spurdog skeletal elements are lipid rich and poorly ossified, and as such have poorer chances of preservation, they are routinely recovered from archaeological sites in central and northern Europe (see Enghoff 2011; Ritchie 2010). The spurdog is a member of the Squalidae family, residing close to the bottom in shallow waters but also down to depths of ca. 400 m. It is migratory, often covering long distances daily (Muus and Dahlstrøm 1964), feeding on fish and various invertebrates. Suitably, the two-spurdog vertebrae from the kitchen midden at Dragsholm had mean $\delta^{13}C$ values of -13.4‰ ± 0.9‰, and $\delta^{15}N$ values of 10.9‰ ± 1.1‰, consequently higher up in the trophic hierarchy of marine taxa.

Although a number of Pleuronectidae (right eye flounders) species are known to naturally occur in the waters of central and northern Europe (for example flounder/plaice/dab), the specimens analysed in this study could not be further identified to the lower taxonomic levels. In general, Pleuronectidae are a demersal taxon, and had the lowest mean $\delta^{15}N$ values (7.4‰ ± 0.7‰). While flounder are known to penetrate into freshwater, three of the specimens (Dragsholm, n = 1 and Nederst, n = 2) analysed here do not possess sufficiently ^{13}C-depleted compositions to be classified as estuarine fish (-11.9‰ to -8.1‰ in $\delta^{13}C$). As such, their isotopic signatures, especially the low $\delta^{15}N$ values resemble either those of plaice or dab (see Fuller *et al*. 2012). However, two of the unidentified specimens (Dragsholm, n =1 and Asnæs Havnemark, n = 1) could be estuarine given their $\delta^{13}C$ values of -16.6‰ and -15.5‰ respectively.

Likewise it was not possible to identify the Gadidae specimens in this study to the lower genus, and taxonomic levels. However, at least six species are known to occur locally in central and northern Europe: Atlantic cod, haddock (*Melanogrammus aeglefinus*), ling (*Molva molva*), pollock (*Pollachius pollachius*), saithe (*Pollachius virens*) and whiting (*Merlangius merlangus*). In light of this, the four Gadidae specimens from the coastal settlement at Asnæs Havnemark, and the Nederst kitchen midden possessed relatively enriched $\delta^{13}C$ and $\delta^{15}N$ values, demonstrating that these species are marine feeders and higher up in the trophic hierarchy. The mean ± SD values for the four

Gadidae are -11.5‰ ± 2.7‰ for $\delta^{13}C$, and 11.0‰ ± 0.9‰ for $\delta^{15}N$, and are consistent with the cod from the coeval Danish sites at Bjørnsholm, Nivågård, and Vængesø III (-10.6‰ ± 1.7‰ for $\delta^{13}C$ and 10.0‰ ± 1.2‰ for $\delta^{15}N$) (Fischer *et al*. 2007), as well as the Swedish sites dating to the Pitted Ware culture at Ire and Köpingsvik (-14.4‰ ± 1.1‰ for $\delta^{13}C$ and 11.4‰ ± 1.2‰ for $\delta^{15}N$) (Eriksson 2004; Eriksson *et al*. 2008).

The two specimens of garfish from the kitchen midden at Dragsholm had mean $\delta^{13}C$ values of -13.4‰ ± 0.4‰, and $\delta^{15}N$ values of 12.3‰ ± 0.5‰ respectively, and are comparable with a single measurement reported by Eriksson *et al*. (2008) from the site of Köpingsvik, Sweden. Garfish are a pelagic migratory species, as such it is not surprising that their $\delta^{13}C$ values are consistent with marine residency. In addition they are piscivorous though not particularly high in the trophic hierarchy that is reflected in their relatively low $\delta^{15}N$ values.

Likewise the mackerel had a similar habitat use and migratory pattern to that of the garfish, and as such had comparable $\delta^{13}C$ values. However, since they are a diurnal species a range in their $\delta^{15}N$ values is expected. As such the four successful specimens analysed in this study from the coastal settlement at Asnæs Havnemark, and the Dragsholm kitchen midden had mean $\delta^{13}C$ values of -15.5‰ ± 0.2‰, and $\delta^{15}N$ values of 11.1‰ ± 1.1‰.

Anadomous Salmonidae

The single Salmonidae specimen analysed from the coastal settlement at Asnæs Havnemark had a relatively low $\delta^{15}N$ ratio (11.3‰), which is consistent with the fact that it mainly feeds on crustaceans and small fish. Although anadromous, this individual displayed a $\delta^{13}C$ value of -15.5‰ consistent with a marine origin, and no evidence of freshwater residency.

Catadromous eels

The 10 successful eel specimens exhibited considerable variation in both their $\delta^{13}C$ and $\delta^{15}N$ values. They possessed mean $\delta^{13}C$ values of -10.0‰ ± 1.6‰, and mean $\delta^{15}N$ values of 9.2‰ ± 0.7‰ respectively. Congruent with the data reported by Robson *et al*. (2012), it is suggested that the eel found at the four coastal sites and kitchen middens in this study have carbon isotope values consistent with populations residing in marine-dominated waters. Similarly, the variations in the $\delta^{15}N$ values are likely to represent the wide range of feeding strategies seen in modern eels (Harrod *et al*. 2005), although they

are comparable with fish feeding at three or four trophic levels above producers (difference/3.5). The two eel from Tågerup that derived from deposits dated to the Kongemose culture epoch had the most ^{13}C-depleted values (-13.6‰ and -11.9‰ respectively), although their δ^{15}N isotope values are within the range established from the study by Robson *et al*. (2012). The two eel from the coastal settlement at Asnæs Havnemark had the most enriched δ^{15}N values, whilst the eel from the shell bearing deposits at Dragsholm and the Nederst kitchen midden had fairly similar δ^{13}C and δ^{15}N values. However, the difference between the δ^{13}C values of the archaeological eel (n = 46) and the approximated modern salinity values for the water bodies closest to the archaeological sites are significantly positively correlated (Pearson Correlation; r = 0.660, n = 59, p < 0.0005), see Figure 10.

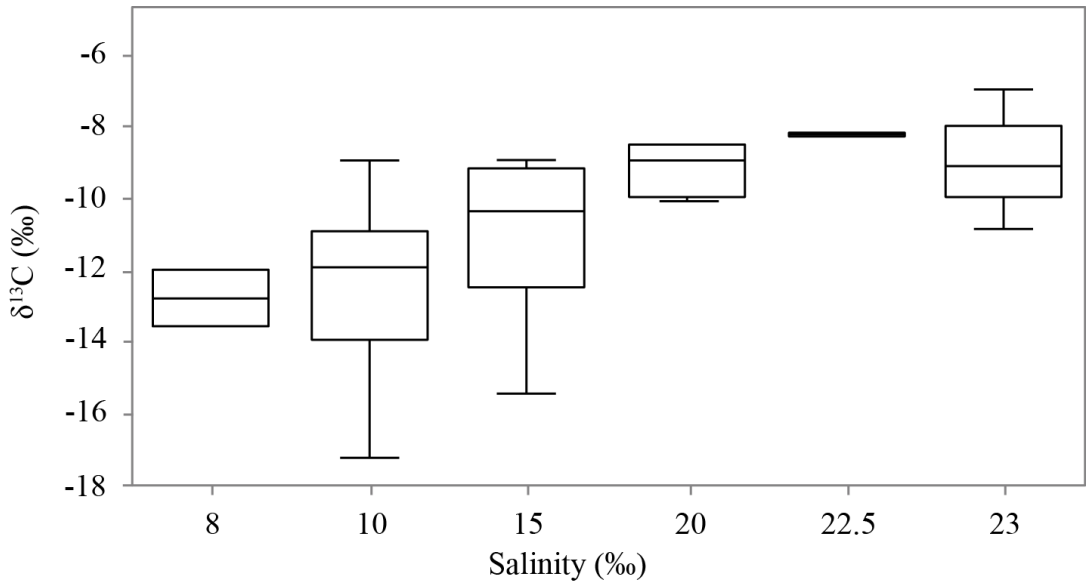

Figure 10: Box and whisker plot representing the mean and standard deviations for the δ^{13}C values from the eel bone collagen samples in this study and those reported by Robson et al. (2012) against the approximated salinity of the water bodies closest to the archaeological sites.

Conclusions

The results of this study emphasize the necessity of the analysis of fish bone collagen for the stable isotopic values of carbon (δ^{13}C) and nitrogen (δ^{15}N) in future dietary reconstruction of human populations dating to the late Mesolithic and the early Neolithic of central and northern Europe. In comparison with previously published

archaeological human bone isotope data (n = 19) from Denmark of late Mesolithic date (Ertebølle culture), the situation is rather complex. They possessed mean $\delta^{13}C$ values of -13.2‰ ± 2.1‰, and mean $\delta^{15}N$ values of 13.2‰ ± 1.7‰ respectively (Fischer *et al*. 2007; Price *et al*. 2007; Richards *et al*. 2003b; Richter and Noe-Nygaard 2003). While exhibiting a broadly similar range in $\delta^{13}C$ to that of the fish, the human $\delta^{15}N$ values are elevated representing the trophic enrichment between prey and consumer. However, given the considerable overlap with both the diadromous (anadromous and catadromous), and marine taxa, a considerable proportion of diet, albeit long term, derived from the consumption of a mixture of available sources of fish, although additional work is needed to determine what possible mixtures could result in the observed human stable isotope values.

Since there is no evidence for long-distance fish trade during these periods (though see Fischer 1982), the specimens analysed in the present study were probably captured in the local waters by the Mesolithic and Neolithic fishers in the region (Enghoff *et al*. 2007), and thus to some extent reflect the species composition of the local waters (Enghoff 1994). Although the data exhibited the expected ranges for freshwater, brackish, and marine fish, they show considerable inter-species variation in both the measured $\delta^{13}C$ and $\delta^{15}N$ values of fish bone collagen. Based on the small sample analysed here, variation between site type, and the success rate (Fuller *et al*. 2012; Szpak 2011) could not be established. However, the future stable isotopic analyses of fish bone collagen dating to both the Maglemose and Kongemose cultures will help to establish whether diachronic variation has taken place. Furthermore, additional work is needed in order to characterise the variation in the isotopic values of inland freshwater eels. Additional work establishing the trophic enrichment factor between diet and collagen, how it compares to muscle tissue and how it varies with salinity is required. Lastly, in order to compare trophic positions without a common baseline relative to primary producers, the use of compound specific stable isotope determinations are required (for example McClelland and Montoya 2002).

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