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Environment and subsistence in north-western Europe during the Younger Dryas: An isotopic study of the human of Rhünda (Germany)

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ABSTRACT

The human skull of Rhünda in Central Germany is one of the rare human remains belonging to the cold episode of the Younger Dryas or GS-1 based on direct radiocarbon dating (10,200 ± 60 uncal BP GrA-15947). The return of periglacial conditions from northern France to northern Germany favoured the expansion of the reindeer herds, as testified by their numerous remains found at the Ahrensburgian sites. The isotopic composition of the collagen ($\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$) of the Rhünda individual provides insight into the relative dietary contribution of terrestrial ungulates, such as reindeer, compared to the intake of aquatic resources. The systematic higher $\delta^{13}C_{coll}$ values found for reindeer compared to horse during the Younger Dryas in northern Germany, the Ardennes and south-western England result from a different diet specialization, i.e. the high consumption of lichen by reindeer. The isotopic pattern evidenced in the Pleniglacial reflects such a niche partitioning, while the isotopic pattern of the Late-Glacial Interstadial reveals overlapping ranges in ^{13}C abundances in the different ungulates species, resulting most likely from a decrease in niche diversity. Despite their isotopic variability linked to trophic position and habitat, the freshwater fishes of the Belgian Ardennes show systematic higher $\delta^{15}N_{coll}$ values (6.6 to 11.7‰) than those of the terrestrial ungulates (<5‰) of the same region and surrounding areas. The high $\delta^{15}N_{coll}$ value of the Rhünda human (13‰) can thus be explained by an important consumption of freshwater resources, while the $\delta^{13}C_{coll}$ value (−20.5‰) is too low to consider a significant input of anadromous fishes and their marine-influenced isotopic signature. The application of a Bayesian model confirms this pattern with a minimum contribution of 40% of aquatic resources as protein source for the human diet. In contrast, the input of protein of terrestrial origin hardly exceeded 40% of horse and 20% of reindeer meat consumption. Although existing archaeological and isotopic evidence already suggests a significant use of aquatic resources during the Late-Glacial, the human of Rhünda illustrates an intensive exploitation of the freshwater ecosystem at a time and latitude where the access to palatable plants must have been challenging.

1. Introduction

The use of aquatic resources by hominid groups can be tracked back to the Early and Middle Pleistocene (e.g. Stewart, 1994; Joordens et al., 2009; Braun et al., 2010). The expansion of the diet to include aquatic components can be viewed as a valuable nutritional alternative, favouring brain development and cognitive capacities (e.g. Broadhurst et al., 2002; Cunnane and Stewart, 2010). In Europe, a significant intensification (or at least systematization) of the use of aquatic resources in coastal as well as in inland contexts is recognized in the late Upper Palaeolithic, especially during the last millennia before the onset of the Holocene, which correspond to the Late-Glacial (e.g. Aura et al., 1998, 2002; Adán et al., 2009; Le Gall, 1992; Van Neer et al., 2007).

The broadening of the diet spectrum may be linked to rapidly changing climate and environment with a period of global warming, the Late-Glacial Interstadial (or GI-1; ca. 14,700–12,850 cal BP), followed by one last important cold and arid event, the Younger Dryas (or GS-1, ca. 12,850–11,650 cal BP). The Interstadial witnessed in most parts of north-western Europe the replacement of the large herds of migrating reindeer by smaller groups of sedentary red deer (e.g. Sommer et al., 2008, 2014) and the development of light forest of *Pinus* and *Betula* in replacement of the *Artemisia* dominated steppe-tundra (e.g. Merkt and Müller, 1999; Litt et al., 2001; Ammann et al., 2013; Mortensen

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et al., 2015). This dramatic change could have led the human population to adapt their subsistence strategies by broadening their food resource spectrum (e.g. Le Gall, 1992) and exploiting their environment on a reduced territory (e.g. Aura et al., 1998; Debout et al., 2012).

In contrast, the Younger Dryas favoured the re-expansion of the steppe plant species such as Graminea and *Artemisia* (e.g. Merkt and Müller, 1999; Litt et al., 2001; Ammann et al., 2013), even if they did not necessarily re-occupy former forested areas under more continental conditions (Theuerkauf and Joosten, 2012). The impact of the Younger Dryas was far more pronounced in the higher latitudes of France, Benelux and Germany, regions where the return of periglacial conditions, including permafrost re-expansion, induced the return of reindeer herds in steppe-tundra landscape (e.g. Renssen and Vandenberghe, 2003; Benecke, 2004). Reindeer seemed to significantly contribute to the subsistence of hunter-gatherers of the Ahrensburgian culture in northern Germany and Belgium (Baales, 1996; Bratlund, 1996a), in southern England (Lewis and Rackham, 2011), and potentially in the area of the Dry North Sea. On the other hand, the discovery of fishhooks from northeast Germany and its surroundings directly dated to the Younger Dryas period (Hanik, 2009; Gramsch et al., 2013) raises the question of the exploitation of fish.

Due to its low archaeological visibility, the consumption of fish and other aquatic prey has been investigated using direct trackers such as carbon and nitrogen isotope abundances in bone collagen (e.g. Richards et al., 2001; Drucker and Henry-Gambier, 2005; Bocherens et al., 2007). Indeed, the $\delta^{13}C$ and $\delta^{15}N$ values of the collagen reflect those of the consumed food, especially those with high protein content (Ambrose and Norr, 1993; Tieszen and Fagre, 1993; Jim et al., 2004). Since the plant tissues have lower nitrogen content than animal meat (1% of nitrogen in terrestrial plants against 14% in animal meat; Phillips and Koch, 2002), their impact on the ^{13}C and ^{15}N abundances of the human consumers is not significant unless they represent more than 50% in weight of the diet (see Bocherens, 2009). Interestingly, the majority of modern hunter-gatherers derives 55 to 65% of their food from animal products (Cordain et al., 2000). As a result, the ^{13}C and ^{15}N abundances in collagen of ancient hunter-gatherers inform us on the origin of the animal protein they foraged over the last years of the individual's life (e.g. Hedges and Reynard, 2007; Bocherens, 2009), such as aquatic vs. terrestrial. Indeed, for a comparable trophic position, specimens from an aquatic ecosystem deliver higher ^{15}N abundances than specimens from terrestrial context (e.g. Schoeninger and DeNiro, 1984; Richards and Hedges, 1999; Dufour et al., 1999).

Here we present the results of $^{13}C_{coll}$ and $^{15}N_{coll}$ abundances of the human specimen of Rhünda from Central Germany. The isotopic analysis of this individual provides an insight into the relative consumption of aquatic to terrestrial resources and thus connects archaeological evidences and the use of the exploited resources at an individual scale during the Younger Dryas in north-western Europe. To this aim, we examined the $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values of faunal remains from archaeological sites as close as possible to the location and dating of the human of Rhünda. An isotopic enrichment in bone collagen of about 0.8 to 1.3‰ in $\delta^{13}C$ values and of 3 to 5‰ in $\delta^{15}N$ values is expected between a consumer and the consumed prey (Bocherens and Drucker, 2003). On the other hand, the isotopic signature of the potential preys depends on their dietary preferences and habitat conditions (e.g. Drucker et al., 2003; Stevens and Hedges, 2004). Hence, the isotopic values obtained on terrestrial herbivores are useful not only as comparative data to reconstruct the diet of the human of Rhünda, but also to reconstruct aspects of the ecosystem of the Younger Dryas.

2. Material and methods

The human of Rhünda was found as an isolated skull on the bank of the river of the same name in Hesse (Germany) after a violent storm in June 1956 (Fig. 1). After being first attributed to a female Neanderthal (Jacobshagen, 1957), the morphological reconstruction by Heberer and Kurth (1963) confirmed that this adult specimen belonged to the species *Homo sapiens*, possibly from the Postglacial period based on indirect dating of surrounding sediment due to the lack of archaeological artefacts (ca. 9000 uncal BP; Jacobshagen et al., 1962). More recently, direct AMS dating was conducted directly on the skull (Rosendahl, 2002) and placed this individual in the Younger Dryas with a result of 10,200 ± 60 uncal BP GrA-15947 (11,695–12,127 cal BP using Calib 7.1 programme based on Intcal13 calibration curve Reimer et al., 2013). A piece of ca. 0.5 g was taken for stable isotope investigation.

We extended the isotopic data set of herbivore collagen of the Younger Dryas of north-western Europe that consisted of seven specimens of reindeer *Rangifer tarandus* (Drucker et al., 2011) and one remain of bison *Bison bonasus* (Bocherens et al., 2015b) directly dated (10,070 ± 50 uncal BP KIA-3331–11,343–11,828 cal BP; Benecke, 2004), all of them coming from the site of Stellmoor in northern Germany (Fig. 1). Additional isotopic data are available for the GS-1 based on direct dating of one horse from Koslar and one reindeer from Kartstein in the Rhineland region, western Germany (Bronk Ramsey et al., 2002; Stevens and Hedges, 2004; Stevens et al., 2008). Several bone remains of horse *Equus* sp. were sampled from the Ahrensburgian assemblage of Stellmoor (n = 4; Bratlund, 1996a), as well as from the Hamburgian occupation of the neighbouring site of Meiendorf (n = 4; Bratlund, 1996b). One of the Ahrensburgian horse (ATV-5 in Table 1) was dated to 10,150 ± 40 uncal BP KIA-48960 (11,690–12,022 cal BP; this work). The additional reindeer bones and one mandible fragment of horse were obtained from the site of Remouchamps located in the Belgian Ardennes (Fig. 1), which provided a significant Ahrensburgian assemblage (Dewez collection; Dewez, 1974). Finally, we selected one horse metapodial from Nichet 2 at Fromelennes (Ardennes, France) that was directly dated to the Younger Dryas chronozone (Bridault, pers. Comm., 2010).

Isotopic analyses of archaeological fish remains are challenging due to their poorer state of preservation in comparison to mammal remains (e.g. Szpak, 2011; Fuller et al., 2012). As a result, higher amounts of bone are necessary for collagen extraction. Unfortunately, small numbers of fish remains are generally present as it is the case of the site of Stellmoor (Heinrich, 2001). So far, the closest geographical and temporal fish material that could be retrieved for this study was coming from the Magdalenian layers of several Belgian sites (Bois-Laiterie, Trou du Sureau, Trou du Frontal, Trou de Chaleux; Van Neer et al., 2007; Fig. 1) corresponding to the early Late-Glacial phase of the end of the cold GS-2a stadial, slightly predating the GI-1e (Sano et al., 2011). The isotopic analyses of three specimens of Atlantic salmon *Salmo salar* from Trou du Frontal were published in Bocherens et al. (2014). Besides some Cyprinidae that could not be identified at the species level (n = 3), we had access to several other species: burbot *Lota lota* (n = 4), nase *Chondrostoma nasus* (n = 1), pike *Esox lucius* (n = 3), and brown trout *Salmo trutta fario* (n = 5). The remains are of anthropogenic origin and come from large individuals with minimum length sizes of 30 cm for the burbot, nase and brown trout, 40 cm for the pike and Cyprinidae, 70 cm for the Atlantic salmon (Van Neer et al., 2007). The represented species include those encountered in the context of the Younger Dryas in northern Germany: mainly pike and burbot at Stellmoor (Heinrich, 2001), mainly pike at Wustermark 22 (Gramsch et al., 2013). When possible, we used a single bone of a given fish species, but in some cases several pieces were combined to obtain the 0.5 g necessary for the collagen extraction.

Collagen was extracted from human and faunal samples following a protocol based on Longin (1971) and modified by Bocherens et al. (1997). In brief, the extraction procedure includes a step of demineralization in HCl 1 M, a step of soaking in 0.125 M NaOH, and a final step of solubilization in acidified water (pH = 2) before the freeze-drying process. The elemental analyses (C_{coll}, N_{coll}) and isotopic measurements ($\delta^{13}C_{coll}$, $\delta^{15}N_{coll}$) were conducted at the Department of Geosciences of Tübingen University using a NC2500 CHN-elemental analyser coupled to a Thermo Quest Delta + XL mass spectrometer. The international

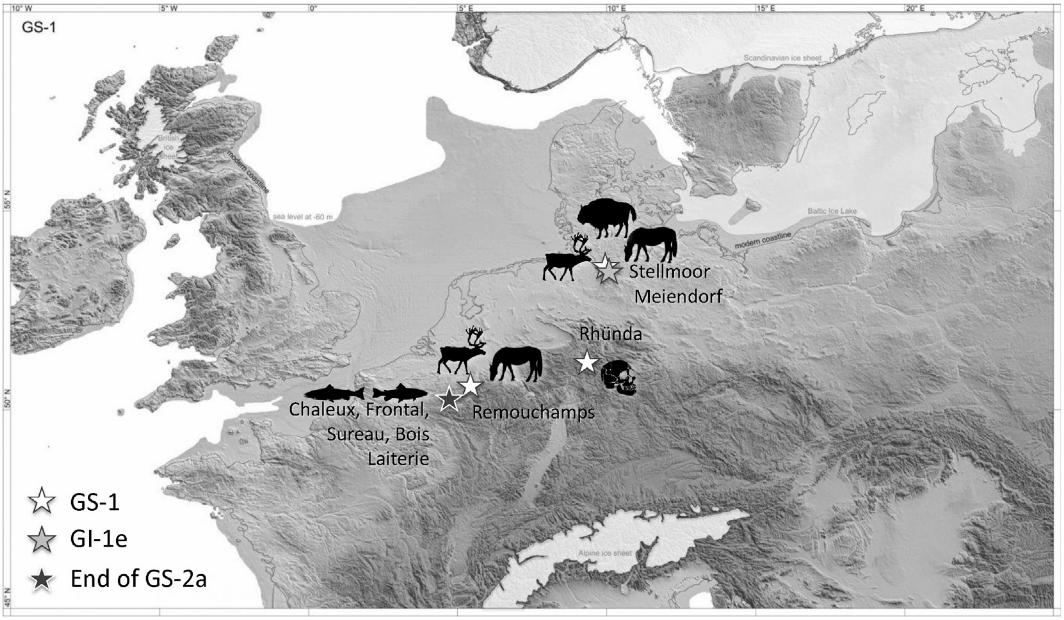

Fig. 1. Geographical location of the archaeological sites with faunal and human remains analysed for this work. Map compiled by Grimm (2009) after Wolstedt (1956), Björck (1995), Konradi (2000), Boulton et al. (2001), Lundqvist and Wohlfarth (2001), Bourillet et al. (2003), Lericolais et al. (2003), Weaver et al. (2003), Evans et al. (2004), Ivy-Ochs et al. (2006), and Gupta et al. (2007).

standards are a marine carbonate (V-PDB) for $\delta^{13}C$ and atmospheric nitrogen (AIR) for $\delta^{15}N$. Measurements were normalized to $\delta^{13}C$ values of USGS24 ($\delta^{13}C = -16.00‰$) and to $\delta^{15}N$ values of IAEA 305A ($\delta^{15}N = 39.80‰$). Analytical error, based on within-run replicate measurement of laboratory standards (albumen, modern collagen, USGS 24, IAEA 305A), was $\pm 0.1‰$ for $\delta^{13}C$ values and $\pm 0.2‰$ for $\delta^{15}N$ values. Reliability of the $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values can be established by measuring the chemical composition of collagen, with C/N_{coll} atomic ratio ranging from

Table 1
Results of the stable isotope analyses of collagen ($\delta^{13}C_{coll}$, $\delta^{15}N_{coll}$) of the remains of reindeer (*Rangifer tarandus*), horse (*Equus* sp.) and bison (*Bison bonasus*) of the Younger Dryas in Germany (Stellmoor), Belgian Ardennes (Remouchamps) and French Ardennes (Nichet 2).

Site	Lab n°	Species	Anatomical part	C_{coll} (%)	N_{coll} (%)	C/N_{coll}	$\delta^{13}C_{coll}$ (‰)	$\delta^{15}N_{coll}$ (‰)	Reference
Stellmoor	RA-STA 11	Reindeer	Tibia	46.1	15.9	3.4	−18.0	2.2	Drucker et al. (2011)
Stellmoor	RA-STA 12	Reindeer	Tibia	40.9	14.0	3.4	−18.3	1.4	Drucker et al. (2011)
Stellmoor	RA-STA 13	Reindeer	Tibia	45.0	15.9	3.3	−18.2	2.1	Drucker et al. (2011)
Stellmoor	RA-STA 14	Reindeer	Tibia	41.7	15.5	3.1	−17.5	1.6	Drucker et al. (2011)
Stellmoor	RA-STA 15	Reindeer	Tibia	45.8	16.1	3.3	−17.8	1.2	Drucker et al. (2011)
Stellmoor	RA-STA 16	Reindeer	Tibia	47.5	15.9	3.5	−18.2	1.6	Drucker et al. (2011)
Stellmoor	RA-STA 19	Reindeer	Tibia	48.0	16.8	3.3	−17.8	2.1	Drucker et al. (2011)
Remouchamps	REM-3	Reindeer	Calcaneum	47.4	16.2	3.4	−18.9	3.1	This work
Remouchamps	REM-4	Reindeer	Left metacarpal	43.4	15.0	3.4	−18.3	2.5	This work
Remouchamps	REM-5	Reindeer	Left metatarsal	38.7	13.4	3.4	−19.2	2.4	This work
Remouchamps	REM-6	Reindeer	Metapodial	42.5	15.0	3.3	−18.3	1.9	This work
Remouchamps	REM-7	Reindeer	Right metacarpal	42.4	15.1	3.3	−18.9	1.9	This work
Remouchamps	REM-8	Reindeer	Left metatarsal	40.9	14.6	3.3	−18.1	1.9	This work
Remouchamps	REM-9	Reindeer	Left metatarsal	38.1	13.5	3.3	−18.9	1.9	This work
Remouchamps	REM-10	Reindeer	Right tibia	42.6	15.1	3.3	−19.1	2.5	This work
Remouchamps	REM-11	Reindeer	Right tibia	42.2	15.0	3.3	−18.2	2.0	This work
Remouchamps	REM-12	Reindeer	Right tibia	43.0	15.3	3.3	−18.7	2.9	This work
Remouchamps	REM-13	Reindeer	Right tibia	41.4	14.8	3.3	−17.6	2.1	This work
Remouchamps	REM-14	Reindeer	Mandible	43.0	15.3	3.3	−18.4	3.5	This work
Remouchamps	REM-15	Reindeer	Left metacarpal	41.2	14.8	3.2	−18.2	1.3	This work
Remouchamps	REM-16	Reindeer	Right metacarpal	40.7	14.5	3.3	−18.8	2.4	This work
						Average	−18.4	2.1	
						SD	0.5	0.6	
Stellmoor	ATV-5	Horse	Left rib	40.2	14.1	3.3	−21.9	2.9	This work
Stellmoor	ATV-6	Horse	Left rib	39.8	13.8	3.4	−21.8	3.0	This work
Stellmoor	ATV-7	Horse	Left metatarsal	41.3	14.4	3.3	−21.4	3.9	This work
Stellmoor	ATV-8	Horse	Third phalanx	42.4	14.8	3.3	−21.5	3.4	This work
Remouchamps	REM-1	Horse	Mandible	40.9	14.2	3.4	−21.5	4.4	This work
Le Nichet-2	NIC-1	Horse	Metapodial	42.9	14.7	3.4	−20.9	4.3	This work
						Average	−21.5	3.7	
						SD	0.4	0.7	
Stellmoor	BIS-13	Bison	Skull	41.0	14.3	3.3	−19.7	2.8	Bocherens et al. (2015b)

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2.9 to 3.6 (DeNiro, 1985) and percentage of C_{coll} and N_{coll} above 8% and 3% respectively (Ambrose, 1990).

The relative contribution of the different food categories to the average diet of the human of Rhünda was simulated using a Bayesian mixing model performed in the SIAR package (Parnell et al., 2010), using R software, version 3.1.3 (R Core Team, 2013). The SIAR package is based on a Bayesian inferences approach that takes into account the uncertainties in the input parameters such as the isotopic variation within sources, and in the trophic fractionation. The model provides not only the range of possible contribution of the different tested dietary sources but also the probability distribution of the estimated proportions. We followed the Trophic Enrichment Factor (TEF) of $+1.1 \pm 0.2$‰ and $+3.8 \pm 1.1$‰ for $\delta^{13}C$ and $\delta^{15}N$ values, respectively (Table 2 in Bocherens et al., 2015a).

3. Results and discussion

3.1. Terrestrial resources

During the GS-1, the reindeer and horse showed distinct $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values in the northern lowlands of Germany (Fig. 2a; Table 1) as well as in the French and Belgian Ardennes (Fig. 2b; Table 1). The reindeer had higher $\delta^{13}C_{coll}$ (-18.3 to -17.5‰) and lower $\delta^{15}N_{coll}$ values (1.2 to 2.2‰) than those of the horse (-21.4 to -19.8‰ for ^{13}C, 1.5 to 2.7‰ for ^{15}N). The same isotopic pattern was observed in the Ardennes, where the reindeer $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values varied from -19.2 to -17.6‰ and 1.3 to 3.5‰ respectively, while the horse showed lower $\delta^{13}C_{coll}$ (-21.5 and -20.9‰) and higher $\delta^{15}N_{coll}$ values (4.3 and 4.4‰). The $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values of the reindeer of Kartstein (-17.6‰ and 2.5‰) and the horse of Koslar (-21.4‰ and 3.3‰) in the Rhineland clustered in the same range as their respective species from the Ardennes (Fig. 2b). Moreover, we considered the isotopic data measured on reindeer and horse from south-western England dated to the GS-1 (Stevens and Hedges, 2004; Jacobi and Higham, 2009; Fig. 2c). The difference in $\delta^{13}C_{coll}$ values was comparable (reindeer: -18.6 to -18.3‰; horse -21.9 to -21.1‰), but the relatively high $\delta^{15}N_{coll}$ values of reindeer (3.7 to 4.6‰) placed them in a range comparable to the horse of the same region (2.0 to 4.5‰).

Niche partitioning could explain such a significant discrepancy between reindeer and horse, with the specific consumption of lichen by the reindeer providing the species with relatively high ^{13}C abundances (e.g. Fizet et al., 1995; Bocherens, 2003; Drucker et al., 2003). Lower consumption of grasses may explain the lower ^{15}N abundance observed in reindeer collagen in northern Germany and the Ardennes compared to the horse of the same regions and the reindeer of south-western England. Indeed, graminoids (grasses and *Carex*) provide forage enriched in ^{15}N abundances in comparison to shrubs and trees (see review in Drucker et al., 2012). Another reason could be linked to the variable ^{15}N abundances found in lichen relative to the vascular plants of the same subarctic ecosystem: intermediate to grasses and shrubs in Barnett (1994), comparable to shrub leaves in Griffith et al. (2002), lower than all the other plants in McLeman (2006).

The significant ^{13}C discrimination among large herbivores related to diet specialization is typical feature of the Pleniglacial ecosystem (e.g. Bocherens, 2003, 2015; Drucker et al., 2003; Fox-Dobbs et al., 2008). In addition to the results described above, the bison specimen of the Ahrensburgian level of Stellmoor exhibited a $\delta^{13}C$ value different from those of the reindeer and horses of the same site (-19.7‰; Table 1). We concluded that the ecosystem of the Younger Dryas is characterized by the same niche partitioning among large ungulates as it was the case in the mammoth steppe of the Pleniglacial, when the diversity of the mega-herbivores was larger.

The high consumption of lichen by the reindeer of the GS-1 illustrates the return to cold tundra-like environment during this cold phase. In contrast, the warmer and wetter conditions of the Late-Glacial Interstadial, which were unfavourable to lichen development, are reflected in the relatively low ^{13}C abundances in reindeer collagen of the northern German lowlands (Drucker et al., 2011; Fig. 2d). Our results on the reindeer from the Rhineland and the Ardennes confirmed that the GS-1 $\delta^{13}C$ values were higher than those obtained for the GI-1e (Germonpré et al., 2009; Stevens et al., 2009; Fig. 2e). Again, the reindeer dated to the Late-Glacial Interstadial from the Somerset region in England (Jacobi and Higham, 2009; Stevens et al., 2010; Fig. 2f) revealed lower ^{13}C abundances than their Younger Dryas counterparts.

In the three considered regions, the $\delta^{13}C$ values of the reindeer were close to, if not overlapping with, those of the horse, due not only to the relative ^{13}C-depletion in reindeer but also to the relative ^{13}C-enrichment in horses. In northern Germany, the $\delta^{13}C_{coll}$ values of GI-1e horses of Meiendorf varied from -21.4 to -19.8‰ (Table 2). The ^{15}N abundances were also lower than those found for the species in

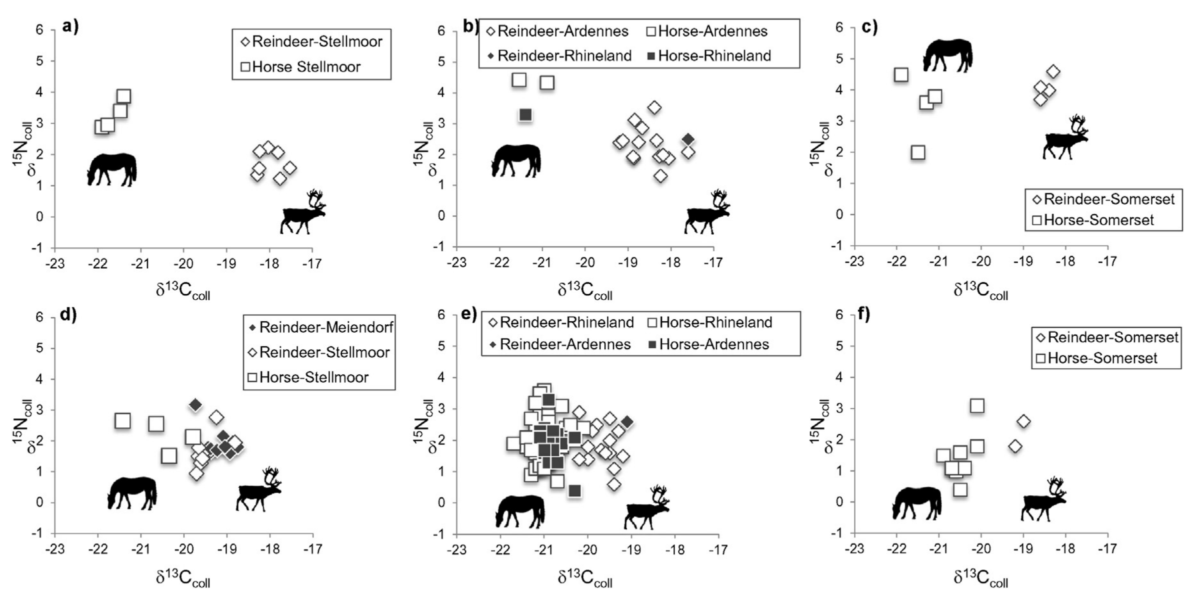

Fig. 2. Measured $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values on reindeer (*Rangifer tarandus*) from northern Germany during (a) the Younger Dryas (Drucker et al., 2011; this work) and (d) the Late-Glacial Interstadial (Drucker et al., 2011; this work), the Ardennes and the Rhineland during (b) the Younger Dryas (this work) and (e) the Late-Glacial Interstadial (Germonpré et al., 2009; Stevens et al., 2009), Southwestern England during (c) the Younger Dryas (Stevens and Hedges, 2004; Jacobi and Higham, 2009) and (f) the Late-Glacial Interstadial (Stevens and Hedges, 2004; Jacobi and Higham, 2009).

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Table 2
Results of the stable isotope analyses of collagen ($\delta^{13}C_{coll}$, $\delta^{15}N_{coll}$) of the horse (*Equus* sp.) of the Late-glacial Interstadial at Meiendorf (northern Germany). The carbon and nitrogen composition of the collagen is given through elemental composition (C_{coll}, N_{coll}) and atomic ratio (C/N_{coll}).

Site	Lab n°	Species	Anatomical part	C_{coll} (%)	N_{coll} (%)	C/N_{coll}	$\delta^{13}C_{coll}$ (‰)	$\delta^{15}N_{coll}$ (‰)
Meiendorf	ATV-1	Horse	Left rib	42.3	14.7	3.4	−20.4	1.5
Meiendorf	ATV-2	Horse	Left rib	40.5	14.1	3.3	−20.7	2.6
Meiendorf	ATV-3	Horse	Right rib	41.4	14.6	3.3	−19.8	2.1
Meiendorf	ATV-4	Horse	Left femur	39.1	13.7	3.3	−21.4	2.7

the Younger Dryas, with $\delta^{15}N_{coll}$ values between 1.5 and 2.7‰ (Table 2). The isotopic data collected from south-western England in Jacobi and Higham (2009) indicated the same tendency, where horse $\delta^{13}C$ values were closer to those of the reindeer because of the isotopic shift of both species between the Late-Glacial Interstadial and the Younger Dryas. During the warmer phase of the Late-Glacial, the spectacular reduction of the range of ^{13}C abundances in large herbivores, which results in some overlap between the species, can be viewed as a decrease in niche diversity leading to increased competition for food and habitat (e.g. Immel et al., 2015).

3.2. Aquatic resources

The analyses of Magdalenian fish of the Belgian Ardennes reflected a high variability in the values of $\delta^{13}C_{coll}$ (−24.1 to −18.7‰) and $\delta^{15}N_{coll}$ (6.6 to 11.7‰) of freshwater resources (Fig. 3; Table 3). The isotopic differential between freshwater and anadromous fish species has been demonstrated, the latter having higher ^{13}C abundances averaging −14.1‰, while their ^{15}N abundances (9.5 to 10.0‰) were comprised in the range observed in freshwater environments. The marine diet and habitat of these anadromous salmonids where they spend most of their life is reflected in their collagen isotopic signature, while the freshwater ecosystem where they spawn has little impact since they generally stop feeding at that time. Among the freshwater species, some differences among fish species are suspected with the pike exhibiting among the highest $\delta^{15}N_{coll}$ values (8.1 to 10.6‰) in accordance with his trophic position as a top carnivore (e.g. Craig, 2008; Fuller et al., 2012). Some of the cyprinids also have relatively high $\delta^{15}N_{coll}$ values, no doubt because they are large mature individuals of between 40 and 60 cm standard length (Häberle et al., 2015). The burbot provided among the lowest $\delta^{13}C$ values (−24.1 to −21.8‰), whereas the brown trout gave among the highest $\delta^{13}C_{coll}$ values (−20.5 to −18.7‰), for $\delta^{15}N$ values ranging from 6.6 to 10.5‰ and 8.7 to 9.4‰ respectively. Diet does not differ significantly between the two species. Thus, the ^{13}C partitioning may be due to contrasting conditions in their respective habitat. A more benthic habitat is generally associated with higher ^{13}C abundances in algae (e.g. France, 1995). The mature burbot occurs in the deeper zones of the lakes and rivers, which seems contradictory to its relatively low ^{13}C abundances; however, they move to shallow inshore parts for feeding (e.g. Fischer and Eckmann, 1997). The brown trout lives in shallow waters until it gets older and larger and then prefers deeper zones, which may be reflected by their rather high $\delta^{13}C$ values. On the other hand, high variability of isotopic signatures depending on the lacustrine system was demonstrated for the same fish species (e.g. Dufour et al., 1999; Katzenberg and Weber, 1999). It is therefore difficult to assign a specific habitat (deep vs. shallow; lake vs. river) from the isotopic values of the collagen.

The comparison between the Late-Glacial fish from the Belgian Ardennes and from south-western France revealed a comparable range of isotopic signature. The measured range on the freshwater specimens of Belgium encompassed the values found at Pont d'Ambon where the freshwater $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values plotted between −23.7 to −20.8‰ and 6.6 to 9.5‰, respectively, for a period ranging from the Late-Glacial to the early Holocene (Drucker and Bocherens, 2004). The salmonids of Pont d'Ambon clustered close to the anadromous fishes of the Belgian Ardennes ($\delta^{13}C = -16.1$‰; $\delta^{15}N = 12.1$‰). The eel from the late Mesolithic site of Noyen-sur-Seine provided $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values which are also included in the range of variation of the Belgian freshwater fishes. Altogether, the ^{13}C and ^{15}N abundances of a given species of fish are comparable between the Magdalenian Belgian sites and other areas in north-west Europe of later chronological phases. Excluding slight differences between locations and time periods, the

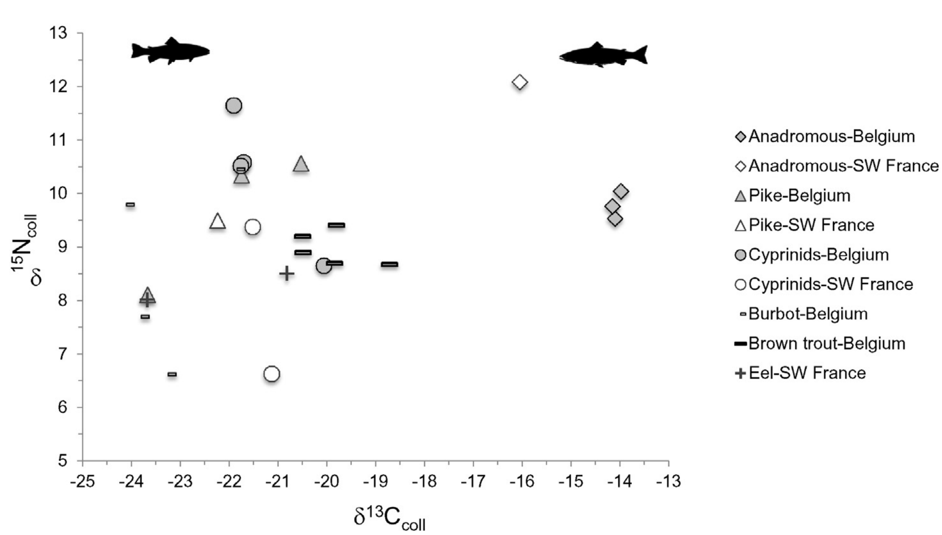

Fig. 3. Measured $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values on fish of the Belgian Ardennes (Bois-Laiterie, Trou du Sureau, Trou du Frontal, Trou de Chaleux; this work) compared to those obtained on fish from south-western France (Pont d'Ambon; Drucker and Bocherens, 2004).

Table 3
Results of the stable isotope analyses of collagen ($\delta^{13}C_{coll}$, $\delta^{15}N_{coll}$) of the Late-Glacial fish remains of Belgium. The carbon and nitrogen composition of the collagen is given through elemental composition (C_{coll}, N_{coll}) and atomic ratio (C/N_{coll}).

Species	Anatomical part	C_{coll} (%)	N_{coll} (%)	C/N_{coll}	$\delta^{13}C_{coll}$ (‰)	$\delta^{15}N_{coll}$ (‰)	Reference
Burbot *Lota lota*	Vertebra	26.2	9.5	3.2	−23.2	6.6	This work
Burbot *Lota lota*	Vertebra	33.3	12.4	3.1	−21.8	10.5	This work
Burbot *Lota lota*	Bones	32.5	12.1	3.1	−24.1	9.8	This work
Burbot *Lota lota*	Vertebra	14.8	5.6	3.1	−23.8	7.7	This work
Nase *Chondrostoma nasus*	Bones	40.5	15.4	3.1	−20.1	8.7	This work
Brown trout *Salmo trutta fario*	Vertebra	37.0	12.2	3.5	−18.7	8.7	This work
Brown trout *Salmo trutta fario*	Vertebra	36.9	13.1	3.3	−20.5	9.2	This work
Brown trout *Salmo trutta fario*	Vertebra	38.6	13.6	3.3	−19.8	9.4	This work
Brown trout *Salmo trutta fario*	Vertebra	35.6	12.8	3.2	−20.5	8.9	This work
Brown trout *Salmo trutta fario*	Vertebra	27.0	9.9	3.2	−19.8	8.7	This work
Pike *Esox lucius*	Bone piece	39.5	13.5	3.4	−20.5	10.6	This work
Pike *Esox lucius*	Bone piece	40.3	14.2	3.3	−23.7	8.1	This work
Pike *Esox lucius*	Vertebra	31.1	11.1	3.3	−21.7	10.3	This work
Cyprinidae	Bone piece	43.3	15.8	3.2	−21.9	11.7	This work
Cyprinidae	Vertebra	42.1	15.2	3.2	−21.7	10.6	This work
Cyprinidae	Vertebra	41.5	14.2	3.4	−21.8	10.5	This work
				Average	−21.5	9.4	
				SD	1.6	1.3	
Salmon *Salmo salar*	Vertebra	37.2	13.7	3.2	−14.1	9.5	Bocherens et al. (2014)
Salmon *Salmo salar*	Vertebra	37.2	14.1	3.1	−14.0	10.0	Bocherens et al. (2014)
Salmon *Salmo salar*	Vertebra	40.1	14.8	3.2	−14.2	9.8	Bocherens et al. (2014)
				Average	−14.1	9.8	
				SD	0.1	0.3	

overall range obtained in the Belgian Ardennes can be considered as representative of the expected range for aquatic resources in the continental context of the Late-Glacial.

3.3. Diet of the human of Rhünda

Diet reconstruction based on collagen $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values of ancient hunter-gatherers aims to define the averaged isotopic signature of potential preys, namely faunal remains of close chronological and geographical origin to the human individual. In the case of the human of Rhünda, we considered the large herbivores of the Younger Dryas occupations of the northern lowlands of Germany and the Ardennes region of Belgium and France. The fish specimens of the Belgian Ardennes provided the best reference for freshwater food despite their older age. As expected, the terrestrial resources represented by horse, bison and reindeer showed a significant overlap in the $\delta^{13}C_{coll}$ values but lower $\delta^{15}N_{coll}$ values than those of the freshwater fishes (Fig. 4). None of the analysed ungulates provided a $\delta^{15}N$ value higher than 5‰, an upper limit that would be maintained if we included the reindeer of the Rhineland and south-western England regions (Stevens and Hedges, 2004; Stevens et al., 2008; Jacobi and Higham, 2009). In these ecosystems and in case of a terrestrial-dominated diet, we expected a $\delta^{15}N_{coll}$ value of the human of Rhünda not higher than 10‰. The measured value of 13‰ (Table 4) implied the consumption of high ^{15}N resources from an aquatic ecosystem. The $\delta^{13}C_{coll}$ of −20.5‰ (Table 4) corresponded to an average diet value of ca. -21.5‰, which excluded marine influenced resources such as the

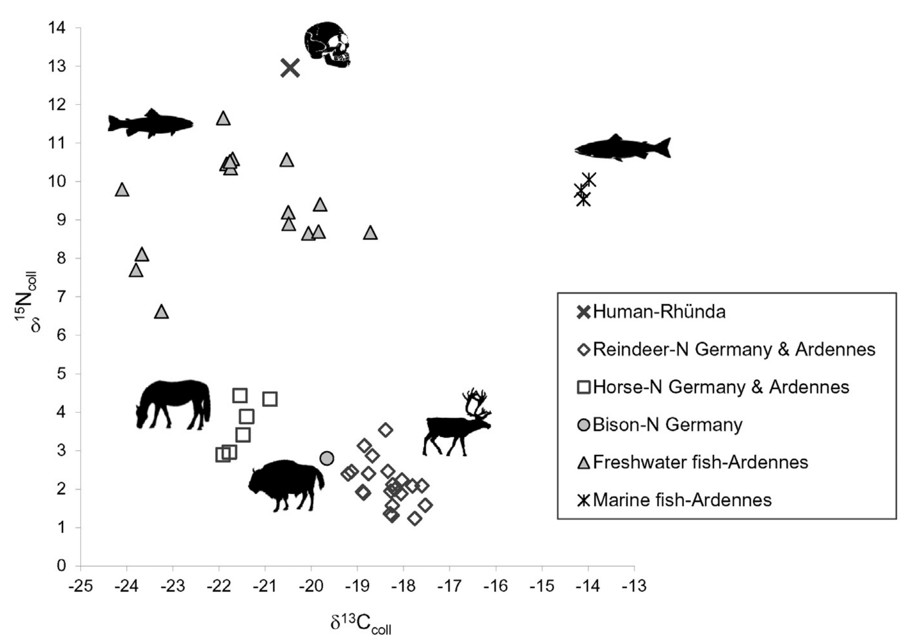

Fig. 4. Measured $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values on the human of Rhünda, reindeer of Remouchamps (n = 14) and Stellmoor (n = 7), horse of Stellmoor (n = 4), Remouchamps (n = 1) and Le Nichet 2 (n = 1), bison of Stellmoor (n = 1; Bocherens et al., 2015b) and fish of the Belgian Ardennes (n = 19).

Table 4
Results of the stable isotope analyses of collagen ($\delta^{13}C_{coll}$, $\delta^{15}N_{coll}$) of the Younger Dryas human of Rhünda (Germany). The carbon and nitrogen composition of the collagen is given through elemental composition (C_{coll}, N_{coll}) and atomic ratio (C/N_{coll}).

Site	Lab n°	Species	Anatomical part	C_{coll} (%)	N_{coll} (%)	C/N_{coll}	$\delta^{13}C_{coll}$ (‰)	$\delta^{15}N_{coll}$ (‰)
Rhünda	RHU-1	Human *Homo sapiens*	skull	37.2	12.5	3.5	−20.5	13.0

anadromous fish. The isotopic signature of the individual of Rhünda pointed clearly to a very high consumption of freshwater resources.

The relative contribution of reindeer, horse, freshwater and anadromous fish as food resources were tested using the Bayesian model SIAR. The results of the simulation pointed to a maximum of 20–30% of contribution of reindeer or anadromous fish, while the most likely scenario was the absence of these food sources in the human diet (Fig. 5). The proportion of horse in the diet may have been as high as ca. 40%. In contrast, the possible contribution of the freshwater resources ranged from ca. 40 to 90% and the most likely proportion was around 75% (Fig. 5). The relatively low contribution of the reindeer over averaged years to the subsistence of the human of Rhünda fits the hypothesis of a seasonal consumption of reindeer in contrast to a subsistence pattern based on herd-following strategy all over the year (see discussion in Gronnøw, 1985; Bratlund, 1996a; Baales, 1996). The seasonal access to reindeer was in this case complemented by the exploitation of the freshwater ecosystem. Access to fish is easiest during their reproduction season, i.e. winter for the salmonids and spring/early summer for the cyprinids (Fig. 4 in Van Neer et al., 2007).

Only few human remains associated with the Younger Dryas have been studied for isotopes so far (see Table 5). In Southern Italy, the Grotta del Romito provided a Late-Glacial context with remains of individual Romito 5, dated to 10,862 ± 70 (LTL-3033A), from the rockshelter zone (Craig et al., 2010). The isotopic signature of this individual ($\delta^{13}C_{coll} = -19.7$‰, $\delta^{15}N_{coll} = 9.3$‰) is similar to that of the other remains dated to Late-Glacial Interstadial at Romito. Despite the close proximity to the coast, a terrestrial-based diet can be considered, since the animal $\delta^{15}N_{coll}$ range from ca. 4 to 6‰ (Craig et al., 2010). A significantly lower $\delta^{15}N_{coll}$ value of 6.8‰ has been found for the human skull of Balma Guilanyà in north-eastern Spain dated to 10,195 ± 255 uncal BP (Ua-34298) (Garcia-Guixé et al., 2009). However, the low $\delta^{15}N_{coll}$ values measured on a limited number of Late-Glacial red deer and wild goat (1.5 to 2‰) can explain this result; indeed, it is most probably linked to the high altitude of the site (1157 m a.s.l; Garcia-Guixé et al., 2009). Finally, one human remain of the Upper Palaeolithic site of Předmostí in the Czech Republic appeared to be far more recent than expected and can be added to the individuals contemporaneous to the GS-1 with a direct radiocarbon date of 10,675 ± 45

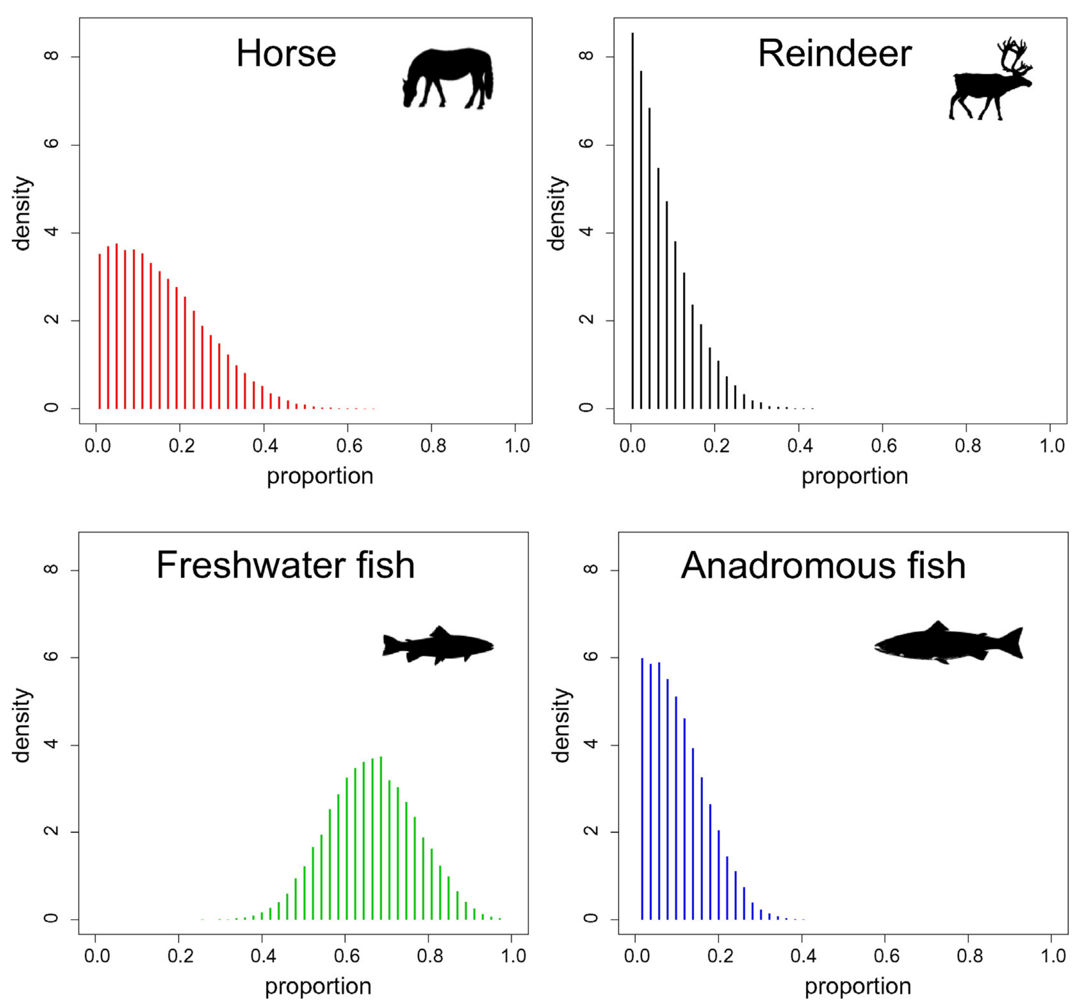

Fig. 5. Proportional contribution of the horse, reindeer, freshwater fish and anadromous fish plotted as histograms based on Bayesian model calculation in SIAR.

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Table 5
Summary of the diet reconstruction of human individuals of the Late-Glacial using stable isotope analyses of collagen.

Location	Context	Site	Period	Remain	Dominant diet	Reference
N Germany	Inland	Rhünda	GS-1	Adult skull	Freshwater	This work
S Italy	Inland	Grotta del Romito	GS-1	Adult femur	Terrestrial	Craig et al. (2010)
NE Spain	Inland	Balma Guilanyá	GS-1/PB	Adult skull	Terrestrial	Garcia-Guixé et al. (2009)
Czech Republic	Inland	Předmostí	GS-1	Adult femur	Terrestrial ?	Bocherens et al. (2015a)
S Italy	Inland	Grotta del Romito	GI-1a/c	Adult bone	Terrestrial	Craig et al. (2010)
Wales	Coastal	Kendrick's Cave	GI-1c	Adult mandible	Marine and freshwater	Richards et al. (2005), Bocherens and Drucker (2006)
SW France	Inland	Abri Faustin	GI-1e	Adult bone	Freshwater and marine	Drucker et al. (2005)
N Sicily	Coastal	San Teodoro	GI-1e	Bone, skulls	Terrestrial and freshwater	Mannino et al. (2011)
N Sicily	Coastal	Addaura Caves	GI-1e	Fibula	Terrestrial	Mannino et al., 2011
SW England	Inland	Gough's Cave, Sun. Hole 2	GI-1e	Adult bones	Terrestrial	Stevens et al. (2010)
N Italy	Inland	Riparo Tagliente	GS-2a	Adult rib	Freshwater	Gazzoni et al. (2013)
S Italy	Inland	Grotta del Romito	GS-2a	Adult bone	Terrestrial and freshwater	Craig et al. (2010)

uncal BP (OxA-37,382) and $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values of −20.1‰ and 9.7‰, respectively (Bocherens et al., 2015a). The lack of associated fauna does not allow for a detailed interpretation of the isotopic signature in terms of dietary habits. Thus, there has been no evidence of aquatic-dominated diet through stable isotope investigation for this period in time in Western Europe.

The $\delta^{15}N_{coll}$ value of 13‰ of the individual of Rhünda reflects a high consumption of freshwater aquatic resources, which so far that has not been directly seen in the Younger Dryas period, even though fishing activity can be suspected from archaeological findings, such as the fish-hooks from northern Germany (Gramsch et al., 2013). From an isotopic point of view, the individual of Riparo Tagliente in the inland context of Northern Italy resembles the case of Rhünda in its considerable freshwater resources consumption, however for a period predating the Late-Glacial Interstadial (end of GS-2a; Gazzoni et al., 2013). Even if less spectacular, the human remains of Romito 9 of roughly the same time also show a consumption of aquatic resources of freshwater origin (Craig et al., 2010). Interestingly, other coastal sites of the Late-Glacial period present isotopic evidence of freshwater dietary intake by human individuals, as seen at San Teodoro in Northern Sicily (Mannino et al., 2011) and Kendrick's Cave in Wales (Bocherens and Drucker, 2006). The Final Magdalenian human of the Abri Faustin can be added to this list as an example of aquatic-based diet in the inland context of south-western France (Drucker et al., 2005). In contrast, the humans dated to the Late-Glacial Interstadial from the Addaura Caves close to San Teodoro (Mannino et al., 2011), the Grotta del Romito in southern Italy (Craig et al., 2010) and the south-western England sites of Gough's Cave and Sun. Hole 2 (Stevens et al., 2010) have not revealed any significant input of aquatic resources in their diet. However, in the latter case of south-western England, the interpretation may be challenged by revisions not only of the radiocarbon dating but also of the stable isotope results on the human remains published by Jacobi and Higham (2009, 2011). Based on stable isotope and archaeological evidence, the high aquatic intake by the individual of Rhünda seems to be in accordance with the multiple indications for freshwater exploitation by the Late-Glacial humans in north-western Europe. Both during the Late-Glacial Interstadial and the Younger Dryas, aquatic consumption may have been more systematic in the north-western compared to the south-western parts of Europe.

4. Conclusions

The return of periglacial conditions in the northern lowlands of north-western Europe is attested archaeologically by the expansion of the reindeer herds. The systematically higher $\delta^{13}C_{coll}$ values of the reindeer during this period compared to the previous warmer episode confirms the dietary contribution of lichen, which had become more abundant as a result of the cold conditions. Reindeer remains are frequently found in the Younger Dryas sites; however, they represent a limited part of the diet of the human of Rhünda (20% maximum of the protein fraction), which is consistent with a seasonal consumption of this prey. Freshwater resources were the main protein source of the Rhünda individual. This seems to be in accordance with the archaeological evidence of aquatic exploitation in the Late-Glacial Interstadial, but is in contrast with the terrestrial-dominated diet demonstrated by stable isotope analyses on humans from more southerly sites. In the case of Rhünda, the impressive contribution of freshwater resources may be linked to its location at higher latitude compared to other contemporaneous sites. Modern hunter-gatherers at higher latitudes compensate for the low amount of edible plants by the exploitation of aquatic ecosystem (Cordain et al., 2000). Freshwater resources also appear to have been an important dietary component for Paleo-Inuits in subarctic environments at a time when the terrestrial megafauna was already extinct but when full access to marine resources was not yet established (Bocherens et al., in this volume). Following a comparable scenario, it can be speculated that, in the northern lowlands, the aquatic resources were used as an alternative during the last cold episode of the Late-Glacial, when the amounts of available ungulates and plant biomass were relatively low.

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