Isotopic evidence for the diets of European Neanderthals and early modern humans

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We report here on the direct isotopic evidence for Neanderthal and early modern human diets in Europe. Isotopic methods indicate the sources of dietary protein over many years of life, and show that Neanderthals had a similar diet through time (≈120,000 to ≈37,000 cal BP) and in different regions of Europe. The isotopic evidence indicates that in all cases Neanderthals were top-level carnivores and obtained all, or most, of their dietary protein from large herbivores. In contrast, early modern humans (≈40,000 to ≈27,000 cal BP) exhibited a wider range of isotopic values, and a number of individuals had evidence for the consumption of aquatic (marine and freshwater) resources. This pattern includes Oase 1, the oldest directly dated modern human in Europe (≈40,000 cal BP) with the highest nitrogen isotope value of all of the humans studied, likely because of freshwater fish consumption. As Oase 1 was close in time to the last Neanderthals, these data may indicate a significant dietary shift associated with the changing population dynamics of modern human emergence in Europe.

Europe | isotopes | collagen | fishing

Isotope evidence is a powerful tool for reconstructing past human diets and subsistence adaptations (1–3), and it has been applied to a number of Neanderthals and early modern humans from Europe (4–12). In 2 earlier studies (10, 11), we argued that Neanderthals had relatively uniform dietary adaptations while early modern humans in Europe had more variable isotope values—and therefore diets—than the Neanderthals. Specifically, we proposed that a number of European early modern humans had higher nitrogen isotope values than any Neanderthal and that these values likely indicated that some of these humans were obtaining much of their protein from aquatic resources, namely freshwater fish (11). This interpretation was largely based on the similarity of these isotope values to those of freshwater fish consumers from Mesolithic Eastern Europe (13, 14). We further postulated that the isotope evidence demonstrated a shift to a broader dietary spectrum by early modern humans (11), which probably included small game, in addition to fish, an inference supported by the faunal evidence (15, 16). Since that study, there have been more isotopic studies of Neanderthals (5–9) and early modern humans (4, 17, 18). Importantly, we present here previously unrecorded isotopic data from an early modern human from the Peçstera cu Oase (4), which overlaps in time with the last Neanderthals (19), allowing us a direct comparison between Neanderthal and modern human diets when they were both present in Europe. Below, we summarize the current isotopic evidence for Neanderthal and modern human diets and suggest that the previously unrecorded data support our original inference that there was a shift in dietary spectra between the Neanderthals and early modern humans in Europe.

Isotopic Analysis. Carbon and nitrogen stable isotope ratios of adult human bone collagen are indicators of the main sources of dietary protein consumed over a number of years (20, 21). Carbon isotope ratios (δ^{13}C values) can indicate if the source of dietary protein was from marine resources or terrestrial resources (22, 23), as there is an ≈7 per mil (‰) shift between dissolved ocean bicarbonate and atmospheric carbon dioxide (the main respective sources of carbon for plants in each ecosystem) (24, 25). Therefore, exclusively marine consumers, such as seals, have δ^{13}C values of –12 ± 1‰, and this value is relatively constant around the world, including in the oceans surrounding Europe (26). Terrestrial consumers have δ^{13}C values close to –20 ± 2‰, depending on the region (27). Organisms in freshwater ecosystems generally have carbon values similar to terrestrial values, but these values are highly variable because dissolved carbon in rivers and lakes can derive from many geological sources with differing carbon isotope ratios (27, 28). Carbon isotope values can also be used to discriminate between the consumption of C_3 and C_4 photosynthetic pathway plants (29); however, there were no edible C_4 plants in Europe during the Late Pleistocene.

Nitrogen isotope ratios (δ^{15}N values) of human bone collagen are between 3 to 5‰ higher than dietary protein (30, 31). This "trophic level effect" is widely used in archeology and modern ecology as a means to determining the positions of organisms in food webs, particularly for identifying the prey species of carnivores as well as the diets of omnivores, such as humans (27). The basis of this pattern is that plants obtain nitrogen from the soil or atmosphere (24), and in Holocene Europe plants generally had δ^{15}N values of between 0 and 2‰. Herbivores that consume plants have body protein (flesh and bone collagen) that is 3 to 5‰ higher than the plants (i.e., 3 to 7‰). Carnivores that consume those herbivores have bone collagen nitrogen isotope values that are again 3 to 5‰ higher than the herbivores (i.e., 6 to 12‰). Omnivore values can fall between the ranges of carnivore and herbivore values depending on the amount of plant vs. animal protein in their diets. Therefore, by comparing the isotope values of omnivores such as humans to the isotope values of herbivores and carnivores from the same site or region, we can determine whether they obtained their proteins from mainly animal sources (carnivore-like) or plant sources (herbivore-like), or a mix of both. The same process applies in aquatic (freshwater and marine) ecosystems. However, as there are often many more steps in the food chain in aquatic ecosystems, top-level aquatic consumers often have much higher δ^{15}N values [i.e., seals have δ^{15}N values of 18 to 20‰ (26)] than their terrestrial counterparts [i.e., wolves generally have values between 10 and 12‰ (9)].

A confounding factor in the use of stable isotope analysis to reconstruct past diets is that carbon and nitrogen isotope values vary between different geographical regions, especially related

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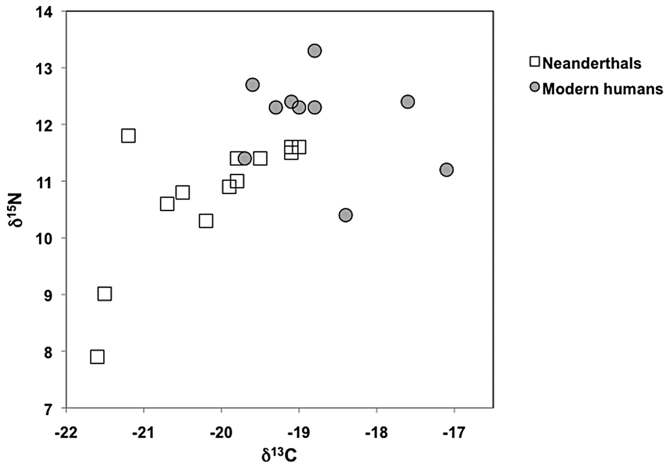

Fig. 1. Carbon and nitrogen isotope values of bone collagen from Neanderthals and early modern humans from Europe. Errors on the isotope measurements are typically ±0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$.

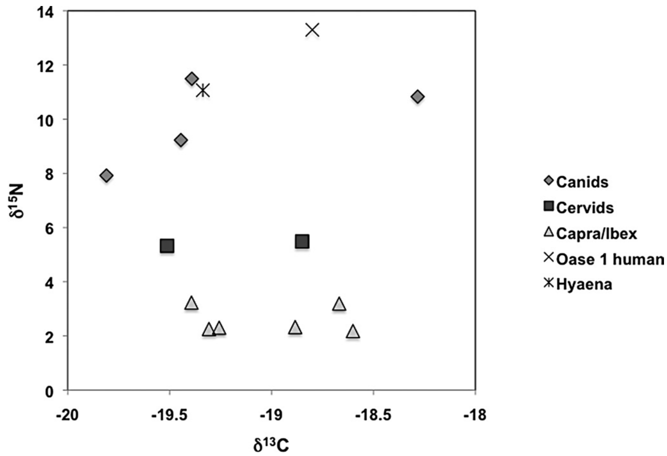

Fig. 2. Carbon and nitrogen isotope data for the Oase 1 human and associated fauna taken from Trinkaus et al. (4) and the present study. Errors on the isotope measurements are typically ±0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$.

to temperature and aridity (24, 32, 33). In Europe, the climate is relatively similar so, to date, there have not been any observed large-scale differences in carbon and nitrogen isotopes of herbivores and carnivores across Europe, especially in the Holocene [where most of the application of isotope analysis has occurred (34)]. However, the climate has changed considerably in the past, and it now appears that these climate changes had an effect on isotope values, especially during and just after the Late Glacial Maximum, when herbivores had $\delta^{15}N$ values of ≥3‰ lower than in the preceding marine isotope stage (MIS) 3 and subsequent Holocene period (34–36). Of note here is that these studies did not observe a significant increase in $\delta^{15}N$ values in the period from 50,000 to 25,000 cal BP. However, the fauna in these studies was exclusively from Northern Europe, and mostly from the United Kingdom, so it is not a valid comparative framework for Eastern and Southern Europe. Regardless, to best interpret human carbon and nitrogen isotope values we should compare the human isotope values to the isotope values of associated fauna that are as close in time and space as possible, and ideally from the same site and stratigraphic context.

Results

Neanderthal Isotope Values. There are currently 13 $\delta^{13}C$ and $\delta^{15}N$ values for European adult Neanderthals [Fig. 1 and supporting information (SI) Table S1] . These Neanderthals range in age from ≈120,000 BP (Scladina) to ≈37,000 cal BP (Vindija), but most of them are <50,000 cal BP. We have excluded the Engis juvenile Neanderthal (8), as there are a number of physiological effects on juvenile isotopic values, such as breastfeeding and weaning (37–39), and therefore juvenile data cannot be directly compared with adult values. Following Bocherens et al. (9), we have excluded 2 of the Neanderthals from Les Pradelles (Marillac) (12), as they apparently have poor collagen preservation (40). Additionally, as we are focusing only on Europe, we do not include the Siberian Okladnikov Neanderthal ($\delta^{13}C$ = –19.1‰, $\delta^{15}N$ = 12.9‰) (41).

The carbon isotope values for all of the Neanderthals (see Fig. 1 and Table S1) are all <–19‰, indicating that dietary protein was from terrestrial sources. Therefore, there is no evidence that marine foods (which have higher $\delta^{13}C$ values, ≈–12 ± 1‰) were consumed in any significant quantities by these Neanderthals, few of which were in close proximity to coastlines.

Because of the potentially fluctuating faunal isotope values over this time period [for which we do not have the baseline faunal data that we do for later periods (34)], we cannot directly compare these Neanderthal nitrogen isotope values to each other. However, in each analysis in which the Neanderthals were compared to contemporary faunal isotope values from the same site or contemporary adjacent sites, the conclusions were the same. Each Neanderthal had $\delta^{15}N$ values that were 3 to 5‰ higher than contemporary herbivores and similar to carnivores (or in some cases slightly higher). In each study, the authors concluded that Neanderthals were top-level carnivores and that their main protein source was large herbivores.

Early Modern Human Isotope Values. There are 14 modern humans from the European earlier (Early and Mid) Upper Paleolithic (MIS 3) that have carbon isotope values, and 10 which have both carbon and nitrogen isotope values (see Fig. 1, Table S2) . The Oase 1 modern human is the oldest directly dated modern human in Europe [≈40,000 cal BP (42)] and the only one in our study that overlaps in time with Neanderthals. The other early modern humans from the Early- to Mid-Upper Paleolithic with isotopic values date to between ≈34,000 and ≈27,000 cal BP and are (or are likely to be) associated with late Aurignacian or especially Gravettian technology.

The Oase 1 human carbon and nitrogen values are plotted with isotope results from associated faunal remains in Fig. 2. The human and faunal remains were largely recovered from surface deposits in the cave, and therefore represent a range of time periods dating to between ≈50,000 (wolf, hyena, and red deer) and ≈20,000 (ibex) cal BP (43). The herbivore isotope values are similar, despite their likely range of ages. The highest wolf $\delta^{15}N$ value is 11.5‰, which is 8.9‰ higher than the *Capra* (ibex) (average 2.6 ± 0.5‰) and 6.1 ‰ higher than the *Cervus* (red deer) (average 5.4‰), while a hyena has a value of 11.1‰, which is 8.5‰ higher than the ibex and 5.7‰ higher than the deer. As there is an enrichment of between 3 to 5‰ in $\delta^{15}N$ between prey and consumer, the wolves and the hyena were likely obtaining most of their protein from the red deer and not the ibex at this site. In contrast, Oase 1 has a $\delta^{15}N$ value (13.3‰) that is 10.8‰ higher in $\delta^{15}N$ than the ibex and 8.0‰ higher than the red deer. The enrichment between both herbivores and Oase 1 is far beyond the 3 to 5‰ trophic level effect in $\delta^{15}N$. The Oase I $\delta^{15}N$ value is also above those of the hyena (11.1‰), and the highest wolf value (11.5‰) from the same site and dating to about the same time. Therefore, Oase 1 must have obtained a significant portion of its protein from a different ecosystem, for which the best candidate is freshwater fish.

Further evidence for the use of aquatic foods by early modern

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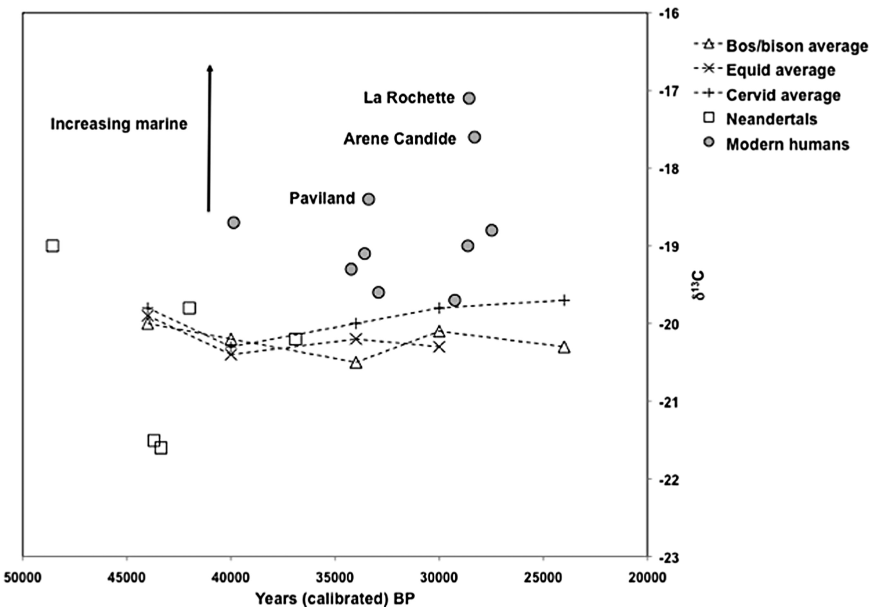

Fig. 3. $\delta^{13}C$ bone collagen values of directly radiocarbon-dated Neanderthals and early modern humans compared to the average $\delta^{13}C$ values of directly radiocarbon-dated herbivores from Northern Europe (34) over the period 50,000 to 20,000 cal BP.

humans comes from the isotope values of 2 later coastal Mid Upper Paleolithic modern humans, Arene Candide IP from coastal Italy (18) and La Rochette 1 from further inland in France (44). Both of these individuals have carbon isotope values >–18‰, which indicate that they consumed significant (i.e., 20–30% of dietary protein) amounts of marine foods, probably high trophic level (carnivorous) fish or marine mammals. These values are evident in a plot of $\delta^{13}C$ values of the Neanderthals and early modern humans (Fig. 3) that have direct radiocarbon dates, combined with the $\delta^{13}C$ values compiled in a large-scale survey of directly radiocarbon-dated European faunal isotope values (34). These 2 humans have very different carbon isotope values from all of the other early modern humans from Europe and all of the Neanderthals (see Fig. 1, Tables S1 and S2), and the associated faunal data shows that there was no unrecognized shift in terrestrial $\delta^{13}C$ values at this time. Therefore, these 2 individuals most likely consumed significant amounts of marine protein. This interpretation is also supported by the associated high $\delta^{15}N$ values (12.4‰ for Arene Candide IP, 11.2‰ for La Rochette 1), as the $\delta^{13}C$ values of marine food consumers are correlated with an increase in $\delta^{15}N$ values (26, 45).

The other early modern humans all have $\delta^{13}C$ values <–18.5‰ (see Fig. 1 and Table S2), which indicate that their protein came from terrestrial C_3 (or freshwater) foods, yet many of them have high $\delta^{15}N$ values, at or above the highest Neanderthal values. To best interpret these high human $\delta^{15}N$ values, they should be compared to associated faunal remains. However, in contrast to the Neanderthals, very few of these humans have associated faunal isotope values. This situation is partly because of the nature of their discovery and excavation, as many of them are from deliberate burials, were not found in association with fauna, and were excavated in the 19th or early 20th century without associated faunal remains or have isotopic data from direct radiocarbon dating. Unfortunately, unlike the $\delta^{13}C$ values, we cannot use the average faunal $\delta^{15}N$ values in studies of directly radiocarbon dated fauna from this period, as these data are exclusively from Northern Europe and so cannot be compared to humans from Southern and Eastern Europe (contra ref. 46). Nonetheless, a plot of those faunal $\delta^{15}N$ data with the human values (Fig. 4) shows no consistent shift across mammalian families in average $\delta^{15}N$ values.

The Eel Point 1 human from South Wales has a $\delta^{15}N$ value of 11.4‰. This value can be compared to those of approximately contemporary fauna from the nearby site of Paviland (47). Two bison bones from Paviland have an average $\delta^{15}N$ value of 8.4‰. The $\delta^{15}N$ value of Eel Point 1 is 3‰ higher than the average $\delta^{15}N$ values of these 2 herbivores, which is within the 1 trophic level increase range. Therefore, Eel Point 1 most likely obtained most of its dietary protein from herbivores, such as bison and horse. The human has very different carbon isotope values than a contemporary brown bear ($\delta^{13}C$ = –17.3‰, $\delta^{15}N$ = 11.3‰), which likely consumed marine foods such as salmon.

The human from Paviland itself has a lower $\delta^{15}N$ value (10.4‰) than Eel Point 1 and also has a more positive $\delta^{13}C$ value (–18.4‰). This human was originally interpreted as having a minor, but detectable, contribution of marine protein in its diet (47). Redating of Paviland 1 to ≈33,000 cal BP (48) means that we can now compare the human isotope values to fauna dating to an earlier period. There are 3 faunal bone samples dating to ≈33,000 to ≈34,000 cal BP, a fox ($\delta^{13}C$ = –19.6 ‰, $\delta^{15}N$ = 9.4‰), a bison ($\delta^{13}C$ = –19.9‰, $\delta^{15}N$ = 6.2‰), and a brown bear ($\delta^{13}C$ = –18.8‰, $\delta^{15}N$ = 10.6‰). The fox and bison have terrestrial $\delta^{13}C$ values, so there is no unusual effect at this site and time to explain the more positive $\delta^{13}C$ values of Paviland 1. Therefore, based on both the $\delta^{13}C$ and $\delta^{15}N$ values of Paviland 1, this human likely had a marine component in its diet, and indeed it has isotope values similar to the contemporary brown bear that was likely to have been a marine consumer.

Several other Early Upper Paleolithic humans have high $\delta^{15}N$ values, higher than any of the Neanderthals (see Fig. 1, Table S1 and S2). These high values may, similar to Oase, indicate the consumption of freshwater foods, but without comparative faunal isotope values it is not possible to definitively conclude this inference. Yet, if we compare the 3 other humans from Romania, Muierii 1 and 2, and Cioclovina 1, with $\delta^{15}N$ values of 12.3‰, 12.4‰, and 12.7‰, respectively (average: 12.5‰), with the herbivore values from Oase, they are ≈10‰ higher than the ibex and 7‰ higher than the deer. Likewise, if we compare the $\delta^{15}N$ values of the 2 humans from the Czech

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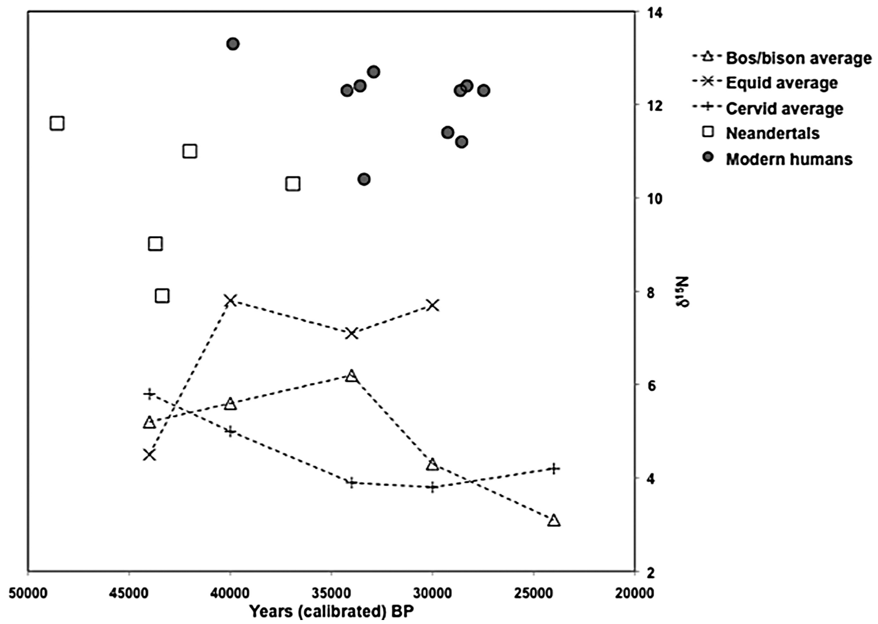

Fig. 4. $\delta^{15}N$ bone collagen values of directly radiocarbon-dated Neanderthals and early modern humans compared to the average $\delta^{15}N$ values of directly radiocarbon dated herbivores from Northern Europe (34) over the period 50,000 to 20,000 cal BP.

republic (Dolní Věstonice 35 and Brno-Francouzská 1), both of which have $\delta^{15}N$ values of 12.3‰, with the single, contemporary, herbivore bone from Brno-Francouzská ($\delta^{15}N$ value of 5.2‰) (4), the humans are 7.1‰ higher than the herbivore from Brno-Francouzská. In both of these cases the humans have $\delta^{15}N$ values that are more than the observed trophic level effect (3–5‰); an explanation may be the inclusion of significant amounts of freshwater resources in their diets. However, these interpretations are preliminary until associated faunal values can be obtained from these 4 sites.

Discussion

Isotopic analysis provides information about the sources of dietary protein over a number of years, even though it does not measure the caloric contributions of different foods. As the method only measures protein intake, many low-protein foods that may have been important to the diet (i.e., high caloric foods like honey, underground storage organs, and essential mineral and vitamin rich plant foods) are simply invisible to this method. There are high-protein plant foods in Europe that Neanderthals and early modern humans could have consumed, such as hazelnuts [commonly consumed in the Mesolithic (49)] that would have been visible in the isotopic analyses, but they are simply not seen. Another important consideration is that this method tracks the bulk protein consumption over a number of years, and provides an average and proportional measure of the protein sources. Therefore, the occasional consumption of resources like fish or marine mammals by Neanderthals (i.e., once a month, 1 month a year) would be largely invisible to this method. Indeed, it is evident that Neanderthals sometimes consumed aquatic resources (50), although the isotope evidence shows that it was not likely to have been an important part of their diet across Neanderthal populations.

Despite these caveats, isotopic analysis is the only direct measure of the protein sources in past diets, and it allows reconstruction of this aspect of Neanderthal and early modern human diets in Europe. The isotopic evidence for Neanderthal diets is notable for its consistency. Although the Neanderthals that have been studied to date come from different regions of Europe and time periods, the isotopic data show that, in each case, they have $\delta^{15}N$ values between ≈3 and 5‰ higher than the local herbivores, and plot close to carnivores from the same or nearby sites. These higher $\delta^{15}N$ values indicate that European Neanderthals had similar dietary adaptations.

Early modern humans in Europe have a more varied range of isotopic values that indicates that some of them consumed significant quantities of aquatic foods, both from freshwater and marine sources. The only human contemporary with the Neanderthals that currently provides isotopic data, Oase 1, has $\delta^{15}N$ values that are the highest of all of the modern humans and higher than all of the Neanderthal values.

The isotope data agree well with results from faunal analyses. Studies of animal remains from Neanderthal sites in Europe have repeatedly shown that Neanderthals consistently hunted large herbivores (51, 52), including seasonal use of reindeer (53). Yet, there is little evidence for the use of small game such as birds or fish (4, 51, 54). Early modern humans also appear to have regularly hunted large herbivores (55–57), but there is also evidence for the use of small game, including fish at some of these sites (15, 16).

The observed isotope difference between Neanderthals and early modern humans may therefore indicate that there were dietary spectra differences between MIS 3 modern humans in Europe and the Neanderthals. Modern humans may well have had a broader dietary spread than Neanderthals, but we need more data from areas where Neanderthals and modern humans overlapped to confirm this inference. It is nonetheless clear that modern humans, in the relatively short period covered by this study (40,000 to 27,000 cal BP), were exhibiting a wide range of diets, while the Neanderthals seem to have had the same general dietary adaptation throughout a much longer time range (120,000 to 37,000 cal BP).

Why do we see these dietary differences between Neanderthals and modern humans in Europe? It is tempting to see the difference as being somehow cognitive, in that Neanderthals were unable to alter their (albeit very successful) subsistence strategies, whereas modern humans were more creative and were able to exploit resources more than the Neanderthals. However, the difference need not be cognitive and instead an increased flexibility in modern human diets could be part of the techno-

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logical and organizational package that allowed the widespread expansion of modern humans out of Africa into Europe ≈40,000 years ago. Indeed, the first clear evidence for the regular use of marine resources comes from modern humans in Africa only after the middle stone age/late stone age transition ≈40,000 BP (58), although, as in Europe, there is scattered earlier evidence of fish consumption in Africa (59). Therefore, the differences in diets may simply be linked to adaptive and technological changes between these 2 time periods, and their cultural complexes, probably analogous to the clear dietary changes from marine to terrestrial foods at the Mesolithic to Neolithic transition in Northern Europe (60, 61). Moreover, the relatively rapid dispersal of modern humans into most of Europe and the evidence for limited if widespread assimilation of Neanderthals into those populations (62) imply markedly higher effective population sizes of those early modern humans. Larger modern human populations may well have promoted the variable exploitation of a broader range of resources, ones requiring greater effort or technological investment for their acquisition.

Stable isotope analysis is therefore a powerful method for reconstructing aspects of past diets, and it has been especially useful in determining the protein sources in Neanderthal and early modern human diets in Europe. There are now enough isotopic data to see patterns in the data, and they show that the Neanderthals and early modern humans had similar dietary adaptations, obtaining most of their dietary protein from animals, although some of the early modern humans obtained significant amounts of their protein from aquatic, and not just terrestrial, sources. Ongoing work on Neanderthal and early modern human isotopic profiles will continue to test whether this difference is real; work in other regions with different available resources, such as the Mediterranean, Russia, and China, will test whether this pattern was more widespread. We will also soon be able to apply much needed new isotopic measurements to evaluate the evidence for the consumption of aquatic resources, such as single amino acid carbon isotope analysis (63) and sulfur isotope analysis (64–66).

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