Stable isotope evidence for increasing dietary breadth in the European mid-Upper Paleolithic

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New carbon and nitrogen stable isotope values for human remains dating to the mid-Upper Paleolithic in Europe indicate significant amounts of aquatic (fish, mollusks, and/or birds) foods in some of their diets. Most of this evidence points to exploitation of inland freshwater aquatic resources in particular. By contrast, European Neandertal collagen carbon and nitrogen stable isotope values do not indicate significant use of inland aquatic foods but instead show that they obtained the majority of their protein from terrestrial herbivores. In agreement with recent zooarcheological analyses, the isotope results indicate shifts toward a more broad-spectrum subsistence economy in inland Europe by the mid-Upper Paleolithic period, probably associated with significant population increases.

early modern humans | subsistence | Middle Paleolithic | Neandertal

Human subsistence patterns during the Late Pleistocene have been inferred principally from faunal remains preserved in archeological sites; from the uses of stone tools based on form, microwear traces, and organic residue analysis; and occasionally from preserved vegetal remains. Although it is recognized generally that Late Pleistocene human diets must have included a variety of plants and animals, the majority of the studies conducted to date have focused on large mammal remains and taphonomic arguments about the changing nature of human exploitation of those animals. By the late Upper Paleolithic period (during oxygen isotope stage 2), however, paleontological, paleobotanical, and technological evidence all indicate substantial broadening of human diets in several regions of the Old World. For the earlier phases of the Upper Paleolithic and the Middle Paleolithic, zooarcheological data relating to the exploitation of resources other than large-bodied terrestrial vertebrates are more geographically variable and rare, but gradually emerging (1, 2). One less-documented family of resources consumed by Late Pleistocene humans before the Last Glacial Maximum [18–20 ka (thousand years) before present (BP)] is animals from aquatic habitats (but see refs. 3–5).

It is possible to assess the relative proportion of aquatic resources in the diets of prehistoric foragers and coextant animals through analyses of bone collagen carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values. These data provide direct information about average dietary protein intake by prehistoric consumers over an approximately 10-year period before their deaths (6, 7). Although generally silent on the exact range of prey species involved, the isotope data can reflect the proportionality or relative importance of certain kinds of foodstuffs obtained from distinct habitats such as freshwater wetlands, sea coasts, and dry terrestrial landscapes.

To compare the relative roles of aquatic resources in European early modern and late archaic human populations, we analyzed the $\delta^{13}C$ and $\delta^{15}N$ values of collagen extracted from nine modern human skeletons dating to the mid-Upper Paleolithic period in Europe and west-central Asia. These data are combined with published results (8–10) on five late archaic humans (Neandertals) from the western portion of the same general geographic region. The latitudinal distribution of the samples is ≈45°N to 60°N, and most of the samples come from inland regions. A critical distinction is made in this study between marine and freshwater animal resources. Marine exploitation is documented from zooarcheological evidence as early as the Middle Paleolithic of the Last Interglacial (oxygen isotope stage 5e) some 110 ka BP (4), but the scale of exploitation seems to increase with time. Exploitation of fish and other animals from freshwater habitats is a rather different story, because zooarcheological evidence for this behavior does not emerge until much later, and it is most abundant in the zooarcheological record after the Last Glacial Maximum (about 20 ka BP; e.g., refs. 11–13). Freshwater aquatic resources potentially include fish, certain large-bodied mollusks, and the many waterfowl species that feed on aquatic plants, invertebrates, and small vertebrates (e.g., rails and ducks).

Materials and Methods

Given that there are few reliably dated modern human remains from the early Upper Paleolithic (≈36–29 ka BP, i.e., the Aurignacian), we have focused on samples from the subsequent mid-Upper Paleolithic (≈28–20 ka BP), including phases variously termed the Upper Perigordian, Gravettian, Pavlovian, and Streletskayan (14). The sample includes specimens from Brno-Francouzská and Dolní Věstonice (Czech Republic), Kostenki, Mal'ta and Sunghir (Russia), and Paviland (Great Britain). All have been dated directly by the accelerator mass spectrometry radiocarbon technique and, with the exception of Kostenki 1, their uncalibrated ages fall between 26–20 ka BP (Table 3). We contrast these data with published $\delta^{13}C$ and $\delta^{15}N$ values for five Neandertals from inland Europe that date to roughly 130–28 ka BP (Table 4). All of the Upper Paleolithic specimens except the Dolní Věstonice 35 femur are from intentional burials (graves). All the Neandertal specimens are isolated skeletal elements. The Upper Paleolithic Mal'ta 1 and Sunghir 2 and 3 fossils and the Neandertal Scladina 1 specimens are juveniles or young adolescents; the remainder were fully mature at the time of death.

Because stable isotope analyses are destructive and require good collagen preservation, suitable human remains are few in number. It is not unusual for bone samples from this time period to fail the requirements for analysis because of significant protein diagenesis. We assume that the available samples are sufficiently representative for our purposes, while recognizing that information (specifically on geographic and interpopulation diversity) is limited by the nature of these samples.

Mammal bone collagen $\delta^{13}C$ values measure the relative amounts of marine vs. terrestrial protein in the diet (15). In arid regions where there are significant numbers of C_4 plants, the

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Table 1. Means and standard deviations (1σ) of δ^{13}C and δ^{15}N values of European Late Mesolithic humans for whom aquatic foods are a significant dietary component

Sites	δ^{13}C	δ^{15}N	N	Diets
Various, Denmark (16)	-12 ± 1‰	14 ± 1.5‰	7	Marine fish/shellfish
Oronsay, Scotland (27)	-12.6 ± 0.8‰	15.5 ± 1‰	5	Marine fish
Schela Cladovei, Romania (26)	-19.6 ± 0.2‰	15.4 ± 0.4‰	7	Freshwater fish
Vlasac, Serbia (27)	-18.9 ± 0.5‰	14.7 ± 0.2‰	4	Freshwater fish

δ^{13}C value also can indicate the relative amounts of dietary protein from C_3 and C_4 plant sources (16); because C_4 plants are unknown from prehistoric Europe (17), it is unlikely that the δ^{13}C values presented here reflect the differential plant consumption documented in arid equatorial environments. Consumer collagen δ^{15}N values are 2–4 ‰ higher than the average δ^{15}N value of the protein consumed. Therefore, in the Pleistocene human foraging context of concern here, δ^{15}N values indicate the trophic level of the organism of interest (18). Aquatic systems have longer food chains than terrestrial ones, and the δ^{15}N values of modern aquatic species such as fish (about 12 ‰) and carnivorous marine mammals (*ca.* 18 ‰) are much higher than those of terrestrial herbivores such as cattle and red deer (*ca.* 4–6 ‰; refs. 9, 19–25). The same would apply to waterfowl feeding on aquatic invertebrates and/or vertebrates (18). Thus, humans who consume significant amounts of aquatic foods will have much higher δ^{15}N values than humans who consume only terrestrial plants and herbivores (16, 25–28). For more extensive discussions of the assumptions and justifications behind these palaeodietary inferences from stable isotope analyses see refs. 29–31.

Additionally, marine organisms are more enriched in ^{13}C than terrestrial organisms (15), such that, in addition to higher δ^{15}N values, marine organisms have more positive δ^{13}C values [e.g., -12 ± 1‰ for marine mammals (19)]. Organisms in freshwater ecosystems can have δ^{13}C values that are more negative than those in terrestrial and marine ecosystems, because carbon in freshwater systems can come from geological sources as well as from the atmosphere (32). Significant consumption of freshwater resources by humans therefore can be indicated by high δ^{15}N values and/or more negative δ^{13}C values [e.g., -23 ± 1‰ (33)]. For comparison, stable isotope values of Holocene late Mesolithic humans from Europe, whose diets (on the basis of zooarcheological evidence) included significant amounts of aquatic foods, are given in Table 1. There are, unfortunately, very few published δ^{15}N values for Eurasian freshwater fish and waterfowl; the available δ^{13}C and δ^{15}N values for a number of Eurasian freshwater and anadromous fish and waterfowl are given in Table 2.

Stable isotope measurements of the mid-Upper Paleolithic human samples were made at the Research Laboratory for Archaeology and the History of Art, University of Oxford (Oxford). The samples were prepared following collagen extrac-

tion procedures outlined in detail elsewhere (28, 34). In brief, bone samples were drilled and then demineralized in 0.5 M HCl. They were gelatinized for 48 h at 75°C in sealed tubes, and the gelatin was filtered and lyophilized before combustion. Isotope measurement was performed in a Europa Geo 20/20 mass spectrometer at the Radiocarbon Accelerator Unit, University of Oxford.

Results

The bone collagen δ^{13}C and δ^{15}N values for the mid-Upper Paleolithic humans are in Table 3, and the δ^{15}N values for those that indicate significant freshwater aquatic food consumption are plotted in Fig. 1 relative to recent herbivore and aquatic prey values, as well as those of five Neandertals. The continental samples from Kostenki, Dolní Věstonice, Brno-Francouzská, and Mal'ta have elevated δ^{15}N values, indicating the consumption of freshwater aquatic foods, probably fish and/or fowl. Their δ^{13}C values differ from the expected terrestrial value of 20‰. This difference likely reflects river carbon δ^{13}C values, which can be a combination of atmospheric and dissolved geological carbon (20, 32). The Kostenki individuals have the highest δ^{15}N values, indicating that well over 50% of the dietary protein came from freshwater animal resources. The Mal'ta, Dolní Věstonice, and Brno-Francouzská individuals do not have as high δ^{15}N values, suggesting that 25–50% of their dietary protein came from freshwater prey. All three individuals from Sunghir have moderately high δ^{15}N values, probably derived mainly from herbivore protein. The δ^{13}C value of the coastal Paviland 1 specimen of -18.4‰ indicates consumption of marine foods (10–15% of dietary protein), as terrestrial herbivores from the same site and time period have δ^{13}C values of -21 ‰ (35, 36).

Limited human stable isotope and zooarcheological evidence from the Mesolithic period (<10,000 years BP) of several regions of Europe indicates that aquatic resources were dietary staples. Freshwater resources were important along the Danube in the Iron Gates region (26) and in the Ukraine along the Dneiper River (33) where human skeletons have elevated δ^{15}N values similar to the earlier humans from Kostenki, Dolní Věstonice, Brno-Francouzská, and Mal'ta (Table 1). Along the Atlantic coast of Europe, there is strong archeological and stable isotope evidence for heavy reliance on marine resources (27, 37–39).

Table 2. Observed average and standard deviations (1σ) δ^{13}C and δ^{15}N values of omnivorous freshwater fish and waterfowl from Eurasian contexts

Species (common name)	Location	N	Habitat	δ^{13}C	δ^{15}N	Age
Esox lucius (pike)	1	2	F	-22.0‰	12.0‰	Modern
Perca fluviatalis (perch)	1	2	F	-21.0‰	11.9‰	Modern
Unknown (anadromous)	2	1	F/M	-15.7‰	12.9‰	7,000–8,500 BP
Unknown (river dweller)	2	1	F	-19.8‰	10.7‰	7,000–8,500 BP
Coregonus lavaretus (whitefish)	3	20	F	-22.6 ± 0.3‰	12.3 ± 0.1‰	Modern
Salvenius alpinus (arctic char)	3	3	F	-22.8 ± 0.1‰	13.2 ± 0.5‰	Modern
Grus grus (crane)	4	1	F	-20.1‰	8.7‰	9,000 BP

1, Lake Baikal, Siberia (25); 2, Danube, Iron Gates region (26); 3, Lake Geneva, Switzerland (20); 4, England; M, marine; F, freshwater.

Site/Sample	Location	δ^{13}C	δ^{15}N	^{14}C age, BP
Brno-Francouzská 2	Czech Rep.	−19.0	12.3	23,680 ± 200 (OxA-8293)
Dolni Věstonice 35	Czech Rep.	−18.8	12.3	22,840 ± 200 (OxA-8292)
Kostenki 1	Russia	−18.2	15.3	32,600 ± 1100 (OxA-7073)
Kostenki 18	Russia	−19.1	13.1	21,020 ± 180 (OxA-7128)
Mal'ta 1	Russia	−18.4	12.2	19,880 ± 160 (OxA-7129)
Paviland 1	U.K.	−18.4	9.3	25,840 ± 280 (OxA-8025)
Sunghir 1	Russia	−19.2	11.3	22,930 ± 200 (OxA-9036)
Sunghir 2	Russia	−19.0	11.2	23,830 ± 220 (OxA-9037)
Sunghir 3	Russia	−18.9	11.3	24,100 ± 240 (OxA-9038)

The δ^{13}C values are reported relative to the Vienna Pee Dee Belemnite (VPDB) standard, and the measurement errors are ±0.2‰. The δ^{15}N values are reported relative to the Ambient Inhalable Reservoir (AIR) standard, and the measurement errors are ±0.3‰.

In contrast, the European Neandertal bone collagen δ^{13}C and δ^{15}N values (Table 4) indicate diets dominated by terrestrial herbivores. As dietary δ^{15}N values can vary over time and among geographic regions (41), the δ^{15}N values of associated herbivores and carnivores were measured in each of these cases. All five of the Neandertal δ^{15}N values were most similar to coextant top-level carnivores such as wolves, large felids, and hyenas (10). There is evidence of neither the highly elevated δ^{15}N values associated with the consumption of aquatic species for these Neandertals, nor is there evidence of the more negative δ^{13}C values associated with the consumption of marine protein. The contrast between the European Neandertal and the Upper Paleolithic early modern human values in our study is illustrated by a Kruskal–Wallis $P = 0.005$ between the two samples for their combined δ^{13}C and δ^{15}N values. We note, however, that the Neandertal samples represent inland populations; those living closer to the Mediterranean Sea are known from zooarcheological evidence to have consumed marine shellfish to some degree.

At two sites in Russia, mammoth bone has yielded high δ^{15}N values (about 10‰) relative to other herbivores (42). It is unclear why this δ^{15}N elevation occurs, but it may be explained by regional climatic factors (41). Some of the central and eastern

European human δ^{15}N values reported here could have been influenced by the consumption of these high δ^{15}N mammoths. Although this inference seems consistent with the abundance of mammoth remains in some sites, the extent of human involvement in the procurement and consumption of mammoths remains unclear and controversial (43–45). Regardless, these points do not seem to account for the broader patterns observed, because most of the observed mammoth δ^{15}N values for Eurasia are much lower, under 8‰ (46, 47). Moreover, the average mammoth δ^{15}N value from the Czech sites of Milovice ($n = 3$) and Dolni Věstonice ($n = 1$) is 7.7 ± 0.7‰ (47), too low to account for the Dolní Věstonice and Brno-Francouzská human δ^{15}N values of 12.3‰.

Discussion

The stable isotope data suggest that the exploitation of aquatic resources, including mammalian and avian predators feeding on smaller aquatic animals, was limited among inland European late archaic (Neandertal) populations. By the mid-Upper Paleolithic, there was relatively heavy use of freshwater aquatic resources in some areas. This difference in the isotope results suggests significant broadening of the resource base between the time of the European Neandertals (including the Vindija 207 and 208 specimens dated to 28–29 ka BP) and that in which mid-Upper Paleolithic human populations existed in Europe. Such a dietary change corresponds to greater "evenness" in the proportions of highly ranked game (high protein or energy yield relative to capture and processing costs) and lower-ranked game, such as fish and fowl, quick-moving animals whose capture costs can be reduced only through greater technological investment.

Neandertals exploited shellfish on occasion, including estuarine mollusks at Vanguard Cave, Gibraltar (48–50); clams, oysters, and mussels at the Grotta di Moscerini, Italy (4); and fish and diverse mollusks at Devil's Tower, Gibraltar (51, 52). However, although the Neandertals' use of marine shellfish in southern Europe is certain, it seems to have been opportunistic, and the question remains whether marine animals of any kind were major or minor sources of protein. Freshwater mollusk
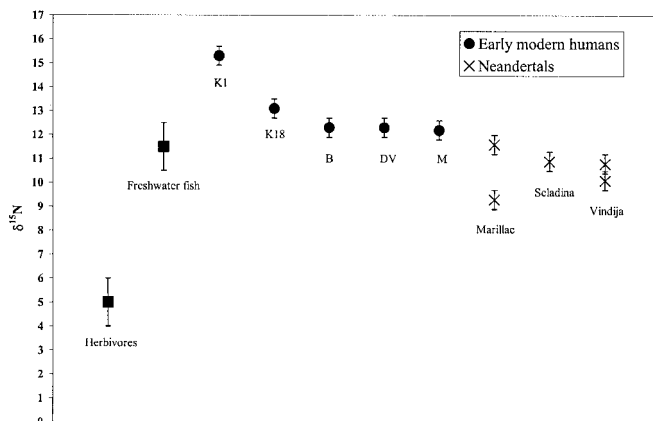

Fig. 1. Bone collagen δ^{15}N values of fauna, Neandertals, and early modern humans showing significant freshwater aquatic resource exploitation from Eurasian contexts. The early modern humans have higher δ^{15}N values, indicating consumption of aquatic foods. Measurement error bars are indicated on the early modern human and Neandertal data points, whereas the bars on the freshwater fish and herbivore points indicate typical ranges of values (see text for references). Abbreviations for the early modern humans are K, Kostenki; B, Brno-Francouzská; DV, Dolni Věstonice; and M, Mal'ta. Early modern humans showing evidence for terrestrial herbivore consumption (Sunghir) and marine resource exploitation (Paviland) are not included.

Table 4. Bone collagen δ^{13}C and δ^{15}N (‰) values of Neandertals (8, 10, 40)

Site/Sample no.	Location	δ^{13}C	δ^{15}N	Age, BP
Marillac 9 (30)	France	−20.2	9.3	About 40–45 ka
Marillac 10 (30)	France	−19.1	11.6	About 40–45 ka
Scladina 1 (29)	Belgium	−19.9	10.9	About 80–130 ka
Vindija 207 (31)	Croatia	−19.5	10.1	About 28–29 ka
Vindija 208 (31)	Croatia	−20.5	10.8	About 28–29 ka

remains occur in the fluviatile sediments of some European Middle Paleolithic sites, but they almost certainly represent the invertebrate background fauna present during site formation in most or all cases.

Aquatic resources are either absent in nonlittoral Aurignacian contexts, with the possible exception of birds, or occur at very low (<1%) percentages of total identified faunal specimens (53). For example, at the Abri Pataud in France, fish remains are absent from the Aurignacian levels, and vertebrae of anadromous salmonids are present in low numbers only in mid-Upper Paleolithic levels 2–4 ($\approx$27–22 ka BP; refs. 54 and 55). However, coastal shellfish exploitation is documented for the early Aurignacian, middle Aurignacian, and Gravettian occupations at the Riparo Mochi on the Mediterranean Sea (Italy), where the importance of shellfish relative to terrestrial game varied mainly with time-dependent eustatic changes in the distance of the shelter from the sea (5). There is also evidence for the exploitation of waterfowl and other birds at Riparo Mochi, beginning with the early Aurignacian, and human diets expanded further in later cultural phases (2). Waterfowl and especially freshwater fish were exploited during the Gravettian at Brillenhöhle, Höhle Fels, and Geissenklösterle (56). Indirect evidence for access to fish comes from rare artistic representations in the Upper Paleolithic of France (57), but these are dated poorly and the majority are probably of late Upper Paleolithic age. There are also fish pendants from the earlier Gravettian at Dolní Věstonice and Pavlov, Czech Republic. In addition, there is evidence for textiles of knotted cord from the central European Gravettian (58) of a form that could have been, but has not been shown to have been, used for nets. However, weaponry specifically designed for the capture of agile or quick small game appears principally in the late Upper Paleolithic (59).

Although scarce and frequently ambiguous, these archeological data may also testify to the growing importance of aquatic resources by the mid-Upper Paleolithic. Direct archeological evidence for aquatic resource exploitation during this time period is still comparatively rare, partly because of the taphonomic challenges of attributing small animal remains to human consumers, but also because small game use has been a low priority in archeological research.

It remains possible that a sampling bias is responsible for the differences we see between our Middle Paleolithic and mid-Upper Paleolithic samples. One is more likely to find evidence for significant exploitation of aquatic resources among those populations that lived in close proximity to maritime, riverine, or lacustrine habitats. Only the Paviland 1 skeleton, of the humans sampled by our study, could be said to have lived close to a marine shoreline, and this aspect of the sample is particularly difficult to evaluate. However, two of the five Neandertal specimens, both from Marillac, lived near an inland riverine habitat (the Tardoire). Among the early modern humans analyzed, those from Dolní Věstonice, Kostenki, and Mal'ta lived close to riverine habitats (the Dyje, the Don, and the Angara, respectively). A Kruskal–Wallis test of the pooled Neandertal and early modern human sample, using proximity to aquatic resources as an indicator variable, provides a $P = 0.109$. It is therefore unlikely that the stable isotope distinction between the consumption of inland aquatic resources by European Neander-

tal and early modern human samples is solely because of geographic sampling bias.

The stable isotope data thus indicate a categorical shift in the importance of aquatic resources in human diets by the mid-Upper Paleolithic. The frequent exploitation of freshwater habitats in particular seems to reflect a trend toward a broader diet base. Consistent with zooarcheological observations for southern Europe and western Asia (2), this process was both more pronounced and began earlier than was thought (cf. 60–63). Recent zooarcheological and isotope findings therefore enlarge the temporal window of what has been called the "Broad Spectrum Revolution" (64). Subsequently, humans exploited fish, shellfish, and certain other small animals even more within the Epipaleolithic and Mesolithic (e.g., ref. 11) periods, and thus their remains are more visible archeologically toward the end of the Pleistocene.

Another implication of the isotope and zooarcheological findings is that Neandertals exploited small animals less consistently in much of Europe. Easily collected small animals such as tortoises and, along coastlines, shellfish certainly were parts of Middle Paleolithic diets in the Mediterranean Basin, where small-animal diversity and abundance tends to be high. But these early foragers tended not to consume quick-moving small animals. Because large game are less biologically productive than small, quick terrestrial game animals, Neandertals would have been more susceptible to seasonal and annual resource fluctuations, a pattern reflected in their paleopathological (65) and mortality distributions (66). Generally low population densities are indicated by the Middle Paleolithic zooarcheological evidence (2). The apparent increase in the exploitation of aquatic resources and quick terrestrial small game before the Last Glacial Maximum could therefore be associated with Upper Paleolithic human population growth.

Conclusions

The stable isotope analysis of early modern human skeletal remains documents a significant shift in faunal exploitation patterns by the mid-Upper Paleolithic based on significant use of freshwater aquatic resources, evidence for an increase in dietary breadth. This trend is correlated with, and probably interrelated with, elaborations in material culture during the mid-Upper Paleolithic, including lavishly decorated burials, abundant personal ornamentation, ceramic figurines, and textiles of knotted cord. Whatever the interrelationships of these cultural evolutionary processes prove to be, the apparently broader dietary spectrum of the early modern human economy may have rendered humans more resilient to natural pressures and the increasingly packed social environments of Late Pleistocene Europe.

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