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Coast–inland mobility and diet in the Danish Mesolithic and Neolithic: evidence from stable isotope values of humans and dogs

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Abstract

Here we present the stable isotope ratios of carbon and nitrogen measured in bone collagen extracted from humans, dogs, herbivores and fish from Mesolithic and Neolithic coastal and inland sites in Denmark. Bones of freshwater fish from several Early Mesolithic lake-side sites have δ^{13}C values surprisingly similar to those seen in marine fish. We propose a model, based on δ^{13}C and δ^{15}N, for the correction for both marine and hard water reservoir effect in radiocarbon dates. A strong reliance on aquatic protein is demonstrated for the Mesolithic inhabitants of the region from the middle of the Early Mesolithic onwards. A significant part of the protein in the diets of the dogs and humans from the Middle and Late Mesolithic was of marine origin, even at inland sites. This observation points to a high degree of (seasonal) coast-inland mobility. The isotopic evidence indicates that during the Neolithic small quantities of aquatic foods were still common sources of dietary protein.

Keywords: Diet; Isotope; Radiocarbon; Reservoir effect; Marine; Freshwater; Denmark; Mesolithic; Neolithic

1. Introduction

For a number of generations archaeologists have debated whether seasonal migrations took place in the Northern and Western European Mesolithic and Early Neolithic, and to what degree the settlement patterns included both coastal and inland regions. Until recently, many scholars considered the Early Mesolithic Maglemose Culture of the North-European lowlands as primarily or solely an inland phenomenon (Mathiassen, 1943: 139; Clark, 1972; Grøn, 1987; cf. Sørensen, 1996: 38, 44; Schilling, 2003). Others argued that Mesolithic settlements in the interior regions of Norway, Sweden, Denmark, England, etc. could have been part of seasonal rounds, which also—or primarily—included habitation at the coast (e.g. Troels-Smith, 1960, 1963; Møhl, 1971; Andersen, 1975; Mikkelsen, 1978; Larsson, 1980; Andersen K., 1983: 195 and 202; Rowley-Conwy, 1983; Fischer and Sørensen, 1983; Donahue and Lovis, 2006).

Over the latest two decades stable isotope analyses of collagen in human and dog bones have played an essential role in this debate (Noe-Nygaard, 1988; Clutton-Brock and

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Noe-Nygaard, 1990; Fischer, 1993, 2003, 2004; Price, 1993; Andersen, 1998; Rasmussen, 1998; Rowley-Conwy, 1998; Karsten, 2001: 85; Schulting and Richards, 2002; Eriksson, 2003: 22; Fischer and Hansen, 2005; cf. Tauber, 1986a). It has been demonstrated that several of the individuals found in the inland bogs of the Vale of Pickering in England, Ringkloster, Åmose, Holmegård and Sværdborg in Denmark and Agerød in Sweden (Fig. 1) have clearly elevated $\delta^{13}C$ values. Based on this observation it has been inferred that these dogs and humans moved from the coast to the interior.

Fig. 1. Sites mentioned in the text. Solid symbols represent samples analysed as part of the present project. Squares: coastal Stone Age sites. Dots: inland Stone Age sites. Triangles: Present-day lake and fjord sites.

Other Mesolithic inland individuals have $\delta^{13}C$ values in which a marine signature is not visible. However, this may in principle simply be a matter of mixed marine and freshwater diet, which can produce $\delta^{13}C$ values indistinguishable from those representing purely terrestrial diet (Fischer, 2003). In order to address this aspect of interpretation, the present project was initiated. It includes combined measurements of $\delta^{13}C$ and $\delta^{15}N$ of all Danish Mesolithic inland samples of humans and dogs presently available to us.

For comparative reasons, a number of humans found at Mesolithic and Neolithic coastal sites and in Neolithic megalithic tombs have been included in the project. As a result we also have new data that are relevant to the long-standing debate over changes in diet at the transition from the Mesolithic to the Neolithic (e.g. Tauber, 1981a,b, 1986a; Fischer, 2002; Richards et al., 2003; Milner et al., 2004; Lidén et al., 2004; Richards and Schulting, 2006). In total the paper presents the results of $\delta^{13}C$ and $\delta^{15}N$ measurements of 75 humans and 27 dogs from the Mesolithic and the Neolithic, several of which have also been AMS dated as part of the project.

To provide a firm basis for dietary interpretation, we have measured $\delta^{13}C$ and $\delta^{15}N$ values for a number of the most common food source animals found on Danish coastal and inland sites spanning from the Early Mesolithic to the Middle Neolithic. The empirical basis for dietary interpretation is, furthermore, supported by a series of $\delta^{13}C$ and $\delta^{15}N$ measurements on a number of organisms that represent a wide range of trophic levels in two present-day lakes and a fjord located in the area where most of our prehistoric samples were found.

In the present paper a site is termed "coastal" only when it originally lay directly at the contemporaneous beach (<100 m from the sea). In most cases such sites are characterised by cultural deposits in marine sediments and/or kitchen middens packed with shells of marine molluscs. The Mesolithic inland sites dealt with here were originally all situated at the water edge of lakes and bogs miles away from the contemporaneous sea shores. The same applies to some of the Neolithic inland sites dealt with in the paper. Most of the other Neolithic samples derive from megaliths on more or less elevated spots in the landscape such as the passage grave of Aldersro, which is located on a hill 2–3 km from the nearest contemporaneous fjord.

2. Paleodietary information from stable isotopes

Measurements of stable isotopes of carbon and nitrogen in bone collagen have proven a useful way of obtaining information on the protein portion of diets (Ambrose and Norr, 1993). Although lipids and carbohydrates in diets may constitute significant parts of the energy intake, they have little influence on $\delta^{13}C$ in bone collagen—at least in protein-rich diets (e.g. Hedges, 2004). Since they contain no nitrogen, they have no effect on $\delta^{15}N$.

The isotopic composition of collagen from the most compact regions of the bones of adult humans represents the average diet over a considerable time (of the order of 20 years) prior to death (Wild et al., 2000; Geyh, 2001). Collagen from non-compact (trabecular) areas of bones from adult humans represents the average diet over about four years (Martin et al., 1998). The bone collagen turnover rate in dogs is much higher than in humans. Thus, in young adult dogs the turnover time is reported to be six months to three years (Martin et al., 1998).

In palaeodietary research the $\delta^{13}C$ value has generally been considered useful for estimating the proportion of marine relative to terrestrial food, despite warnings against pitfalls (Lanting and van der Plicht, 1998). As mentioned above, mixtures of marine and freshwater food may yield $\delta^{13}C$ values that simulate terrestrial food, but this ambiguity can to some extent be resolved through measurement of $\delta^{15}N$. The $\delta^{15}N$ value reflects the trophic level of a diet, so carnivores have significantly higher $\delta^{15}N$ values than herbivores (Schoeninger and DeNiro, 1984). Since aquatic (i.e. marine and freshwater) food chains are longer than their terrestrial counterparts, diets dominated by food from fresh and/or marine waters can often be distinguished from more terrestrial diets through their elevated nitrogen values.

Both $\delta^{13}C$ and $\delta^{15}N$ values of consumer bone collagen are higher than the corresponding values of their prey. We adopt the generally accepted offsets of approximately 1‰ for $\delta^{13}C$ and 3.5‰ for $\delta^{15}N$ (Post, 2002; Bocherens and Drucker, 2003; cf. Masao and Wada, 1984; Schoeninger and DeNiro, 1984; Lidén, 1995: 17; Richards and Hedges, 1999; Sponheimer et al., 2003).

3. Methods and data evaluations

3.1. Methods and equipment

The stable carbon and nitrogen isotope ratios expressed as $\delta^{13}C$ and $\delta^{15}N$ values were measured on mass spectrometers in Aarhus and Bradford while only $\delta^{13}C$ measurements were made in Reykjavik. In addition six samples were measured in Oxford. All samples were prepared according to standard extraction procedures (Richards and Hedges, 1999). Most samples prepared in Bradford prior to 2005 were also ultrafiltered (Brown et al., 1988), while the samples prepared in Aarhus and in Bradford from 2005 onwards were not. The modern samples of fish, molluscs, etc. were first run through a lipid dissolving sequence of hexane, acetone and lastly ethanol; each step implied the application of an ultrasonic bath at 45 °C for 15 min. The samples were then rinsed with water (2 × 15 min in ultrasonic bath).

There were multiple determinations in several cases, so that the same bone was measured in Bradford as well as in Aarhus. In both laboratories the precision was ±0.2‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$. If the measured carbon-to-nitrogen ratio (C:N) was outside the accepted range of 2.9 to 3.6 (DeNiro, 1985), the $\delta^{13}C$ and $\delta^{15}N$ values were not used in this study. Further, the quality guidelines given by Van Klinken (1999) have been applied to remove collagen samples of unsatisfactory quality: carbon content <25%, nitrogen content <10%, collagen yield <1% (in case of ultrafiltered samples, collagen yields as low as 0.1% are, however, considered valid). At the Science Institute in Reykjavik, $\delta^{13}C$ values were measured with a precision of ±0.1‰ on all samples that have been dated at the AMS ^{14}C Dating Centre in Aarhus.

Table 1
Measurements produced by the present project

Site name	Cultural epoch	Lab. no.	Species (and sex)	Anatomical part and ontogenetic age	^{14}C age
					BP
Inland samples					
Aldersro X621	N	Poz-17033/ACQ59: 20+31	Human	Femur dxt., adult	3855 ± 35
Aldersro X622	N	Poz-17023/ACQ59: 9+28	Human	Femur dxt., adult	3950 ± 35
Bodal A	E/N	AAR-4769/30035	Dog	Mandibula sin., adult	5380 ± 50
Bodal AL	E	AAR-4767/32176	Dog	Radius sin., adult	5765 ± 45
Bodal AV	E/N	AAR-4771/32175	Dog	Tibia sin., adult	5250 ± 50
Bodal C	E/N	AAR-4766/30053	Dog	Mandibula dxt., adult	5355 ± 45
Bodal C	N	AAR-6945/34768	Domestic cattle	Phalanx, adult	5110 ± 40
Bodal C	E/N	AAR-7199/34768	Dog	Os temporale, adult	5430 ± 48
Bodal E	E/N	AAR-4770/ZMK 43/1988	Dog	Calvarium, adult/senilis	5340 ± 80
Bodal K	E	AAR-4765/BCH198: 12a+b	Human	Humerus sin., adult	6275 ± 50
Bodal K	E/N	AAR-4772/31020	Dog	Atlas, adult >1.25 y	5240 ± 45
Bodal K	N	AAR-6826/29-03-00; AS 02/01	Human M	Tibia sin., adult	4970 ± 60
Bodal K	N	AAR-6943/ZMK 23/1982	Domestic cattle	Os frontale, adult	5115 ± 50
Bodal K	N	AAR-6944/36614	Domestic cattle	Radius, adult	5135 ± 45
Bodal K	E/N	AAR-7194/36614	Dog	Mandibula dxt., sub-adult	5209 ± 41
Boelkilde	N	K-4593/T4	Human M	Femur dxt., >30 y	4670 ± 65
Ferle Enge	N	K-6299/BCH199: 16+44	Human F	Tibia sin., 25–35 y	4940 ± 95
Flixton School	N	AAR-7669/FL9301UF	Dog	Adult	4990 ± 50
Føllenslev	N	K-3747/BCH198: 46a+b	Human M	Femur sin, adult	3530 ± 120
Hallebygård	N	Poz-17025/ACQ59: 17+27	Human M	Femur dxt., adult	4800 ± 40
Hedegård	M	AAR-4554/BCH198: 40a+b	Human M	Cranium, adult	8680 ± 40
Hesselbjerggårds Mose	N	AAR-7310/1943	Human	Os frontale, adult	4867 ± 32
Holmegård I	M	AAR-4381/M-56696	Dog	Calcaneus sin.	7980 ± 70
Holmegård I	m	AAR-8658-1/1922	Red deer	Femur sin., adult	
Holmegård I	m	AAR-8658-2/1922	Red deer	Femur sin., adult	
Holmegård I	m	AAR-8659-1/1922	Roe deer	Femur dxt., adult	
Holmegård I	m	AAR-8659-2/1922	Roe deer	Femur dxt., adult	
Holmegård I	m	AAR-8854/1922 c	Pike	Articulare	
Holmegård IV	m	AF52B	Otter	Humerus, adult	
Holmegård IV	m	T6	Otter	Humerus, adult	
Holmegård IV	m	1944-38D	Pike	Vertebra	
Holmegård V	M	AAR-4382/M-56697	Dog	Pelvis, adult	8580 ± 60
Holmegård V, A	M	AAR-8558	Human M	Humerus dxt., >35 y	8465 ± 35
Holmegård V, A	M	AAR-8559	Human M	Ulna dxt., >35 y	
Holmegård V, B	M	AAR-8560/M57435	Human	Humerus dxt., ∼18–20 y	8315 ± 45
Holmegård V, C	M	AAR-8561	Human M	Ulna dxt., adult	8500 ± 65
Hulbjerg	N	K-6042/T5	Human	Femur	3680 ± 65
Jorløse Mose	N	K-6302/BCH199: 17+45	Human M	Tibia sin., 30–40 y	4430 ± 90
Klokkehøj	N	K-2954/SHg1143	Human	Costae and os coxa, adult	4550 ± 65
Klokkehøj	N	K-3012/BCH198: 24a+b	Human	Femur dxt., adult	4250 ± 90
Klokkehøj	N	K-3014/SHg1150	Human	Femur, adult	4200 ± 90
Koelbjerg	M	AAR-8613/FS B 2268–2270	Human F	Femur dxt., ∼25 y	9285 ± 50
Kongemose, 1979	M	AAR-6788/A51207, AS40/00	Human	1st permanent molar, 6–12 y	8060 ± 65
Kongemose B	N	AAR-7195/31176	Dog	Mandibula sin., >2.5 y	4690 ± 41
Mullerup, Neegaards island	m	BCH198: 21a+b	Pike	Vertebra	
Mullerup, Neegaards island	m	5/ACQ59: 19+40	Pike	Vertebra	
Mullerup, Neegaards island	m	9/ACQ66a:24+43	Pike	Cleithrum	
Mullerup, Sarauws island	M	AAR-8554/NM1 A18269	Human	Femur sin., adult	8310 ± 55
Mullerup, Sarauws island	m	BCH198: 7	Human	Mandibula dxt., 7–8 y	
Nissehøj	N	K-6101/T3 (M70957)	Human	Fibula dxt.	3620 ± 90
Porsmose	N	K-3748/Hg24297	Human M	costae, 35–40 y	4710 ± 90
Præstelyng	E/N	K-3773/AFP1	Dog		5260 ± 65
Ringkloster	E/N	K-4133/M57431	Dog		5420 ± 210
Sigersdal A	N	K-3744/BCH198: 8a+b	Human F	Costae, 18–20 y	4650 ± 140
Sigersdal B	N	K-3745/BCH198: 87+23	Human F	Costae and pes, 16 y	4680 ± 75
Storelyng VI	n	AAR-7061	Goat	Metacarpus, adult	4500 ± 45
Storelyng VI	n	AAR-7062	Goat	Metararpus, ∼.25 y	4420 ± 50
Storelyng VI	n	AF285	Roe deer	Pelvis	
Storelyng VI	n	AF4300	Roe deer	Tibia	
Storelyng VI	n	AF9107	Roe deer	Radius+ulna	

$\delta^{13}C$	$\delta^{15}N$	C:N	$\delta^{13}C$	Reservoir correction model		Corrected ^{14}C age	%C	%N	% col.
VPDB (‰)	AIR (‰)	atom	CPH	$\delta^{13}C$	$\delta^{15}N$	BP	average/range		
−20.1	8.5	3.4		14%	7%	3800	33.8	11.6	4.2
−20.1	9.3	3.3		14%	16%	3884	34.7	12.3	5.3
−19.3	9.7	3.2		21%	20%	5296	37.1−37.8	13.1−13.8	10.5−14.2
−13.5	10.0	3.2		71%	24%	5481			8.7
−23.6	9.3	3.1		−	16%	5250	40.1	15.0	8.9−16.9
−15.1	10.2	3.2		57%	27%	5127	34.5	12.7	9.1−14.7
−21.4	5.0	3.3				5110	40.6	14.2	5.9−19.6
−14.5	10.4	3.1		62%	28%	5183	36.1−39.5	13.1−14.8	9.5
−20.1	7.9	3.4		14%	1%	5283	31.3	10.5	6.8−12.0
−16.1	13.4	3.2		48%	61%	6031	41.1−41.3	14.8−15.3	14.7−19.4
−24.4	7.6	3.4		−	−	5240			7.8−11.7
−21.5	9.7	3.4		2%	21%	4887	40.5−42.2	13.2−14.9	2.2−6.1
−21.7	4.7	3.4				5115	42.9	14.7	22.2
−21.3	4.3	3.5				5135	41.6	14.0	7.8−23.1
−22.4	9.2	3.1		−	15%	5149	40.1−43.7	14.4−16.2	15.2
−19.7	12.0	3.2	−20.8	17%	46%	4487	30.8	11.1	6.3
−22.6	9.3	3.4	−20.6	−	16%	4875	35.7	12.2	7.1
−21.1	6.0	3.3		5%	−	4969	44.8	16.4	16.5
−20.7	9.4	3.3	−20.7	8%	18%	3459	40.2	14.2	9.2
−21.1	9.9	3.3		5%	22%	4711	41.0	14.4	9.9
−20.3	11.5	3.2		12%	41%	8518	40.4	14.8	15.8
−20.5	9.8	3.2		11%	22%	4778	38.3−41.1	13.6−15.2	7.6
−18.3	9.5	3.2		30%	19%	7861	40.4	14.8	
−22.7	4.7	3.4					44.3	15.1	2.7
−22.9	4.6	3.3					40.9	14.3	0.8
−24.3	3.8	3.4					45.3	15.7	5.7
−22.6	3.1	3.4					44.6	15.2	5.6
−15.4	7.8	3.6					33.8−39.8	11.7−12.9	1.1−9.3
−20.7	10.2	3.5					32.4	10.8	10.3
−14.8	9.6	3.4					37.6	13.0	7.9
−22.8	10.0	3.6					43.4	14.1	1.7
−17.8	8.8	3.1		33%	11%	8446	39.0	14.6	
−18.6	11.8	3.1		26%	44%	8289	36.7	13.6	5.1
−18.5	11.8	3.2					40.8	14.9	5.7
−20.0	12.4	3.2		15%	50%	8114	43.2	15.7	6.7
−20.2	11.6	3.2		13%	41%	8336	38.3	14.0	5.4
−20.8	10.6	3.3	−20.1	8%	30%	3558	44.1	15.6	19.0
−20.5	10.8	3.5	−20.3	10%	32%	4301	40.9	13.3	11.1
−19.7	9.7	3.4	−18.1	17%	21%	4466	43.4	15.0	9.5
−20.2	9.6	3.2	−19.2	13%	19%	4174	36.8	13.4	
−20.1	9.2	3.4	−18.9	14%	15%	4140	41.8	14.2	6.3
−22.3	7.9	3.4		−	1%	9281	44.2−46.3	13.2−15.4	6.9−23.5
−22.3	11.5	3.5		−	40%	7900	46.2	15.3	1.8−8.3
−20.3	9.2	3.1		12%	15%	4629	40.6−42.9	15.0−16.0	12.4
−9.3	9.4	3.6					35.8	11.8	1.9
−8.0	9.2	3.4					42.6	14.6	7.0
−9.5	8.7	3.3					39.6	14.2	7.9
−18.5	9.7	3.2		28%	20%	8199	39.8	14.4	16.1
−21.4	10.0	3.6					41.9	13.8	9.8
−20.3	8.4	3.2	−20.0	12%	7%	3572	37.2	14.2	15.1
−20.4	8.6	3.1	−19.4	11%	9%	4664	39.8	15.0	
−21.3	8.5	3.2	−21.6	3%	7%	5232	43.8	16.0	14.5
−16.6	16.2	3.4	−18.8	44%	92%	5053	39.2	13.3	11.0
−20.4	10.0	3.3	−19.9	11%	24%	4554	35.9	12.9	
−19.2	10.5	3.3	−19.3	21%	29%	4564	37.1	13.7	
−21.6	4.5	3.2					42.6	15.0	19.7
−21.1	5.1	3.2					40.4	14.5	18.5
−21.6	4.2	3.1					41.2	15.3	21.4
−21.4	3.4	3.1					39.3	14.7	18.3
−22.5	2.5	3.2					43.7	16.1	19.3

(*continued on next page*)

Table 1 (*continued*)

Site name	Cultural epoch	Lab. no.	Species (and sex)	Anatomical part and ontogenetic age	^{14}C age
					BP
Storelyng VI	n	AF4533	Pike	Cleithrum	
Storelyng VI	(n)	AF7016	Pike	Dentale	
Storelyng VI	(n)	AF7521	Pike	Dentale	
Storelyng VI	n	AF8148	Pike	Ceratohyale	
Storelyng VI	k/e	AF9093	Pike	Vertebra	
Storelyng VI	k/e	AF9440	Pike	Articulare	
Storelyng VI	n	BCH198: 25a+b	Pike	Dentale	
Storelyng VI	n	AF351	Tench	Operculum	
Storelyng VI	n	AF2709	Tench	Operculum	
Storelyng VI	n	AF2875	Tench	Pharyngeum inferius	
Storelyng VI	n	AF2947	Tench	Operculum	
Storelyng VI	n	AF3065	Tench	Cleithrum	
Storelyng VI	n	AF3071	Tench	Pelvis	
Tagmosegård	N	K-6297/BCH199: 49	Human	Femur dxt., 7–8 y	4920 ± 95
Tingbjerggård Vest	E/N	AAR-7032/T.v.704, A47874	Human F	Femur, adult	5452 ± 48
Trudstrupgård	N	AAR-6881/KAM 20724	Human M	Os coxa dxt., 40–50 y	4870 ± 45
Trudstrupgård 2	N	AAR-8614/KAM 5694	Human M	Femur dxt., adult	3715 ± 25
Tømmerupgårds Mose	M	Poz-17031/ACQ11+43	Human	Cranium, adult	8730 ± 50
Ulkestrup Lyng M	N	AAR-7673/ZMK 15/1985	Dog	Mandibula dxt., adult	4680 ± 48
Ulkestrup Lyng M	N	K-4979/BCH200: 20+40	Domestic ox	Adult	4630 ± 85
Ulkestrup Lyng U	N	AAR-7196/ZMK 83/1988	Human	Cranium, juvenile/adult	4820 ± 38
Undløse Bro	E/N	AAR-4773/BCH198: 49a+b	Dog	Maxilla, adult	5386 ± 42
Veksø Mose	N	Poz-17006+17030/BCH198: 13a+b	Human F	Femur sin., 30–40 y	4985 ± 27
Øgårde boat III	N	K-3746/ACQ59: 8+38	Human (M)	Adult	4570 ± 60
Østrup homo II	N	AAR-10248/BCH198: 34a+b	Human	Femur sin., 35–45 y	4523 ± 37
Åkonge	n	K-4883/BCH198: 26a+b	Red deer	Limb bone	5010 ± 65
Åkonge	n	K-4881/BCH198: 37a+b	Red deer	Scapula	5060 ± 65
Åkonge	n	K-4882/BCH198: 17a+b	Red deer	Limb bone	5070 ± 65
Åkonge	n	K-4884/BCH198: 19a+b	Red deer	Scapula	4990 ± 65
Åkonge	n	K-4885/BCH198: 43a+b	Red deer	Limb bone	4950 ± 60
Åkonge	n	K-4886/BCH198: 10a+b	Red deer	Limb bone	4990 ± 65
Åkonge	n	AAR-4452/KML 49,5/76,0: 5038	Domestic cattle	Metacarpus sin., ∼.25 y	5120 ± 40
Åkonge	n	BCH198: 38a+b	Pike	Vertebra	
Åkonge	n	BCH198: 36a+b	Pike	Vertebra	
Åkonge	n	AAR-4573/KML 49,5/75,0: 20	Pike	Dentale	5250 ± 45
Åkonge	n	AAR-4576/KML 49,5/75,0: 15	Tench	2 operculae	5565 ± 40
Åkonge	n	AAR-4574/KML 49,5/75,0: 20	Tench	2 operculae	5395 ± 40
Coastal samples					
Argus	(k)	BCH198: 32a+b	Human	Tibia dxt., 2–3 y	
Argus	(k)	AAR-8856	Human	Femur sin., 2–3 y	
Argus	(k)	AAR-8857	Human	Femur sin., 4–5 y	
Argus	K	K-4354/AS 7/01, F 58-54	Human F	Humerussin., 18–20 y	7080 ± 75
Argus	(k)	AAR-8858	Human F	Humerus dxt.,18–20 y	
Argus	(k)	AAR-8859	Human M	Humerus sin., adult	
Argus	(k)	F 58-54 b	Human M	Tibia dxt., adult	
Argus	(k)	ZMK 112/1956	Dog	Tibia, adult	
Argus	(k)	AAR-4093	Dog or Roe deer	Tibia, ∼.5 y	6870 ± 50
Argus	(k)	AAR-8607	Otter	Humerus, adult	
Argus	(k)	AAR-8608	Grey seal	Bulla, new born	
Argus	(k)	AAR-8609	Harp seal	Os occipitale, adult	
Argus	(k)	AAR-8610	Roe deer	Femur sin., adult	
Argus	(k)	AAR-8610-2	Roe deer	Femur sin., adult	
Argus	(k)	AAR-8610-3	Roe deer	Femur sin., adult	
Argus	(k)	AAR-8611	Red deer	Humerus dxt., adult	
Argus	(k)	AAR-8611-2	Red deer	Humerus dxt., adult	
Argus	(k)	AAR-8611-3	Red deer	Humerus dxt., adult	
Argus	(k)	AAR-8605	Pike	Vertebra, adult (∼1.0m)	
Bjørnsholm	e	AFADSC1	Cod	2 vertebrae	
Bjørnsholm	e	AFADSC2	Cod	2 vertebrae	
Bjørnsholm	e	AFADSC3	Cod	2 vertebrae	
Bjørnsholm	n	AFDY1	Cod	3 vertebrae	

δ^{13}C	δ^{15}N	C:N	δ^{13}C	Reservoir correction model		Corrected ^{14}C age	%C	%N	% col.
VPDB (‰)	AIR (‰)	atom	CPH	δ^{13}C	δ^{15}N	BP	average/range		
−22.6	7.9	3.2					35.4	12.9	6.0
−25.3	8.0	3.1					41.8	15.7	10.6
−22.8	7.6	3.2					37.5	13.6	5.7
−24.0	8.1	3.1					37.9	14.3	5.8
−24.0	7.8	3.2					37.6	13.9	6.6
−25.9	6.6	3.4					42.0	14.3	13.3
−22.6	9.1	3.3					41.7	15.0	11.8
−25.6	5.0	3.6					35.1	10.6	4.4
−25.0	5.5	3.4					41.2	14.0	4.1
−25.7	5.4	3.3					40.2	14.2	4.5
−25.4	5.5	3.3					38.0	13.3	5.9
−25.9	5.6	3.3					38.1	13.6	6.5
−26.2	5.8	3.6					35.7	11.6	5.7
−22.4	8.9	3.3	−20.4	−6%	12%	4873	36.3	12.7	8.2
−21.9	12.2	3.2		−	48%	5261	40.9	15.2	20.6
−20.7	9.5	3.3		9%	18%	4798	42.5−43.2	14.2−15.8	3.3−17.2
−19.9	9.3	3.1		16%	16%	3650	41.9	15.7	11.0
−20.9	8.3	3.3		7%	5%	8702	41.9	14.8	15.1
−22.7	8.3	3.2		−	6%	4658	39.3−42.9	14.1−16.0	11.5
−22.5	5.0	3.3	−21.6				42.9	15.3	14.3
−20.1	9.2	3.1		14%	15%	4758	40.5−42.3	14.8−15.7	15.8
−19.7	10.0	3.4		17%	24%	5289	42.5	14.7	3.1−9.5
−20.5	9.6	3.3	−20.3	10%	20%	4907	41.5	14.9	20.9
−20.1	9.2	3.2	−19.8	14%	15%	4509	43.6	15.8	15.0
−19.4	10.5	3.3	−20.7	20%	29%	4405	44.3	15.9	22.0
−22.6	4.5	3.2	−21.4				44.6	16.1	19.1
−22.5	4.6	3.2	−20.8				44.6	16.4	22.6
−22.8	5.4	3.2	−20.9				42.7	15.5	19.5
−22.1	4.8	3.2	−21.6				42.5	14.4	19.7
−23.0	5.0	3.2	−22.6				43.5	15.8	20.0
−22.6	4.2	3.2	−21.9				43.0	15.6	18.0
−22.0	4.3	3.1					39.2	14.6	16.2
−22.3	7.9	3.5					39.2	13.2	9.1
−22.4	8.8	3.5					42.2	14.3	8.0
−21.9	7.3	3.5				#	37.8−41.4	13.0−13.6	0.8−2.8
−25.7	5.6	3.4				#	35.1	12.2	0.7−3.6
−25.5	4.7	3.4				#	36.1	12.4	4.4
−15.2	16.9	3.3					40.7	14.5	16.8
−15.1	16.9	3.3					46.5	16.2	4.1−17.7
−15.2	14.8	3.4					38.4	13.4	7.3−13.9
−14.3	12.8	3.3	−14.3	64%	54%	6825	44.2	15.7	8.3
−14.5	13.4	3.4					42.9	14.9	6.2−13.4
−17.3	13.5	3.4					28.8	10.0	5.8−8.3
−16.3	12.7	3.2					44.2	16.0	8.0
−14.3	11.3	3.4					42.9	14.8	3.5
−20.1	6.6	3.2					38.9	14.5	12.7−13.5
−17.3	10.6	3.3					32.1−38.8	11.5−13.7	13.4
−15.5	15.5	3.3					34.2	12.3	1.3
−16.8	12.1	3.2					35.7−47.7	12.9−17.6	14.6
−23.5	3.9	3.3					35.5−44.4	12.9−15.7	12.1
−24.0	5.0	3.3					43.2	15.3	2.2
−22.8	4.6	3.2					43.7	15.8	2.4
−22.6	4.9	3.3					34.2−40.7	12.5−14.5	11.4
−23.6	4.6	3.5					42.9	14.4	0.9
−21.5	6.0	3.3					42.5	15.1	1.4
−13.3	11.8	3.5					42.8	14.2	5.0
−9.8	9.7	3.3					36.9	13.1	3.9
−9.5	10.1	3.2					39.1	14.4	2.5
−11.6	11.1	3.4					41.6	14.5	5.1
−8.9	9.1	3.3					35.6	12.5	4.1

(*continued on next page*)

Table 1 (*continued*)

Site name	Cultural epoch	Lab. no.	Species (and sex)	Anatomical part and ontogenetic age	^{14}C age
					BP
Bjørnsholm	n	AFDY2	Cod	2 vertebrae	
Bjørnsholm	n	AFDY3	Cod	Vertebra	
Bjørnsholm	N	K-5819/T1 (M70906)	Human (F)	Adult	4600 ± 75
Bjørnsholm	N	K-5820/T2(M70907)	Human (M)	Adult	4130 ± 65
Bjørnsholm	N	AAR-4028/BCH198: 20a+b	Human	Juvenile	4490 ± 55
Blak II	K	Ka-6454/ACQ59: 23+36	Human	Mandibula, adult	7440 ± 90
Bøgebjerg	e	AAR-8855	Pike	Vertebra, adult (∼1.1 m)	
Carstensminde	K	AAR-4092	Dog	Humerus, adult	7280 ± 45
Dyrholm	E	Poz-17034/ACQ59: 16+26	Human	Calvarium, juvenile	6680 ± 50
Ertebølle	E	AAR-8555/E. 2842	Human	Tibia dxt., >25 y	5790 ± 30
Kassemose	N	K-4592/M71190	Human M	Femur sin, adult	3980 ± 60
Korsør Glasværk	E	K-4185/BCH198: 44a+b	Human M	Os parietale sin., adult	6180 ± 95
Korsør Nor, inhumation	E	AAR-10246/BCH206: 13+20	Human	Tibia sin., 30–50 y	6263 ± 36
Krabbesholm	e/n	Poz-12127/BCH195: 12+26	Red deer	Metacarpus, adult	5147 ± 36
Køge Sønakke	M	K-5099/M70831	Human	Humerus dxt., adult	8250 ± 85
Melby	E	AAR-8551/AS 18/73	Human M	Femur sin., adult >35 y	6280 ± 35
Møllegabet	E	K-6040/BCH200: 19+39	Human	Os sacrum	6170 ± 85
Nivågård	e	AAR-8860-3/Niv-1,1	Cod	Vertebra	
Nivågård	e	AAR-8861-3/Niv-2	Flounder	Vertebra	
Norsminde	E	AAR-8556	Human	Femur sin., 30–40 y	5800 ± 35
Pandebjerg	N	Poz-17032/ACQ59: 10+39	Human	Mandibula	4770 ± 40
Rødhals	N	AAR-8552	Human M	Femur dxt., ∼25 y	5360 ± 50
Tybrind Vig Female	K	K-3558/BCH195: 20+36	Human F	Femur sin., young adult	6740 ± 80
Tybrind Vig Child	K	BCH198: 27a+b	Human	Pars petrosa, ∼0 y	
Tybrind Vig, individual 1	K	AAR-9341/AAR-9341	Human M	Mandibula, adult	6820 ± 55
Tybrind Vig, individual 2	K	AAR-9342/AAR-9342	Human F	Costa, young adult	6905 ± 55
Vængesø I	E	AAR-4499/BCH198: 33a+b	Human	Adult	5805 ± 45
Vængesø II	E/N	K-3920/BCH198: 45a+b	Human F	Femur etc., adult	5500 ± 70
Vængesø II	E/N	K-3921/BCH195: 13+14	Human M	Costa, vertebra etc., 20–30 y	5540 ± 65
VængesøIII	e	AFVS1	Cod	Vertebra	
VængesøIII	e	AFVS2	Cod	Parasphenoid	
VængesøIII	e	AFVS3	Cod	Praemaxilare sin.	
Vængesø III	e	ACQ59: 4+25	Cod	Vertebra	
Vængesø III	e	ACQ59: 4+23	Cod	Vertebra	
Discarded samples					
Argus	(k)	AND-11	Human	Femur sin., 2–3 y	
Argus	(k)	AAR-8605	Pike	Vertebra, adult (∼1 m)	
Argus	(k)	AAR-8606	Perch	Vertebra	
Argus	(k)	AAR-8608	Grey seal	Bulla, new born	
Bloksbjerg		AAR-9883	Human	Humerus sin.	
Bodal AL	E	AAR-4767	Dog	Radius, adult	5765 ± 45
Bredgården (Sweden)	M	Ua-6629/ACQ59: 18+33	Human M	Femur sin., 45–60 y	8645 ± 95
Dragsholm	e	S-EVA-132	Codfish	Vertebra	
Dragsholm	e	S-EVA-133	Flounder	Vertebra	
Dragsholm	e	S-EVA-134	Cod	Vertebra	
Holmegård I	m	1922 a	Pike	Vertebra	
Holmegård I	m	1922 b	Pike	Articulare	
Holmegård IV	m	IV-1944-52D	Pike	Quadratum	
Holmegård IV	m	IV-1944-54D	Pike	Dentale	
Holmegård V	m	AAR-6808/NÆM 962x1993: 38	Wolf	Mandibula sin.	
Flixton School	m?	FL9302UF	Dog	Adult	
Kildegård		AAR-7060	(White-beaked) dolphin	Atlas	
Klokkehøj	n	K-3013/BCH198: 82	Human	Femur sin., adult	4140 ± 90
Krabbesholm	e/n	BCH198: 81a+b	Eel	2 vertebrae	
Lundby	m	ACQ66a	Human	Skull cap	
Mullerup, Neergaards island	m	S-EVA-135	Pike	Vertebra	
Mullerup, Neergaards island	m	S-EVA-136	Pike	Vertebra	
Mullerup, Neegaards island	m	4/AQC59: 91+34	Pike	Vertebra	
Mullerup, Neegaards island	m	6/ACQ59: 92+42	Pike	Dentale	
Mullerup, Neegaards island	m	7/ACQ59: 9+32	Pike	Palatinum	
Mullerup, Neegaards island	m	8/ACQ66a:27+51	Pike	Dens	

δ^{13}C	δ^{15}N	C:N	δ^{13}C	Reservoir correction model		Corrected ^{14}C age	%C	%N	% col.
VPDB (‰)	AIR (‰)	atom	CPH	δ^{13}C	δ^{15}N	BP	average/range		
−9.1	8.2	3.4					41.3	14.5	5.5
−9.9	9.6	3.3					41.6	14.7	8.3
−19.7	9.5	3.2	−20.4	17%	18%	4526	34.6	12.5	4.0
−19.8	10.2	3.3	−19.6	17%	26%	4026	35.0	12.5	7.3
−20.9	7.4	3.2		7%	−5%	4462	37.2	13.7	9.7
−17.9	12.8	3.5	−18.5	33%	54%	7222	37.1	12.4	8.6
−23.1	12.5	3.3					29.2	10.3	1.3
−13.8	13.0	3.3		68%	56%	7009	38.6	13.2	9.1−10.2
−10.8	13.3	3.3		94%	59%	6305	39.2	13.9	12.9
−15.2	13.3	3.2		56%	60%	5550	42.4	15.5	4.5
−20.5	8.9	3.2	−19.7	10%	12%	3933	40.2	14.8	19.0
−11.3	14.2	3.2	−14.5	89%	70%	5822	32.0	11.7	
−15.9	12.3	3.3		50%	48%	6064	31.1	11.2	19.4
−22.3	3.1	3.2					40.7	14.8	7.4
−16.8	12.4	3.3	−14.7	42%	50%	8052	33.1	11.9	9.6
−10.7	13.3	3.2		95%	59%	5901	43.5	15.6	5.6
−12.6	15.7	3.4	−12.5	78%	86%	5828	40.8	14.1	11.3
−12.3	8.8	3.3					32.5	11.6	0.1
−13.1	6.5	3.3					40.3	14.4	0.7
−11.8	15.3	3.2		86%	82%	5457	32.4	11.9	9.5
−18.8	11.4	3.3		25%	39%	4613	44.6	15.9	13.7
−11.7	12.7	3.2		87%	54%	5014	42.2	15.3	10.7
−15.7	13.4	3.5	−15.7	52%	61%	6496	37.9	12.8	7.5
−14.7	16.4	3.3					36.6	12.9	7.2
−11.5	16.3	3.3		88%	92%	6452	41.0	14.60	5.0
−11.1	16.3	3.3		91%	92%	6537	39.8	14.30	13.2
−11.7	15.3	3.2		86%	82%	5460	32.4	11.7	5.3
−12.7	15.7	3.3	−11.2	78%	86%	5156	39.8	13.9	8.5
−12.6	16.1	3.3	−11.1	78%	90%	5181	42.6	14.9	14.3
−9.9	9.9	3.2					36.2	13.1	4.0
−11.5	10.4	3.3					38.2	13.5	3.1
−8.8	9.9	3.3					33.5	12.0	4.6
−9.1	9.5	3.2					37.2	13.4	3.4
−13.3	13.0	3.4					37.3	12.9	3.3
−15.7	16.4	3.8					38.2	11.9	4.1
−11.3	10.6	3.4					24.6	8.4	7.3
−21.3	15.3	0.5					6.4	15.4	
−17.2	14.8	3.7							0.7
−13.8	10.1	3.2					25.9	9.4	12.7
−18.8	11.0	3.2					18.6	6.9	
−15.5	9.7	5.5					34.2	7.3	0.2
−10.9	6.0	3.7					37.5	12.0	0.4
−15.0	9.9	5.5					35.8	7.6	0.3
−16.6	7.0	3.9					42.5	12.8	0.5
−18.3	6.5	4.4					42.0	11.3	0.4
−19.7	6.0	4.7					40.4	10.0	0.3
−23.3	5.0	3.7							
−22.7	9.0	3.8	−19.9				35.6	11.0	5.5
−11.0	9.0	3.1					40.3	9.0	7.8
−18.5	8.6	7.0					22.6	3.8	0.3
−23.6	10.4	4.6					41.5	10.6	0.3
−23.2	10.9	3.8					41.2	12.6	2.1
−9.5	8.7	3.6					41.3	13.3	3.1
−13.0	9.3	4.2					39.1	10.8	1.4
−8.4	9.3	3.8					38.2	12.0	1.5

(*continued on next page*)

Table 1 (*continued*)

Site name	Cultural epoch	Lab. no.	Species (and sex)	Anatomical part and ontogenetic age	^{14}C age BP
Mullerup, Neegaards island	m	10/ACQ66a:28+52	Pike	Vertebra	
Mullerup, Neegaards island	m	11/ACQ66a:26+53	Pike	Vertebra	
Nivågård	e	AAR-8860-1	Cod	Vertebra	
Nivågård	e	AAR-8860-2	Cod	Dentale	
Nivågård	e	AAR-8861-1	Flounder	Vertebra	
Nivågård	e	AAR-8861-2	Flounder	Vertebra	
Ravnstrup	(m)	AS 14744	Human	Cranium, adult	
Ringkloster	e/n	K-4132/Hg24968	Dog		5230 ± 70
Tagmosegård	N	K-6297/BCH199: 14	Human	7–8 y	4920 ± 95
Tingbjerggård Z		AAR-4768	Dog	Femur, adult	
Tybrind Vig female	E	K-3558/BCH198: 39	Human	Young adult	6740 ± 80
Ulkestrup Lyng Z		AAR-7198/ZMK 12/1990	Dog or fox	Mandibula, adult/senilis	5100 ± 55
Undløse Bro	e/n	AAR-4773/ZMK 128/1986	Dog	Maxilla, adult	5386 ± 42
Øgårde		AND 1	Dog	Vertebra cervicalis	
Øgårde		AND 2	Dog	Pars petrosa	
Øgårde		AAR-7059/IC10, 2	Grey seal	Femur	
Øgårde		AND 4	Human	Ulna sin.	
Øgårde		AND 7	Dog	Vertebra lumbalis	
Øgårde		AND 8	Dog	Os zygomaticus dxt.	
Øgaarde		BCH198: 14	Human	Ulna	
Åkonge	n	AAR-4576/KML 49,5/75,0: 15	Tench	2 operculae	
Åkonge	n	AAR-4578/KML 49,5/75,0: 7	Tench	Opercylum	
Åkonge	n	AAR-4579/KML 49,5/75,0: 2	Pike	Vertebra + maxilare	

Cultural epochs: M, Maglemose; K, Kongemose; E, Ertebølle; N, Neolithic; E/N, could date to either the late Ertebølle or the earliest Neolithic. Letters in upper case imply that the affiliation to cultural epoch is based on a ^{14}C date of the sample. Letters in lower case refer to affiliations obtained through the archaeological context of the samples only. The use of the sign "−" in the columns for marine and aquatic reservoir correction implies that the stable isotope measurements fall outside the range of the reservoir correction model, and that the reservoir effects in these samples may not be fully accounted for in the corrected ^{14}C age given in the table. Samples for which no stable isotope data are presented had no collagen preserved. For some of the measurements produced in an early stage of the project no information on %C and %N is available. Samples characterised by one or more of the following criteria are listed as discarded because of unsatisfactory quality: C:N value outside the range 2.9 to 3.6, carbon content <25%, nitrogen content <10%, collagen yield <1% (in case of ultrafiltered samples, 0.1%).

3.2. Comparisons between laboratories

Table 1 summarises the results of all our measurements on bone collagen from humans, dogs, and food source animals of Mesolithic and Neolithic date. In several cases the stable isotope ratios were measured in all three laboratories: Bradford, Aarhus and Reykjavik. An inter-laboratory comparison of the δ^{13}C and δ^{15}N results shows satisfactory agreement. The average and standard deviation of the δ^{13}C difference between Bradford and Aarhus was 0.2 ± 0.4‰ ($n = 31$), the average difference between Bradford and Reykjavik was -0.2 ± 0.4‰ ($n = 29$) and between Aarhus and Reykjavik it was -0.3 ± 0.5‰ ($n = 34$). For δ^{15}N, the average difference between Bradford and Aarhus was found to be -0.2 ± 0.4‰ ($n = 31$). Thus, the inter-laboratory deviations are within experimental errors. In the following, we therefore use mean values of measurements from the individual laboratories. Table 1 presents these averages.

3.3. Comparisons with previously published analyses

Forty-eight of the human bones/individuals with acceptable C:N values in our assemblage have previously been radiocarbon dated (47 of these by decay counting) and have had their δ^{13}C values measured by the former ^{14}C laboratory in Copenhagen. In 32 of these cases there was sufficient material remaining for new measurements on the very same bone as had previously been sampled by the Copenhagen laboratory. In the remaining 16 cases we undertook analyses on other bones from the same individual.

The data from the two laboratories are presented and compared in Table 2. As can be seen, ^{14}C dates agree generally, apart from two outliers. The weighted mean value and standard error is 15 ± 43 ^{14}C years (the two outliers removed). The observed scatter in the differences is no more than expected statistically (χ^2: $2.2 < 9.5$). As indicated by the low K-number, the outlier Melby (K-1776/AAR-8551) was produced during an early stage in the development of radiocarbon dating of bone at the Copenhagen laboratory, where raw bone was used for dating instead of extracted collagen (personal communication from K.L. Rasmussen, former head of the laboratory). The date, which has not been fractionation corrected as no δ^{13}C value was available at the time, is therefore not suitable for comparison. The Copenhagen laboratory's δ^{13}C value of this sample is, on the other hand, better suited for comparison as it was produced later and was made on extracted collagen. All the other Copenhagen dates were on collagen and with δ^{13}C measurement and isotopic fractionation correction as standard procedure. We do not have an explanation for why the Ertebølle (K-4933/AAR-8555) result is a clear outlier, but the very large age difference makes it meaningless to include it in the weighted mean and scatter statistics.

The mean value of the difference between our δ^{13}C values and those from the Copenhagen laboratory is 0.0‰ with an

$\delta^{13}C$ VPDB (‰)	$\delta^{15}N$ AIR (‰)	C:N atom	$\delta^{13}C$ CPH	Reservoir correction model $\delta^{13}C$	$\delta^{15}N$	Corrected ^{14}C age BP	%C average/range	%N	% col.
−20.7	11.9	3.5					10.6	2.2	1.9
−14.8	9.7	4.8					16.9	4.1	1.7
−13.8	10.1	3.2					21.2	7.6	3.6
−11.1	10.2	3.1					18.7	7.1	3.5
−14.7	11.7	3.2					15.8	5.8	2.0
−11.3	7.7	3.2					16.9	6.1	2.6
−18.0	13.5	3.7					42.3	13.3	5.1
−19.8	9.9	3.7	−20.4				33.6	10.7	8.2
−23.2	10.1	5.7	−15.7				10.5	2.2	1.9
−20.4									
−19.7	10.3	3.7					40.4	12.8	4.6
−25.2	4.9	3.7					39.5	12.9	0.6−7.2
−26.1	5.8	4.0					43.5	12.9	1.2
−21.8	8.1	3.7					30.5−41.9	9.7−13.4	0.7−2.9

observed standard deviation of 1.6‰. This standard deviation on the $\delta^{13}C$ differences is very large compared to measurement uncertainties. Considering the excellent agreement between the isotopic values between the three laboratories involved in the present work, we assume that this large deviation stems from the Copenhagen data. The fact that the most significantly deviating Copenhagen measurements were produced in the early days of collagen preparation may be taken in support of this assumption.

In the following we include dates from the Copenhagen ^{14}C dating laboratory and consider them to be equally valid as the more recent AMS dates. In addition we include $\delta^{13}C$ values of food source animals in Fig. 3 (lower part) and of humans and dogs in Fig. 5A–D (lower parts) and 6 (upper part) with the reservations stated above and with the additional note that most of them have not been through the C:N quality check. They are only included due to problems in getting access to new samples from the bones/individuals in question.

4. Results

4.1. Modern fish and mollusc

Table 3 shows the $\delta^{13}C$ and $\delta^{15}N$ values for bone collagen and flesh of a variety of present-day fish, and for the flesh of molluscs, lugworms and crabs. These animals were collected in Kalundborg Fjord and in Lake Tissø and Lake Aunsø, Eastern Denmark (Fig. 1). As can be seen from the table, there is in most cases a systematic offset between flesh and bone values. The average and standard deviation of bone-flesh differences among the freshwater fish from Tissø is 2.6 ± 0.6‰ for $\delta^{13}C$ and -1.2 ± 0.7‰ for $\delta^{15}N$, excluding the two aberrant tench samples T4 and T6 (which may represent individuals that had changed habitat shortly before they were caught—as the turn-over rate of flesh is significantly shorter than in bone). For the Kalundborg Fjord fish the average and standard deviation of bone-flesh differences is 2.1 ± 0.6‰ for $\delta^{13}C$ and -0.6 ± 0.4‰ for $\delta^{15}N$. Both sets of data confirm that the bone value can serve as a proxy for the flesh value. The data are presented graphically in Fig. 2, which illustrates that $\delta^{15}N$—and to some degree $\delta^{13}C$—increases with trophic level. Thus, predators are found at the upper (right) ends, while low-trophic species (not least bivalves) are at the lower (left) ends of the plots.

Owing to differences in the environment, it cannot be taken for granted that the isotope values of the modern samples are directly comparable to those from prehistoric fish bones. Present-day influx of commercial nitrogen-rich fertilisers may, for instance, have caused a systematic increase of the $\delta^{15}N$ values of the modern samples relative to prehistoric ones from the same lake. This appears clearly exemplified by the $\delta^{15}N$ values of 6.6–12.5‰ in our archaeological samples of pike as opposed to 20.8–22.6‰ in our modern pike samples (compare Fig. 3 upper diagram and Fig. 2A, respectively). What matters in relation to this study is that the relative position of the individual species should be relatively constant over time—implying that Stone Age protein diet rich in low trophic marine and/or freshwater food (not least molluscs) will be reflected in relatively low $\delta^{13}C$ and $\delta^{15}N$ bone collagen values.

Table 2
Comparison between analyses produced by the former radiocarbon laboratory in Copenhagen and those produced through subsequent measurements of the same bones/individuals

Site name	Copenhagen Laboratory			Sample identity	This and previous studies			Comparison			References
	Lab. No.	^{14}C age BP	δ^{13}C VPDB (‰)		Lab. No.	^{14}C age BP	δ^{13}C VPDB (‰)	Difference in ^{14}C age	^{14}C age deviation in σ	Difference in δ^{13}C	
Argus Bank	K-4354	7080 ± 75	−14.3	1	K-4354		−14.3			0.0	Tauber, 1981b; Fischer et al., in press
Bjørnsholm	K-5819	4600 ± 75	−20.4	1	T1 (M70906)		−19.7				Rasmussen and Rahbek, 1993: 377
Bjørnsholm	K-5820	4130 ± 65	−19.6	1	T2 (M70907)		−19.8				Rasmussen and Rahbek, 1993: 277
Blak II	Ka-6454	7440 ± 90	−18.5	1	ACQ59: 23+36		−17.9				Rahbek and Rasmussen, 1996: 311
Boelkilde	K-4593	4670 ± 65	−20.8	1	T4		−19.7				Tauber, 1987: 186
Bøgebakken, grave 3	K-2781	6050 ± 75	−15.3	2			−13.6			−1.7	Tauber, 1981b; Richards et al., 2003; T.D. Price, pers. commun.
Bøgebakken, grave 5	K-2782	6290 ± 75	−13.4	2			−16.5			3.1	Tauber, 1981b; Richards et al., 2003; T.D. Price, pers. commun.
Ertebølle	K-4933	5340 ± 70	−16.5	1	AAR-8555	5790 ± 30	−15.2	*−450 ± 76*		−1.3	Tauber, 1988
Ferle Enge	K-6299	4940 ± 95	−20.6	1	BCH199: 16+44		−22.6				Rahbek, 1995: 279
Føllenslev	K-3747	3530 ± 120	−20.7	1+2	BCH198: 46a+b		−20.7				Bennike and Ebbesen, 1987; pers. commun. Copenhagen ^{14}C Lab.
Holmegård V, B	K-4153	8340 ± 90	−19.7	1	AAR-8560	8315 ± 45	−20.0	25 ± 101	0.4	0.3	H. Tauber, personal communication
Hulbjerg	K-6042	3680 ± 65	−20.1	1	T5		−20.8				Rahbek and Rasmussen, 1996: 303
Jorløse Mose	K-6302	4430 ± 90	−20.3	1	BCH 199: 17+45		−20.5				Rahbek, 1995: 280
Kassemose	K-4592	3980 ± 60	−19.7	1	M71190		−20.5				Tauber, 1987: 188
Klokkehøj	K-2954	4550 ± 65	−18.1	1	SHg1143		−19.7				Tauber, 1981b:123; Thorsen, 1981: 120
Klokkehøj	K-3012	4250 ± 90	−19.2	1	BCH198: 24a+b		−20.2				Tauber, 1981b:123; Thorsen, 1981: 130
Klokkehøj	K-3014	4200 ± 90	−18.9	1	SHg1150		−20.1				Tauber, 1981b:123–4; Thorsen, 1981: 130
Koelbjerg	K-4063	9250 ± 85	−20.7	2	AAR-8613	9285 ± 50	−22.2	−35 ± 99	−0.2	1.5	Tauber, 1986b
Korsør Glasværk	K-4185	6180 ± 95	−14.5	1	BCH198: 44a+b		−11.3				Fischer and Pedersen, 1997: 320
Køge Sønakke	K-5099	8250 ± 85	−14.7	1	M70831		−16.8				Tauber, 1989: 213
Melby	K-1776	6006 ± 110	−14.0	2	AAR-8551	6280 ± 35	−10.8	*−274 ± 115*		−3.2	Tauber, 1981b
Mullerup	K-4151	8410 ± 90	−16.5	1	AAR-8554	8310 ± 55	−18.5	100 ± 105	1.1	2.0	H. Tauber, personal communication
Møllegabet	K-6040	6170 ± 85	−12.5	1	BCH200: 19+39		−12.6				Rahbek and Rasmussen, 1994: 280
Nissehøj	K-6101	3620 ± 90	−20.0	1	T3 (M70957)		−20.3				Rahbek, 1995: 281
Norsminde	K-5199	5790 ± 95	−12.1	1	AAR-8556	5800 ± 35	−11.8	−10 ± 101	0.1	−0.3	Tauber, 1990
Porsmose	K-3748	4710 ± 90	−19.4	1	Hg24297		−20.4				Bennike and Ebbesen, 1987, pers. commun. Copenhagen ^{14}C Lab.
Præstelyng	K-3773	5260 ± 65	−21.6	1	AFP1		−21.3				Noe-Nygaard, 1988
Ringkloster	K-4133	5420 ± 210	−18.8	1	M57431		−16.6				Rasmussen, 1998
Rødhals	K-3622	5280 ± 50	−12.2	2	AAR-8552	5360 ± 50	−11.8	−80 ± 71	−0.9	−0.4	H. Tauber, personal communication
Sigersdal A	K-3744	4650 ± 140	−19.9	1	BCH198: 5a+b		−20.4				Bennike and Ebbesen, 1987, pers. commun. Copenhagen ^{14}C Lab
Sigersdal B	K-3745	4680 ± 75	−19.3	1	BCH198: 57+23		−19.2				Bennike and Ebbesen, 1987, pers. commun. Copenhagen ^{14}C Lab.
Tagmosegård	K-6297	4920 ± 95	−20.4	1	BCH199: 49		−22.4				Rahbek, 1995: 279
Tybrind Vig Female	K-3558	6740 ± 80	−15.7	2	BCH195: 20+36		−15.7				Andersen, 1984
Ulkestrup Lyng M	K-4979	4630 ± 85	−21.6	2	BCH200: 20+40		−22.5				Tauber, 1988: 236
Veksø Mose	K-6303	5140 ± 100	−20.3	2	Poz-17006+17030	4985 ± 27	−20.5				Rahbek, 1995: 278

Vængegård	K-6300	4760 ± 95	−20.2	2	DK-4		−20.3		0.1	Rahbek, 1995: 280; Richards and Koch, 2001; E. Koch, pers. commun.
Vængesø II	K-3920	5500 ± 70	−11.2	2	BCH198: 45a+b		−12.7			Andersen et al., 1986
Vængesø II	K-3921	5540 ± 65	−11.1	2	BCH195: 13+14		−12.6			Andersen et al., 1986
Øgårde boat III	K-3746	4570 ± 60	−19.8	2	ACQ59: 8+38		−20.1			Koch, 1998: 312; pers. commun. Copenhagen ^{14}C Lab.
Østrup homo II	K-5741	4530 ± 90	−20.7	2	AAR-10248	4523 ± 37	−19.4			Richards and Koch, 2001
Østrup Mose	K-5741	4530 ± 90	−20.7	2	DK-3		−20.0		−0.7	Rasmussen, 1992; Richards and Koch, 2001; E. Koch, pers. commun.
Østrup Mose	K-5742	4510 ± 90	−19.5	2	DK-2		−19.6		0.1	Rasmussen, 1992; Richards and Koch, 2001; E. Koch, pers. commun.
Åkonge	K-4883	5010 ± 65	−21.4	1	BCH198: 26a+b		−22.6			Fischer and Heinemeier, 2003
Åkonge	K-4881	5060 ± 65	−20.8	1	BCH198: 37a+b		−22.5			Fischer and Heinemeier, 2003
Åkonge	K-4882	5070 ± 65	−20.9	1	BCH198: 17a+b		−22.8			Fischer and Heinemeier, 2003
Åkonge	K-4884	4990 ± 65	−21.6	1	BCH198: 19a+b		−22.1			Fischer and Heinemeier, 2003
Åkonge	K-4885	4950 ± 60	−22.6	1	BCH198: 43a+b		−23.0			Fischer and Heinemeier, 2003
Åkonge	K-4886	4990 ± 65	−21.9	1	BCH198: 10a+b		−22.6			Fischer and Heinemeier, 2003
								−15 ± 43	−0.0 ± 1.6	

Sample identity categories: category 1, samples taken from the same bone; category 2, samples taken from different bones that belong to the same individual. Two outliers, written in italics, are excluded from the statistical comparison of ^{14}C age deviations, the result of which is given on the bottom line. The correction for isotope fractionation of the Melby sample was done by us. In the original publication its ^{14}C date was presented without correction for isotope fractionation as 5830 ± 110 BP (K-1776).

4.2. Mesolithic and Neolithic food source animals

Thanks to the existence of very large and well-organised collections of bones from the Danish Stone Age, it has been possible to get access to a sizable and chronologically diverse assemblage of bones from mammal and fish species that served as food sources for humans (and dogs) during the Mesolithic and Neolithic (Table 1). Variation in climate, forest cover, lake water chemistry, etc. may cause variation in isotopic values among individuals of one and the same animal species (Heaton, 1999; cf. Fizet et al., 1995; Noe-Nygaard, 1995; Dufour et al., 1999; Fig. 3, this study). For the purpose of minimizing this source of error, the food reference samples were collected as close as possible, geographically and chronologically, to our Stone Age samples of bones from humans and dogs. The pairs of δ^{13}C and δ^{15}N values resulting from measuring the collagen in these animal bones are shown in Fig. 3.

We have drawn boxes in Fig. 3 (from minimum to maximum values of δ^{13}C and δ^{15}N) in an attempt to distinguish five dietary protein sources: terrestrial herbivores (roe deer, red deer, goat, and domestic cattle, all in one box), two freshwater species (pike and tench, in two separate boxes) and two marine food sources (fish and seal, each in a separate box). Measurements of freshwater species of Early Mesolithic date are excluded from the boxes for reasons described below.

Since some of our boxes in Fig. 3 are based on relatively few measurements we have supplemented our inland data assemblage with δ^{13}C values from the literature. Most of these samples, dating from the Mesolithic and Neolithic, come from Åmose—the Stone Age bog in which many of our inland samples of humans and dogs have been found.

Our Stone Age terrestrial herbivore samples span the δ^{13}C range −21.1‰ to −24.3‰, and the δ^{15}N range of 2.5‰ to 6.0‰. This agrees well with previously published δ^{13}C ranges for this dietary resource (Fig. 3, lower diagram; cf. Lidén et al., 2004).

For the freshwater food source animals dating to the Middle Mesolithic onwards we found the δ^{13}C range −21.9‰ to −25.9‰. A previous study (Noe-Nygaard, 1995; cf. Fischer and Heinemeier, 2003) found a similar, but even wider range: −21.9‰ to −27.4‰ for pike (excluding the Early Mesolithic site Ulkestrup Lyng). A wide range is to be expected. First of all, δ^{13}C values for freshwater sources may show large variation relating to differences in lake size (Post, 2002) and contributions of inorganic and biologically derived carbon of various origins (cf. Dufour et al., 1999). Secondly, a source critical factor may be at play, since most of the data from the previous study were not subjected to the quality tests we apply on our own data (including C:N value and % nitrogen). Our re-measurements of bones from red deer, domestic cattle, pike and tench from the Åkonge site, (c.f. Table 1 versus Fischer, 2002; Fischer and Heinemeier, 2003) has demonstrated the actual existence of this factor—especially in the fish bones.

Our δ^{15}N values for pike span a wide interval of 6.6‰ to 12.5‰. The lower boundary is close to the upper boundary

Table 3

$\delta^{13}C$ and $\delta^{15}N$ values for flesh and bone collagen of present-day fish and mollusc from two lakes and a fjord in Eastern Denmark

Species	Lab. No.	Flesh collagen			Bone collagen			Difference bone−flesh	
		$\delta^{13}C$ VPDB (‰)	$\delta^{15}N$ AIR (‰)	C:N atom	$\delta^{13}C$ VPDB (‰)	$\delta^{15}N$ AIR (‰)	C:N atom	$\delta^{13}C$ VPDB (‰)	$\delta^{15}N$ AIR (‰)
Aunsø									
Bivalve (*Dreissena polymorpha*); 4 cm	Aunsø 1	−35.1	14.6	4.6					
Bream (*Abramis brama*); 6 cm, 2 g	Aunsø 8	−34.2	20.3	3.7					
Pike (*Esox lucius*); 79 cm, 3570 g	Aunsø 2	−31.3	22.6	3.7					
Pike (*Esox lucius*); 55 cm, 1290 g	Aunsø 3	−31.1	21.8	3.7					
Roach (*Rutilus rutilus*); 19 cm, 100 g	Aunsø 10	−33.9	21.0	3.8					
Roach (*Rutilus rutilus*); 5 cm, 1 g	Aunsø 9	−34.0	21.2	3.7					
Tissø									
Bream (*Abramis brama*)	AAR-8370	−28.7	19.8	3.7	−26.3	18.5	3.1	2.5	−1.2
Eel (*Anguilla anguilla*); silver, ca. 70 cm	AAR-8835	−27.4	17.3	3.7	−24.2	15.9	3.2	3.2	−1.4
Eel (*Anguilla anguilla*); silver. 58 cm	AFT1	−26.9	19.9	4.7	−22.9	18.8	3.2	4.1	−1.0
Eel (*Anguilla anguilla*); silver. 70 cm, 750 g	AFT7	−25.8	20.2	3.7	−24.0	19.7	3.3	1.8	−0.5
Eel (*Anguilla anguilla*); yellow. ca. 30 cm	AAR-8836	−26.6	18.6	3.7	−24.6	17.5	3.2	1.9	−1.1
Flounder (*Platichthys flesus*); ca. 20 cm	AAR-8834	−25.9	19.6	3.7	−23.4	18.5	3.1	2.5	−1.1
Freshwater bivalve (*Unionidae*); 8 cm, 18 g	AFT13	−27.2	14.8	4.9					
Freshwater bivalve (*Unionidae*); 8 cm, 25 g	AFT12	−27.4	14.2	4.3					
Freshwater bivalve (*Unionidae*); 8 cm, 26 g	AFT11	−27.1	15.0	4.5					
Freshwater bivalve (*Unionidae*); 8 cm, 26 g	AFT10	−27.5	14.2	3.9					
Freshwater bivalve (*Unionidae*); 8 cm, 27 g	AFT9	−27.4	14.7	4.2					
Freshwater bivalve (*Unionidae*); 10cm	AAR-8375	−30.7	14.0	4.2					
Perch (Percafluviatilis); ca. 25 cm	AAR-8373	−27.8	21.1	3.6	−25.2	19.8	3.0	2.7	−1.3
Pike (*Esox lucius*); ca. 60 cm	AAR-8369	−26.5	20.8	3.8	−23.7	21.0	3.1	2.8	0.3
Pike(*Esox lucius*); ca. 60 cm	AFT8	−26.0	21.6	3.7	−23.7	19.9	3.3	2.3	−1.8
Roach (*Rutilus rutilus*)	AAR-8372	−28.1	17.7	3.8	−24.9	16.0	3.1	3.2	−1.7
Tench (*Tinca tinca*); 19 cm	AFT3	−33.9	15.4	3.7	−31.6	14.2	3.2	2.3	−1.2
Tench (*Tinca tinca*); 40 cm	AFT4	−29.0	17.3	3.7	−29.4	14.9	3.2	−0.4	−2.4
Tench (*Tinca tinca*); 45 cm, 1820 g	AFT6	−27.0	18.5	3.7	−29.5	16.6	3.3	−2.5	−1.9
Zander/pike-perch (*Stizostedion lucioperca*)	AAR-8833	−27.3	22.1	3.7	−24.6	19.6	3.1	2.7	−2.5
Zander/pike-perch (*Stizostedion lucioperca*)	AAR-8371	−25.9	21.1	3.7	−23.9	20.5	3.0	2.0	−0.5
								2.1 ± 1.6	−1.3 ± 0.7
Kalundborg Fjord									
Whiting (*Merlangius merlangus*); 26 cm, 135 g	KLB77	−17.9	13.9	3.6	−15.4	13.3	3.1	2.5	−0.6
Cod (*Gadus morhua*); 38 cm, 500 g	KLB56	−18.2	13.9	3.6	−15.5	13.2	3.1	2.7	−0.7
Bull-trout (*Myoxocephalus scorpius*); 13 cm, 50 g	KLB71	−17.3	13.5	3.7	−15.0	12.8	3.3	2.4	−0.7
Dab (*Limanda limanda*); 28 cm, 240 g	KLB73	−17.7	13.5	3.6	−15.6	13.5	3.4	2.2	0.0
Cod (*Gadus morhua*); 49 cm, 1100 g	KLB76	−17.2	13.4	3.7	−14.6	12.9	3.2	2.7	−0.5
Norway bullhead (*Micrenophrys liljeborgi*); 11 cm, 25 g	KLB70	−16.8	13.2	3.7	−15.1	12.3	3.2	1.8	−0.9
Dab (*Limanda limanda*); 25 cm, 165 g	KLB74	−18.2	12.8	3.6	−16.5	12.2	3.3	1.6	−0.6
Eel (*Anguilla anguilla*); 37 cm, 95 g	KLB62	−17.5	12.7	3.7	−14.5	12.0	3.2	3.0	−0.6
Eelpout (*Zoarces viviparus*); 25 cm, 60 g	KLB57	−17.4	12.3	3.7	−15.5	11.9	3.2	1.9	−0.4
Eelpout (*Zoarces viviparus*); 25 cm, 75 g	KLB58	−17.4	12.2	3.7	−15.3	12.1	3.2	2.1	−0.2
Eel (*Anguilla anguilla*); 46 cm, 210 g	KLB63	−17.4	12.1	3.8	−16.5	11.7	3.9	1.0	−0.4
Shore crab (*Carcinus maenas*); 35 g	KLB81	−18.1	12.0	3.7					
Flounder (*Platichthys flesus*); 28 cm, 340 g	KLB72	−18.4	11.5	3.7	−17.7	10.7	4.1	0.7	−0.8
Shore crab (*Carcinus maenas*); 35 g	KLB80	−18.8	11.4	3.7					

Goldsinny (*Ctenolabrus rupestris*); 9 cm, 15 g	KLB64	−17.8	11.4	3.7	−15.8	10.4	3.2	1.9	−1.0
Cuckoo wrasse (*Labrus bimaculatus*); 16 cm, 90 g	KLB68	−17.1	11.1	3.7	−14.7	9.5	3.1	2.5	−1.6
Lugworm (*Arenicola marina*); 2 g	KLB54	−16.1	9.6	4.1					
Periwinkle (*Littorina littorea*); 2 cm, 1 g	KLB43	−15.4	9.1	4.6					
Common mussel (*Mytilus edulis*); 5 cm, 3 g	KLB52	−19.2	8.7	3.9					
Common mussel (*Mytilus edulis*); 6 cm, 3 g	KLB53	−18.9	8.7	3.8					
Common mussel (*Mytilus edulis*); 8 cm, 6 g	KLB34	−20.1	8.7	3.8					
Periwinkle (*Littorina littorea*); 3 cm, 1 g	KLB42	−16.8	8.7	4.5					
Common mussel (*Mytilus edulis*); 7 cm, 5 g	AFK2	−19.2	8.6	3.9					
Common mussel (*Mytilus edulis*); 7 cm, 5 g	AFK1	−19.6	8.5	4.4					
Cockle (*Cerastoderma edulis*); 4 cm, 0.8 g	AFG1	−20.0	8.4	4.2					
Lugworm (*Arenicola marina*); 2 g	KLB55	−16.4	8.3	4.6					
Periwinkle (*Littorina littorea*); 2 cm, 1 g	KLB37	−16.3	8.2	4.8					
Common mussel (*Mytilus edulis*); 5 cm, 5 g	KLB46	−21.2	8.2	4.5					
Common mussel (*Mytilus edulis*); 6 cm, 7 g	KLB48	−20.0	8.1	3.9					
Periwinkle (*Littorina littorea*); 2 cm, 0.5 g	KLB44	−16.7	8.0	4.5					
Cockle (*Cerastoderma edulis*); 2 cm, 0.7 g	KLB41	−20.8	7.9	4.2					
Common mussel (*Mytilus edulis*); 8 cm, 4 g	AFK3	−19.7	7.9	4.2					
Common mussel (*Mytilus edulis*); 5 cm, 3 g	KLB47	−20.8	7.6	3.8					
Cockle (*Cerastoderma edulis*); 3 cm, 2 g	KLB39	−21.7	7.4	4.5					
Periwinkle (*Littorina littorea*); 2 cm, 1 g	KLB36	−16.6	7.3	4.5					
Cockle (*Cerastoderma edulis*); 2 cm, 0.6 g	AFG3	−21.4	7.1	5.6					
Cockle (*Cerastoderma edulis*); 2 cm, 0.6 g	AFG2	−21.2	6.8	5.0					
								2.1 ± 0.6	−0.6 ± 0.4

Mollusc weights are exclusive of shells.

of the herbivore samples. The δ^{15}N values for tench, ranging from 4.7‰ to 5.8‰, fall within the range of the terrestrial herbivores.

The δ^{13}C values of the fish from Stone Age sites originally located at the shores of more or less brackish fjords span from −8.8‰ to −13.3‰. Their δ^{15}N values show a large spread from 6.5‰ to 13.0‰. The box drawn around our marine samples would likely have been even wider in all four directions if we had measured a larger collection of fish bones representing a larger variety of species and coastal site locations.

The δ^{13}C values of our samples of seal fall in the range −15.5‰ to −16.8‰, and their δ^{15}N values lie between 12.1‰ and 15.5‰. These values are comparable to published data (e.g. Eriksson and Lidén, 2003; Lidén et al., 2004; Craig et al., 2006), but quite different from those of most other marine species from the Danish area. As seal bones are rare in most faunal assemblages from the Danish Mesolithic (e.g. Møhl, 1971), we have chosen to simplify the model for reservoir corrections given below by disregarding the contribution made by these species.

4.3. ‘‘Marine’’ signatures in Early Mesolithic freshwater fish

Our samples from Early Mesolithic (Maglemosian) freshwater food source animals derive from three settlement sites in the bogs of Holmegård and Mullerup, eastern Denmark (Fig. 1). The isotopic results are remarkable. Four out of five pike bones and both of our otter bones have δ^{13}C values that would usually be classified as clearly ‘‘marine’’. We assume that these elevated δ^{13}C values stem from fossil $CaCO_3$ of marine origin, which has been dissolved from carbonate mineral particles in the glacial moraines surrounding these lake-side sites (cf. Day, 1996).

In our assemblage of pike bones from freshwater deposits the most elevated δ^{13}C values are from Neegaard's Island in Mullerup Bog, which on the basis of its lithic material is dated to an early stage of the Maglemose Culture (Petersen, 1973). According to an earlier study (Noe-Nygaard, 1995) the δ^{13}C values of the pike bones from the Ulkestrup Lyng sites have significantly more negative values than those from Neegaard's Island. The Ulkestrup Lyng sites are dated typologically to the middle of the Maglemose Cultural period (Petersen, 1973). In our assemblage the most negative δ^{13}C value seen in a pike bone from a Maglemose Culture inland site (−22.8‰) is derived from Holmegård IV, which represents the middle and late stages of the Maglemosian epoch (Petersen, 1973). Furthermore, the δ^{13}C values observed for Åmose freshwater fish bones from the Middle and Late Mesolithic and from the Neolithic are all much lower than those seen in our samples of marine fish (Fig. 3, upper and lower part). In the following discussion we therefore assume that ‘‘marine’’ isotopic signatures in freshwater fish from Denmark do not occur after the Early Mesolithic.

Fishing equipment and fish bones in the Early Mesolithic (Maglemose Culture) settlement deposits of the Danish interior indicate that fishing in the local lakes was an important part of the subsistence strategy of the humans who inhabited these sites (cf. e.g. Becker, 1945; Andersen K. et al., 1982). Consequently, the elevated δ^{13}C and δ^{15}N values of the dogs and humans of the Mullerup and Holmegård sites may result—partly or totally—from the consumption of local freshwater food.

The new data emphasizes the importance of using reference samples from as close as possible, geographically and chronologically, to the individuals in question. As long as we do not know what chemical and biological processes gave rise to the "marine" signals in the Mullerup and Holmegård fish, and since lake chemistry notoriously differs from lake to lake we cannot say if the phenomenon is restricted to (some) humans and dogs from the Holmegård and Mullerup sites or if it also applies to other of the Early Mesolithic inland individuals from North-Western Europe (Star Carr, Seamer Carr, Sværdborg I, Agerød V and Hanaske) from where elevated δ^{13}C values have also been reported (Noe-Nygaard, 1988; Clutton-Brock and Noe-Nygaard, 1990; Schulting and Richards, 2002; Fischer, 2003; Lidén et al., 2004; see also Bredgården, Table 1 in the present paper). In the following discussions, we therefore do not make any specific inferences about the possible existence or non-existence of Early Mesolithic coast-inland mobility.

4.4. Mesolithic and Neolithic humans and dogs

Some of the human bones in this study belong to genuine burials (Aldersro, Bjørnsholm, Ertebølle, Hulbjerg, Kassemose, Klokkehøj, Korsør Nor, Melby, Nissehøj, Rødhals, Tybrind Vig, Vængesø, and probably Argus Bank). Others belong to mostly complete skeletons that ended up in freshwater sediments, possibly as result of drowning accidents, violence or sacrificial activities (Boelkilde, Ferle Enge, Føllenslev, Hallebygård, Jorløse, Koelbjerg, Porsmose, Sigersdal, Tagmosegård, Trudstrupgård, Veksø, Øgårde boat III, Tømmerupgård and Østrup). The bones of the three humans from Holmegård V were found closely together in a contemporaneous culture layer and are interpreted as the outcome of a ceremonial deposition.

The remaining human bones and all the dog bones are stray elements from more or less disturbed settlements. None of them seem to have been fractured for the purpose of extracting the marrow, and only one (Bodal AL) has cut marks that may relate to butchering. Therefore, we consider it likely that they derive from eroded burials or sacrificial deposits perhaps relating to a cult of the dead (cf. Meiklejohn et al., 2005; Smith and Kooijmans, 2006). Sacrificial activity may also be responsible for wear and cut marks identified on the fragment of a Mesolithic child's skull from Dyrholm. Consequently we assume these stray bones are remains of members of the social groups that inhabited the region in which they were found.

Several of our sites are represented with more than one sample, and in three cases we cannot exclude the possibility that more than one bone from the same individual has been measured. In the case of the two dog bones from Bodal C

Table 4
Previously published radiocarbon data and combined δ^{13}C and δ^{15}N measurements from Danish Stone Age Human bones

Site name and publication	Lab. no.	Age and sex	δ^{13}C VPDB (‰)	δ^{15}N AIR (‰)	^{14}C Age BP	Reservoir correction model		Corrected ^{14}C age	Cultural epoch
						δ^{13}C	δ^{15}N	BP	
Richards et al., 2003									
Bøgebakken, grave 5	K-2782	Adult M	−15.0	11.9	6290 ± 75	**58%**	45%	6059	E
Bøgebakken, grave 8	K-4154	ca. 20 F	−14.4	10.6	6130 ± 90	**63%**	30%	5878	E
Bøgebakken, grave 3	K-2781	40–50 y F	−14.5	11.3	6050 ± 75	**62%**	38%	5802	E
Richards and Koch, 2001									
Bodal Mose	AAR-5360	Adult M	−20.8	8.0	5025 ± 40	**8%**	2%	4994	N
Vængegård	K-6300	Adult F	−20.3	8.2	4760 ± 95	**12%**	4%	4712	N
Østrup Mose	K-5741	Adult M	−20.4	10.0	4530 ± 90	11%	**24%**	4434	N
Østrup Mose	K-5742	Adult F	−19.6	9.9	4510 ± 90	18%	**23%**	4419	N
Aldersro	AAR-6545	Adult F	−19.5	8.0	4410 ± 55	**19%**	2%	4334	N
Aldersro	AAR-6548	Adult	−19.6	9.3	4410 ± 55	**18%**	16%	4338	N
Aldersro	AAR-6550	Adult	−19.2	9.0	4350 ± 50	**22%**	13%	4264	N
Aldersro	AAR-6546	Adult M	−19.7	8.0	4190 ± 60	**17%**	2%	4121	N
Aldersro	AAR-6551	Adult	−20.0	8.7	4100 ± 50	**15%**	10%	4041	N
Aldersro	AAR-6547	5–7 y	−20.2	6.3	4060 ± 45	**13%**	–	4008	N
Aldersro	AAR-6544	Adult F	−20.7	7.5	4010 ± 50	**9%**	–	3976	N

^{14}C reservoir corrections are calculated by the use of both δ^{13}C and δ^{15}N values in accordance with the correction model presented in this study. Bold values refer to the estimated diet fraction used for ^{14}C reservoir correction (% of 400 years).

Table 5
Previously published δ^{13}C (and δ^{15}N) data on Danish Mesolithic and Early Neolithic human and dog bones that can be referred to a specific cultural epoch

Site name	Site location	Cultural epoch	Species	δ^{13}C	δ^{15}N	Lab. No.	^{14}C age BP	Reservoir correction δ^{13}C	Res. Corr. (years)	Corr. ^{14}C age BP	References
Maglemose											
Ulkestrup Lyng	i	m	Dog	−21.9							Noe-Nygaard, 1995: 248
Ulkestrup Lyng	i	m	Dog	−~~25.2~~							Noe-Nygaard, 1995: 248+250
Holmegård, 1944	i	m	Dog	−17.4							Noe-Nygaard, 1988: 90
Sværdborg I	i	m	Dog	−19.5							Fischer, 2003
Kongemose											
Nivå 10	c	K	Human	−16.2		AAR-7058	6900 ± 60	47%	189	6711	Jensen, 2006
Nivågård	c	K	Human ∼5 y	−13.5		Ka-6610	6845 ± 65	71%	283	6562	Jensen, 2001
Korsør Nor	c	K	Human	−14.9		K-4263	6760 ± 75	59%	234	6526	Fischer and Pedersen, 1997: 320
Kongemose	i	k	Dog	−17.0							Noe-Nygaard, 1988: 90
Kongemose	i	k	Dog	−14.0							Noe-Nygaard, 1988: 90
Ertebølle											
Rønbjerg	c	E	Human	−14.3		AAR-832	6680 ± 140	64%	255	6425	Heinemeier et al., 1993: 300
Lollikehuse	c	E	Dog	−12.4		AAR-3629	6390 ± 60	80%	321	6069	Friborg, 1999, Noe-Nygaard, pers. commun.
Holmegård, Jylland	c	E	Human	−11.9		OxA-533/K-3559	6057 ± 64	84%	338	5719	Gillespie et al., 1984; Andersen et al., 1986
Salpetermosen	i	E	Dog	−14.7		K-5230	5820 ± 120	60%	241	5579	Kramer, 2001
Bøgebakken 14	c	E	Human	−14.1		K-2784	5810 ± 105	66%	262	5548	Tauber, 1981b; Albrethsen and Petersen, 1977
Smakkeruphuse	c	E	Dog	−10.2		AAR-3318	5700 ± 65	99%	397	5303	Hede, 2003; Price and Gebauer, 2005: 123
Norsminde	c	E	Human	−14.9		K-385					Andersen, 1991: 39
Maglemosegårds Vænge	c	e	Human	−14.1							Noe-Nygaard, 1988: 90
Maglemosegårds Vænge	c	e	Dog	−14.7		K-373					Noe-Nygaard, 1988: 90
Maglemosegård	c	e	Dog	−14.3							Noe-Nygaard, 1988: 90
Bøgebakken, grave 4	c	e	Human	−13.4	13.8						Richards et al., 2003
Bøgebakken, grave 9	c	e	Human	−13.6	13.0						Richards et al., 2003
Early Neolithic											
Dragsholm	c	N	Human	−21.7		K-2291	4893 ± 100				Tauber, 1981b
Lohals	c	N	Human	−19.3		K-2277	4711 ± 100				Tauber, 1981b

Site location: i, inland; c, coast (<100 m from the beach). Note that information on the scale of measuring uncertainty and data on sample quality (C:N, % col., % C and % N) in most cases are not available. The δ^{13}C value shown with a deletion mark is considered unreliable since it was reported that the sample appeared to be charred. Two females from a mutual burial at Dragsholm (K-2224 and K-2225) are excluded from the table due to reported suspicion of sample contamination. Abbreviations and ^{14}C reservoir corrections follow the principles outlined in Table 1. The age correction for isotope fractionation of the two Early Neolithic samples was done by us. In the original publication the ^{14}C dates of these two samples were presented without correction for isotope fractionation as 4840 ± 100 BP (K-2291) and 4620 ± 100 BP (K-2291).

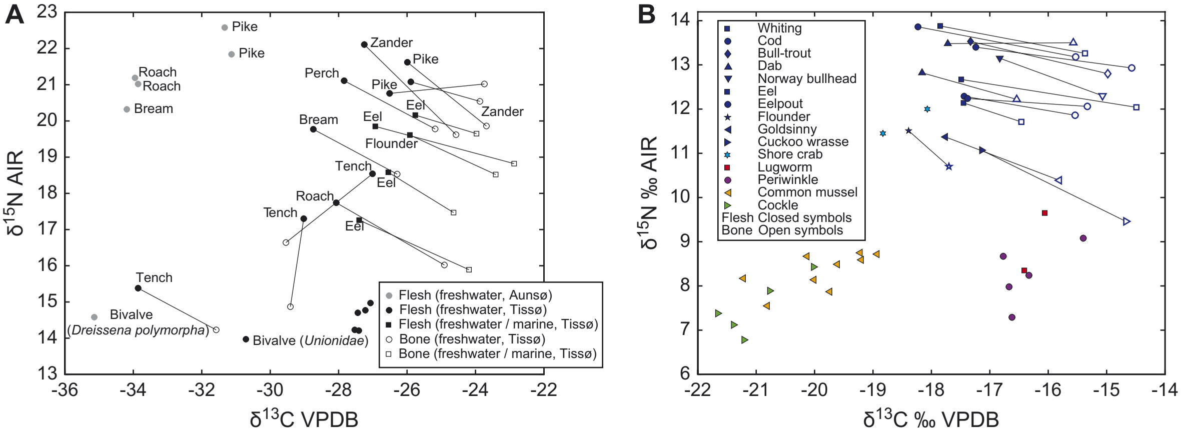

Fig. 2. δ^{13}C and δ^{15}N values measured for present-day fish and mollusc from the two lakes Aunsø and Tissø as well as from Kalundborg Fjord, Denmark. Tissø is located in the same river valley as the Åmose bog, from where many of our Stone Age samples derive. The diagram illustrates that δ^{13}C and δ^{15}N generally increase with increasing trophic level. Note that the molluscs have much lower δ^{15}N values than the fish. Some of the mollusc species also have significantly lower δ^{13}C than any of the fish species living at the respective localities. The solid lines connect flesh values (filled symbols) and bone collagen values (open symbols) of specific individuals. In panel A dots represent freshwater species, while squares represent species that begin their life in the sea and later on migrate to freshwater systems.

neither zoological examination, stable isotope analysis, nor ^{14}C dating could show that we were dealing with two different individuals. Likewise, the two young adult female bones and the two 2-year-old bones from the Argus site cannot be distinguished on the basis of their ontogenetic age or their isotopic values (Fischer et al., in press). In Figs. 4–6, these pairs of samples are marked with two symbols connected by a line. In the case of the two infant bones from the Argus site, the two measurements are so close that they cannot be distinguished from one another in Figs. 4–6. In the following calculations we consider these three cases to represent three individuals only.

5. Paleodietary interpretation of stable isotope data

In Fig. 4 we have drawn four boxes taken from the food-source diagram in Fig. 3 (upper part; seal data omitted) and displaced them +1‰ for δ^{13}C and +3.5‰ for δ^{15}N to account for the diet-to-consumer shift. Thus, these boxes define the isotopic range in which a human or a dog would end up if consuming only food from one of these food categories. Consumer isotopic values outside the boxes indicate a mixture of two or more different food sources. Unfortunately, a more detailed reconstruction is not possible. First of all, freshwater food enters as an important third resource in addition to the marine-terrestrial two-component dietary system applied in previous literature on the topic. Secondly, as seen from Fig. 4, these three main food categories are represented by extended boxes rather than by single, well-defined isotopic values.

For the purpose of clarifying the issue of human coast-inland mobility, the key question is how to identify those individuals who had significant contributions of marine food in their diets. On the basis of the data available at present this should be the case with individuals located on the right hand side of the dashed line in Figs. 4 and 5.

Most of the Neolithic human and dog δ^{13}C and δ^{15}N values from the present study fall in the upper part of, or slightly above, the terrestrial herbivore box (Fig. 5D). In principle they may, therefore, have subsisted totally or primarily on terrestrial foods. In Figs. 2 and 4 it can, on the other hand, be seen that the consumption of mixed diets consisting of a large proportion of low trophic freshwater molluscs or fish and somewhat smaller quantities of low trophic marine fish may result in bone collagen stable isotope values identical to those seen in individuals that feed on terrestrial herbivores only. This is worth noting since shells of freshwater molluscs and bones of low trophic level fish such as tench constitute a significant part of the food remains found at several of the well-preserved Early and Middle Neolithic inland sites in the Åmose (Enghoff, 1995; Noe-Nygaard, 1995; Koch, 2003; Fischer and Heinemeier, 2003)—i.e. in the same inland bog from which many of our Early Neolithic human and dog bone samples derive.

As can be seen on Fig. 5B and C, we found that the Middle and Late Mesolithic humans and dogs, even the five to seven individuals from inland settlements, all have pronounced marine isotopic signatures. Only one of the eight securely dated Neolithic individuals from coastal sites in our assemblage (Fig. 5D), an adult man found in a kitchen midden at Rødhals, also had a diet rich in marine food (Fischer, 2002; Fischer et al., 2005).

6. ^{14}C reservoir correction based on isotopic data

Both marine and freshwater organisms can—for different reasons—be depleted in ^{14}C relative to the atmosphere, producing apparent ^{14}C ages that are too old compared to terrestrial organisms. This age difference is called the reservoir age. Thus, present-day marine organisms living in the upper, mixed layer of the open ocean in the North Atlantic appear about 400 ^{14}C years older than terrestrial organisms. In the Danish shallow seawaters, the reservoir age is often somewhat higher,

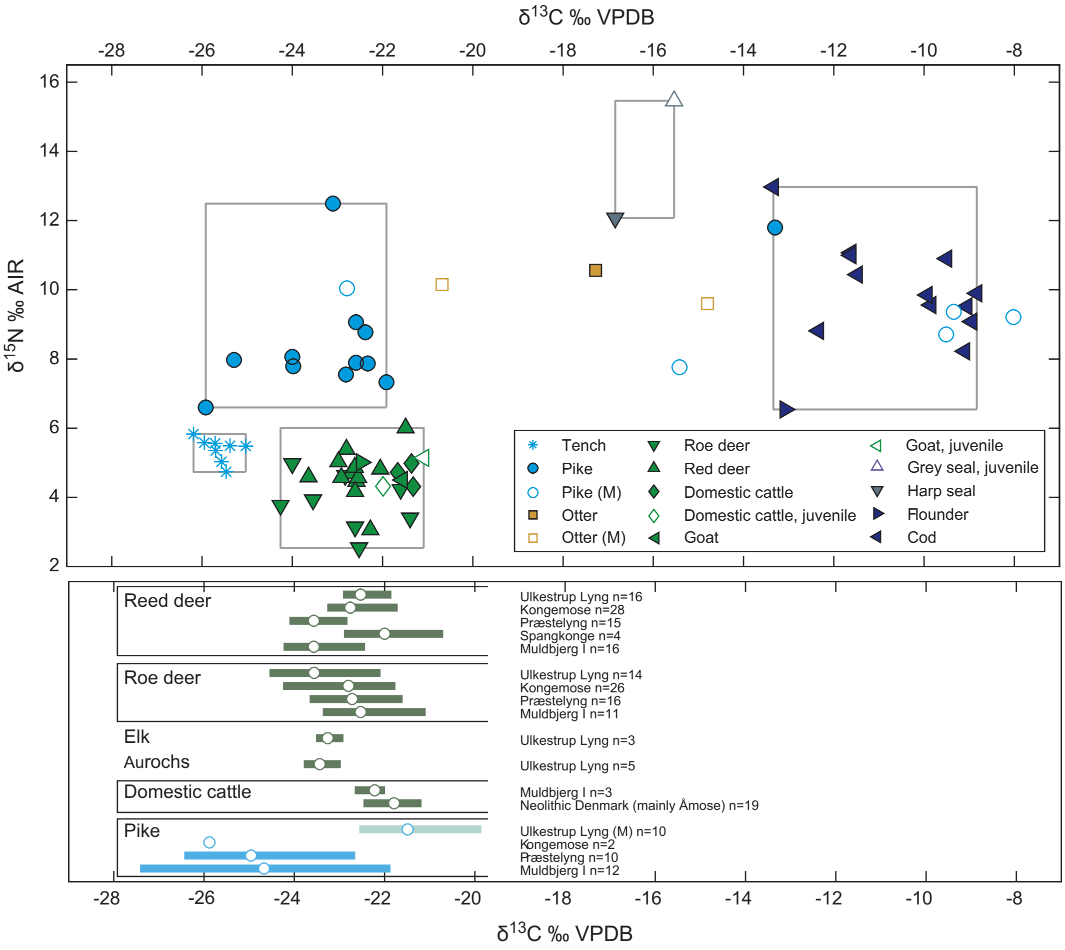

Fig. 3. (Upper diagram) δ^{13}C and δ^{15}N values measured for bone collagen of selected Danish Mesolithic and Neolithic animals, which served as food sources for humans (and dogs). Data points are combined into five groups (rectangular boxes) according to their habitat and position in the food web. (Lower diagram) Previously published δ^{13}C values for food source animals from Danish Stone Age inland sites (Noe-Nygaard, 1995; Fischer, 2002; Noe-Nygaard et al., 2005). The horizontal lines represent ranges of δ^{13}C values for different species, and the dots indicate their average values. The sites are listed in chronological order. Ulkestrup Lyng represents the Early Mesolithic Maglemose Culture. Kongemose represent the Middle Mesolithic, Præstelyng the Late Mesolithic Ertebølle Culture, while Spangkonge and Muldbjerg I are from the Early Neolithic Funnel Beaker Culture. In both diagrams, pikes (and otters) found at Early Mesolithic inland sites are plotted with special symbols, which in the legend are marked with "(M)" for Maglemose.

depending on time and coastal geography (Heier-Nielsen et al., 1995). Organisms that have their carbon from freshwater and brackish environments can appear even older than their marine counterparts, because they may contain fossil carbon (dissolved $CaCO_3$) from influx of groundwater.

The freshwater reservoir age is known to vary considerably with time and location (Lanting and van der Plicht, 1998; Heier-Nielsen et al., 1995; Olsen, 2006: 233). Six fish bones from the Early Neolithic inland site Åkonge showed freshwater reservoir effects from ca. 115 to ca. 480 ^{14}C years (Fischer and Heinemeier, 2003). The difference in apparent age between the Neolithic human Østrup homo II from the Åmose inland area (see Table 1) and a tinder fungus deposited with the body (AAR-10248) is 82 ± 57 ^{14}C years (ignoring the age at death of the fungus). An AMS date of a present-day pike from Lake Aunsø (Table 3, Aunsø sample 2) showed an apparent age of 684 ^{14}C years (AAR-10139), while AMS dates of ten present-day fish and molluscs from Lake Tissø revealed an average reservoir effect of 1034 ^{14}C years (Fischer and Heinemeier, 2003).

To simplify matters for the purposes of this study, we make the assumption that both marine and freshwater reservoir ages are 400 ^{14}C years, knowing that this number is a crude estimate only, especially concerning the freshwater effect. To determine the proportion of marine protein in diets we apply a linear δ^{13}C model (Arneborg et al., 1999) with estimated δ^{13}C endpoints of $-21.7‰$ and $-10.1‰$, corresponding to 0% and 100% marine diet, respectively (Fig. 4, top margin). The first number is the average δ^{13}C value of the faunal samples in the terrestrial box in Fig. 4, i.e. corrected for 1‰ trophic level shift. The second number is the average δ^{13}C value of the marine box in same figure.

Estimating the proportion of freshwater protein in diets is a more complicated matter. We propose a δ^{15}N model (cf. Cook et al., 2001) to distinguish aquatic (i.e. marine and/or freshwater) diet from terrestrial diet. It is based on the assumption that the marine and freshwater food chains are equal in length and have identical isotopic endpoints. The consumer's isotopic "endpoints", corresponding to 0% and 100% aquatic relative

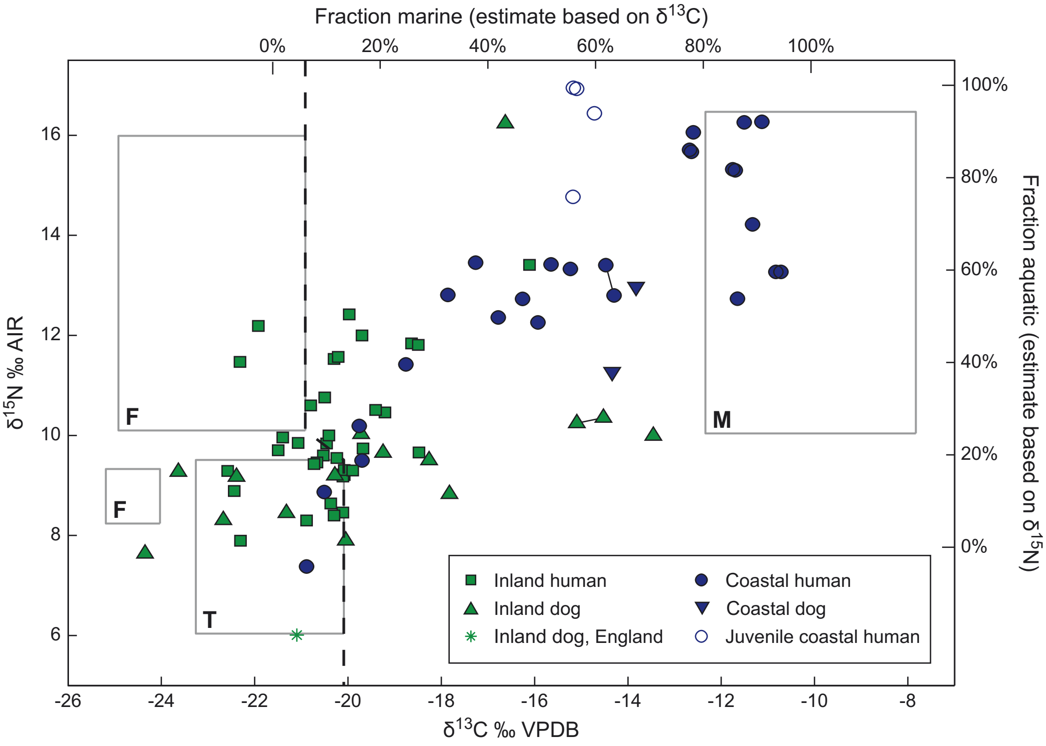

Fig. 4. All $\delta^{13}C$ and $\delta^{15}N$ values of bone collagen of humans and dogs measured as part of this study. Short connecting lines indicate pairs of data point that may stem from the same individual. The rectangular boxes are taken from Fig. 3 and have been shifted by +1‰ on the $\delta^{13}C$ axis and +3.5‰ on the $\delta^{15}N$ axis to account for the trophic shift in isotope values from food source to consumer. The T and M boxes mark the areas in the diagram where hypothetical individuals that subsisted entirely on terrestrial and marine diets, respectively, would be located. The two boxes labelled F relate to consumers of two freshwater species from distinctly different levels of the food web: omnivorous tench (near the lower left corner) and carnivorous pike (higher up and further to the right). Open symbols denote juvenile individuals, which probably have elevated $\delta^{15}N$ values due to lactation. Adult individuals on the right hand side of the dashed line are considered to have consumed significant quantities of marine food. The percentage scales for marine and aquatic components on the top and right margins relate to modelled radiocarbon reservoir effect corrections.

to terrestrial derived protein, are chosen to be $\delta^{15}N$ equal to 7.3‰ and 17.0‰, respectively. The former number is defined by the average $\delta^{15}N$ value of the terrestrial (herbivorous) box (Fig. 4). The latter number is estimated from the highest $\delta^{15}N$ value for our marine and freshwater fish, corrected for a 3.5‰ trophic level shift.

The percentages of marine and aquatic protein in relation to total protein consumption are shown in Fig. 4 as alternative axes in the margins of the graph. The reservoir age correction of a sample is simply estimated as a percentage of 400 years by applying the $\delta^{13}C$ and $\delta^{15}N$ models and then choosing the largest reservoir correction predicted by either of them. We must, however, emphasise that our method only allows a rough estimate of the reservoir effect, not least because the factors influencing the freshwater reservoir effect are very complex.

All estimated ^{14}C reservoir ages are listed in Table 1. Note that for three of our freshwater fish bone samples of reliable quality reservoir ages have actually been measured. They are all from the Åkonge site (AAR-4573, −4574 and −4576, see Table 1) and show reservoir ages of 153 ± 39, 310 ± 46 and 480 ± 46 ^{14}C years, respectively (cf. Fischer and Heinemeier, 2003).

The model cannot be used for individuals with $\delta^{13}C$ values less than −21.7‰, even though their ^{14}C dates may be influenced significantly by the reservoir effect. This is the case with eight inland individuals. In Table 1 the negative percentage values of these individuals, calculated on the basis of the reservoir correction model, are substituted by the sign "–". In Fig. 6 the symbols representing two dogs with extremely negative $\delta^{13}C$ values (to the left of the terrestrial box in Fig. 5D), are marked with arrows, indicating that the reservoir effects in these samples are clearly underestimated.

7. Part-time or full-time inland dwellers

Fig. 5 shows the same data as presented in Fig. 4, divided chronologically into the Maglemose, Kongemose and Ertebølle Cultures and the Neolithic. This is done in order to show the importance of marine and freshwater food over time. Several of our samples are dated so close to 5150 BP (the estimated ^{14}C date for the introduction of farming) that it cannot be decided with certainty if they belong to the latest Mesolithic or the earliest Neolithic. This applies to individuals with ^{14}C dates belonging to the time interval 150 years before to 100 years after 5150 BP. The asymmetric interval of uncertainty has been decided upon in order to take account of possible (freshwater) reservoir effects. For reasons of clarity we have placed these results in either panel Fig. 5C or D according to their association with Ertebølle/marine or

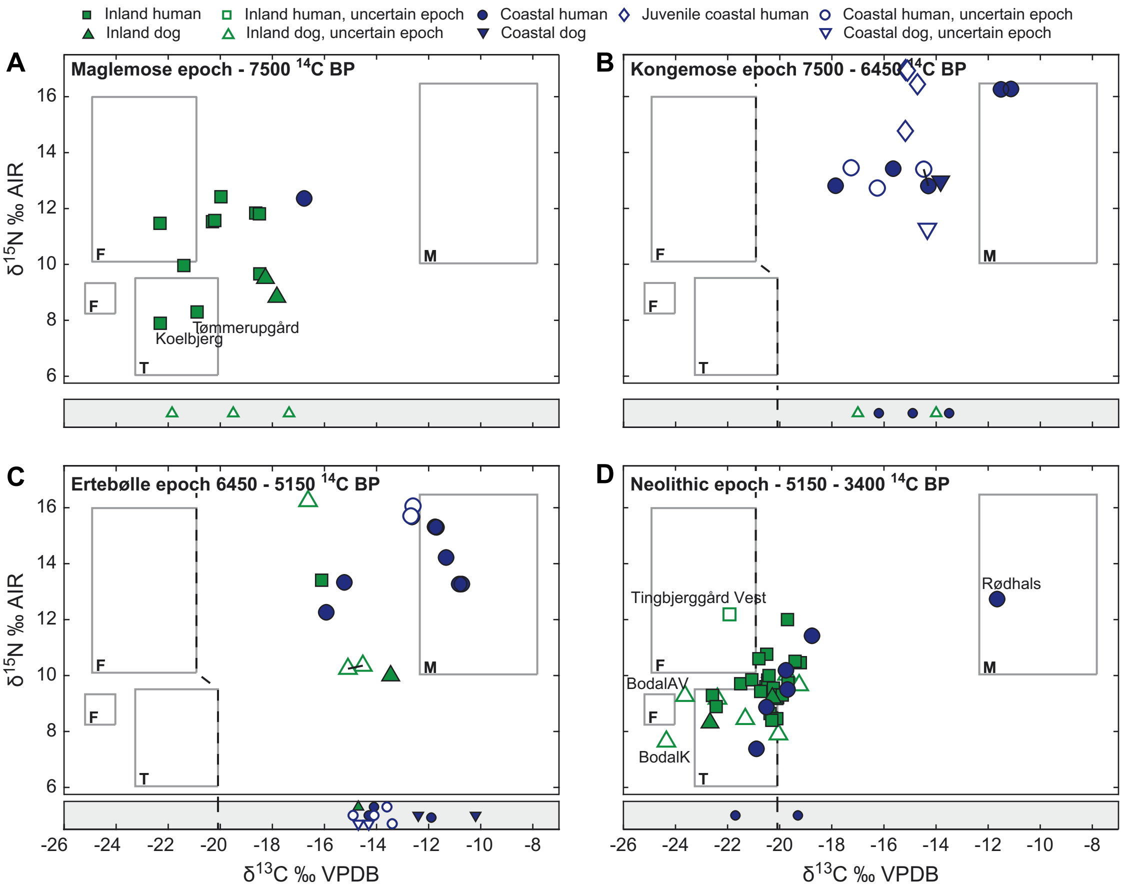

Fig. 5. Bone collagen δ^{13}C and δ^{15}N for Danish humans and dogs sorted in time periods. All the Middle and late Mesolithic inland individuals on the right hand sides of the dashed line (panels B and C) have marine signatures, which support the thesis of high geographical mobility in the Mesolithic. Short connecting lines indicate pairs of data point that may stem from the same individual. The open symbols in the shaded panels represent individuals that are not radiocarbon dated and are referred to the period in question on the basis of their archaeological context only. In panels C and D, upper parts open symbols mark samples with a reservoir corrected ^{14}C age within the interval 150 years before to 100 years after the Mesolithic–Neolithic transition at 5150 ^{14}C BP. For reasons of clarity we have placed this type of samples in either panel C or D, upper parts according to their association with Ertebølle/marine or Neolithic/terrestrial dietary behaviour respectively, based on their δ^{13}C values being higher or lower than $-17.5‰$. The lower, shaded parts of the panels present data published in previous studies (only δ^{13}C available). (A) Maglemose Culture. The bones of most of these Early Mesolithic individuals have been found inland (the contemporaneous coast line is now deeply submerged). Their isotopic values appear to be marine, but special geochemical conditions in the lakes of the Early Mesolithic make it impossible to determine, if these individuals have actually consumed sea food. (B) Kongemose Culture. The protein in the diets of these Middle Mesolithic individuals was mainly of marine origin. Nonetheless, two of them were found in the inland, miles away from the contemporaneous coast. (C) Ertebølle Culture. All individuals ascribed to this period have clear marine signals, even the three inland samples that indisputably belong to this period. (D) Neolithic period (the shaded part of the panel contains previous results from the Early Neolithic only). The concentration of samples with isotopic signatures close to the marine/terrestrial borderline stands in strong contrast to distribution pattern of the previous Kongemose and Ertebølle periods. The protein in the diets of the dogs from Bodal K and Bodal AV, located in the far lower left of the diagram, consisted of high amounts of freshwater food.

Neolithic/terrestrial dietary behaviour respectively, based on their δ^{13}C values being higher or lower than $-17.5‰$.

The highly varied, in some cases clearly marine-like, δ^{13}C values found in some Early Mesolithic freshwater food source animals (pike and otter) make it impossible to determine with certainty if the dogs and humans from Maglemose Culture inland sites had consumed marine food. The very low δ^{13}C and δ^{15}N values seen in our two oldest humans (Koelbjerg and Tømmerupgård) may, however, be taken as an indication that aquatic food, including marine species, was of little or no significance in the diets of these two individuals, dating from the first half of the Early Mesolithic.

As observed in Fig. 5B and 5C, two Kongemose dogs and three Ertebølle individuals from the inland have consumed very significant proportions of marine food despite the fact that they were deposited at sites many miles from the contemporaneous coasts. In addition the two dog bones from Bodal C (possibly only one individual) and a dog bone from Ringkloster, both/all dated to the Mesolithic–Neolithic transition, have clearly marine isotopic signatures.

Bones of anadromous fish species (i.e. salmon/trout) appear in very low frequencies even in the most well preserved Danish Stone Age inland sites (Enghoff, 1994). Therefore, it is very unlikely that widespread consumption of these species could explain the marked marine isotopic signatures in the inland human and dog bones. Also, in the Stone Age, the means of preserving and transporting seafood from the coast to the interior seem to have been limited, and from

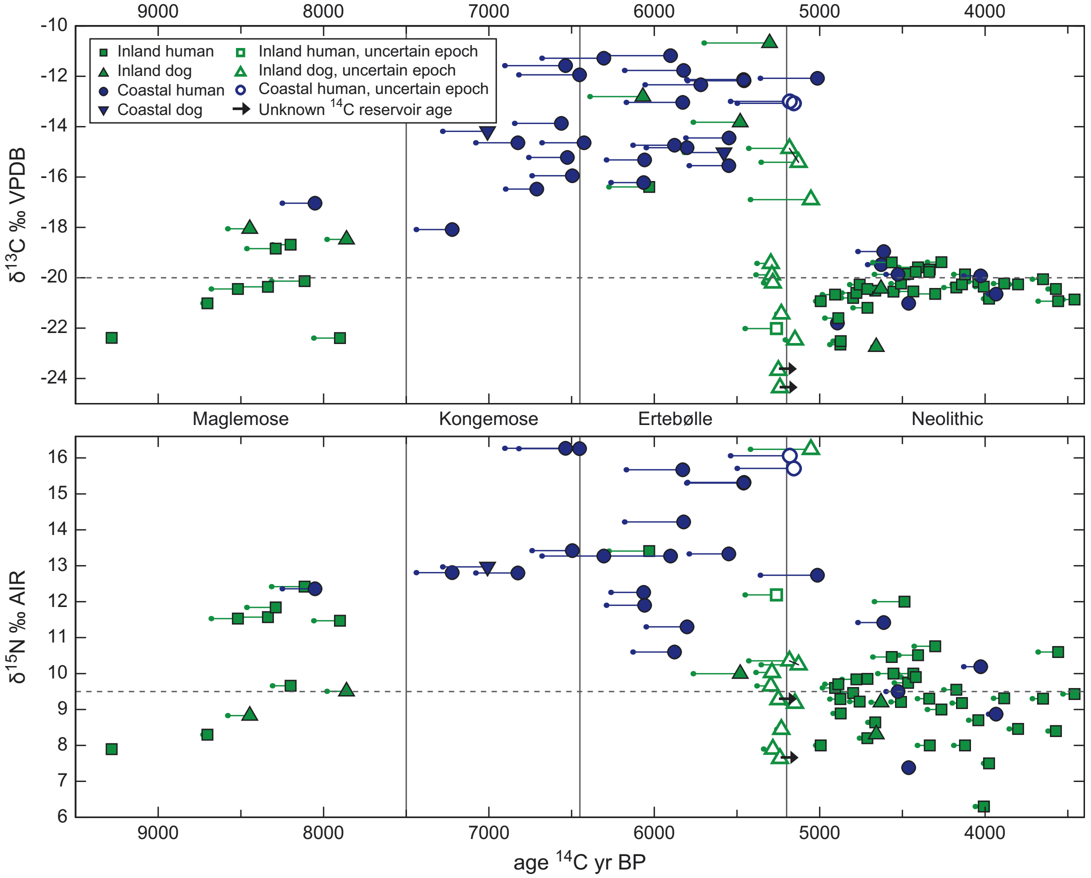

Fig. 6. δ^{13}C and δ^{15}N values for bone collagen of Mesolithic and Neolithic humans and dogs from Denmark plotted versus time. The illustration includes all individuals listed in Tables 1, 4 and 5. The one-sided "error bars" represent reservoir correction. Individuals marked by open symbols belong to the Mesolithic–Neolithic transition (5300–5050 ^{14}C years BP). Open signatures supplemented with an arrow represent samples where the reservoir effect is inadequately accounted for. The horizontal dashed line at $\delta^{13}C = -20‰$ indicates a limit above which there is solid indication of a non-negligible marine dietary component. Individuals somewhat below the line may also have consumed some small quantities of marine food. Based on the presently available data (Fig. 3) the individuals (adults) above the horizontal dashed line at $\delta^{15}N = 9.5‰$ must have consumed aquatic food regularly, and the same may apply to individuals below the line if substantial parts of this dietary component derived from low trophic level organisms such as shellfish.

the very rare occurrences of remains of marine mammals, fish and shellfish in inland fauna assemblages it appears to have taken place only occasionally (Enghoff, 1994; Fischer, 2004). It is therefore unlikely that the marine isotopic signatures of the Mesolithic human and dog bones found on inland sites are the result of transport of quantities of marine food from the coast to the interior. It is more likely that it was the people who moved: the isotopic "marine" inland Middle and Late Mesolithic individuals have most probably spent a considerable part of their lives at the coast eating seafood. Consequently, coast-inland mobility must have been a regular phenomenon in Mesolithic Denmark. The typical location of the Mesolithic inland habitation in Europe—at the edge of rivers and lakes (e.g. Mathiassen, 1937, 1959)—may indicate that the transport between the coast and the interior usually took place by boat (Fischer, 2004).

8. The Mesolithic–Neolithic transition

Fig. 6 displays isotopic values of all ^{14}C dated Danish Stone Age human and dog bones, excluding some Middle and Late Neolithic individuals from which no δ^{15}N value is available) as a function of time across the Mesolithic–Neolithic transition. All the radiocarbon dates have been reservoir corrected using the model described above.

We define the onset of the Neolithic as the time when husbandry and/or agriculture was introduced in the area in question. Our AMS dates of domestic ox bones from the Åmose show that cattle husbandry was introduced in this area no later than 5135 ± 45 ^{14}C years BP (Table 1, AAR-6944). Considering all presently available data (Fischer, 2002; Fischer and Gotfredsen, 2006; cf. Noe-Nygaard et al., 2005), we assume that farming was practised on a regular basis from around 5150 ^{14}C years BP in the Åmose region and probably in most other parts of Denmark too.

In Fig. 6 a marked change in diet is seen around the onset of the Neolithic. Our results agree with a number of earlier studies that there is a sharp decline in the use of marine resources at the time when farming products became available (e.g. Tauber, 1981a,b; Noe-Nygaard, 1988; Persson, 1999; Richards et al., 2003). On the basis of the data presented in Figs. 2 and 3 the decline in δ^{13}C and δ^{15}N values around the beginning of the Neolithic may be explained by either the one or the other of the following two processes:

- a widespread substitution of high trophic level seafood with terrestrial (agricultural) food, as first suggested by Henrik Tauber;
- a widespread substitution of high trophic level marine fish with terrestrial food in combination with a mixture of low trophic level freshwater and marine food.

In support of the latter interpretation it shall be mentioned that shells of freshwater molluscs form significant parts of the culture layers in Åmose from around the onset of the Neolithic (cf. Skaarup, 1973: 120; Noe-Nygaard, 1995: 64; Koch, 1998, 2003; Fischer and Heinemeier, 2003). In addition we notice that a number of our Åmose humans and dogs from the Mesolithic–Neolithic transition have freshwater isotope signatures. This applies most clearly to two inland dogs, which display δ^{13}C values $\leq -23.6‰$ (Bodal AV and Bodal K). It is obviously also the case with the human from Tingbjerggård Vest, who combines a relatively elevated δ^{15}N value with a relatively low δ^{13}C value (Fig. 5D). Moreover, the apparent minimum in δ^{13}C values observed during the Mesolithic–Neolithic transition and shortly afterwards (Fig. 6, upper panel) is most simply explained as an expression of a period of especially high dependence on freshwater food.

9. Consumption of seafood in the Neolithic

It appears from Fig. 5D that the majority of the Neolithic individuals represented in our study have somewhat elevated δ^{13}C and δ^{15}N values. One possible explanation for this might be large-scale consumption of juvenile herbivores. However, we interpret these isotopic values as the result of eating aquatic food, primarily of marine origin. Such an interpretation is perhaps unsurprising given the numbers of Neolithic coastal shell middens recorded, as well as the numbers and in some cases rather impressive sizes of Neolithic fish weirs observed along the contemporary Danish coasts (Pedersen, 1995; Andersen, 2004; Milner et al., 2004; Fischer, 2007).

Only one Neolithic individual in our assemblage has had a clearly marine diet. That is an Early Neolithic male buried in the Rødhals kitchen midden on the island of Sejerø. It should be noted that the geographical location of this site was rather unique as in the Early Neolithic it was a small archipelago several kilometres away from any other land (Fischer et al., 2005).

With this single exception the consumption of marine food was clearly much less important in the Neolithic than during the Middle and Late Mesolithic. There seems, however, no longer to be substantial reason for postulating a severe methodological contradiction between traditional archaeological data versus isotopic observations (as suggested by Milner et al., 2004), nor to uphold a strict view that the population of Denmark turned their back on the sea at the transition from the Mesolithic to the Neolithic (e.g. Schulting, 1998).

10. Conclusions

Our stable isotope analyses indicate that Middle and Late Mesolithic humans and dogs found in the Danish interior have all consumed significant amounts of marine food. Considering the apparently limited means of transporting and preserving food at the time, these individuals must have spent large periods of their lifetimes at the coast. However, we are only able to measure a small number of individuals (at least five, most likely seven) so we do not want to interpret data more broadly.

In principle the marine isotopic signatures of humans and dogs from Middle and Late Mesolithic inland sites can be explained in two different ways. Either they moved frequently between the coast and the interior, or they arrived and settled permanently in the interior as results of exchange—i.e. gift exchange of dogs and exogamous marriage relations between coastal and inland groups. Although the available samples are few the 100% frequency of human and dog bones with clear marine isotopic signatures found in the interior suggests that the exchange hypothesis is unlikely. Most probably the Middle and Late Mesolithic population in the coastal zones of Denmark moved seasonally between the seashore and the interior.

Our analyses show that some of the Early Mesolithic freshwater food source animals from carbonate rich moraine areas in Denmark have δ^{13}C and δ^{15}N values similar to those seen in marine animals. It is therefore not possible to determine if the elevated stable isotope values seen in most of the Early Mesolithic humans and dogs from Danish inland sites are a result of coast-inland mobility or of full-time inland habitation.

Aquatic food, primarily high trophic level fish, appears to have formed a protein source of fundamental importance for the Mesolithic inhabitants of present-day Denmark from the middle of the Early Mesolithic onwards. Around the onset of the Neolithic a very distinct decline in δ^{13}C and δ^{15}N values is observed—among individuals from the coast as well as from the inland. The data now available clearly points to a general change of diet where significant proportions of marine fish were substituted with terrestrial food and possibly some low trophic level freshwater food. It appears, however, that small quantities of marine foods remained a common source of dietary protein throughout the Danish Neolithic.

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