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Environment and human subsistence in Northern France at the Late Glacial to early Holocene transition

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Abstract

The Late Glacial and early Holocene (ca. 15,000–6,000 cal BP) witnessed major changes in the environmental conditions which led to the establishment of temperate vegetation and animal species, thereby offering new subsistence opportunities to the population of hunter-gatherers. Measurements of the relative abundances in ^{13}C and ^{15}N were applied to large herbivores from northern France to document the change in their habitat. During the early Holocene, red deer show a decrease in δ^{13}C values most likely reflecting the effect of a dense canopy and an increase in δ^{15}N values probably linked to the increased soil activity of soils in foraged territories. Aurochs and roe deer δ^{13}C values also revealed a more densely forested habitat at the end of the Preboreal, while the δ^{13}C values of the wild boar indicate dependence on fruits and underground tubers that were not affected by the canopy effect. Three human individuals from Val-de-Reuil and La Chaussée-Tirancourt dated to the Preboreal period provided relatively high δ^{15}N values when compared with the local fauna and other early Mesolithic humans, which might have resulted from the consumption of freshwater resources especially at Val-de-Reuil. The δ^{34}S values appear to depend more on the geographical location of the individual, as demonstrated by the difference among wild boar δ^{34}S values between sites, rather than related to the protein source of the diet, namely, terrestrial *versus* aquatic. Our results confirm the influence of the forest ecosystem on the environment and diet of the considered early Mesolithic human of northern France, while the possible contribution of the aquatic ecosystem still needs to be documented.

Keywords Preboreal · Northern France · Stable isotopes · Environment · Diet · Aquatic resources

Introduction

Over the past decades, the stable isotope analysis of bone collagen has become a common tool of investigation of the subsistence of ancient hunter-gatherers(e.g., Richards 2002;

Bocherens 2009; Schulting 2011). Periods of climatic and/or cultural changes have especially been explored through the isotopic reconstruction of human diet, such as the Mesolithic to Neolithic transition (e.g., Lubell et al. 1994; Lillie and Richards 2000; Richards et al. 2003; Bonsall et al. 2004;

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Bocherens et al. 2007; Fischer et al. 2007; Guiry et al. 2016). Indeed, the collagen ^{13}C and ^{15}N abundances of a consumer depend on those of their food with a factor of enrichment, which is limited in ^{13}C (ca. 1‰) but significant in ^{15}N (ca. 3 to 5‰) (e.g., Bocherens and Drucker 2003). Marine food resources are well characterized by higher ^{13}C and ^{15}N abundances than food products of continental origins (e.g., Schoeninger and DeNiro 1984). Freshwater resources may be detected through higher ^{15}N abundances than in terrestrial ones, while the ^{13}C abundances might provide overlapping ranges between the two sources (review in Guiry 2019). In the case of human consumers, the isotopic abundances of bone collagen can thus indicate the source of the dietary protein consumed over the last decade of their life (e.g., Hedges and Reynard 2007). More recently, the abundances in ^{34}S have been considered for dietary reconstruction since marine resources display higher ^{34}S than terrestrial ones (e.g., Richards et al. 2001). The freshwater resources, however, may or may not differ from the terrestrial ones depending on the context (e.g., Privat et al. 2007) and following a non-predictable pattern since the ^{34}S abundances in terrestrial resources depend on the geological context (review in Nehlich 2015). A very limited, if any, change in ^{34}S abundances has been detected between a consumer and its diet (e.g., Richards et al. 2001; Krajcarz et al. 2019).

Isotopic investigation of human diet and environment has only recently focused on the Late Glacial to early Holocene transition in Europe. It was a period of abrupt climatic change between the last cold spell of the Younger Dryas (or GS-1, ca. 12,800–11,600 cal BP) characterized by an open steppe tundra landscape and the start of the global warming of the early Holocene during the Preboreal (ca. 11,600–9900 cal BP). The increasing temperature and humidity allowed the development of a succession of forest formations (birch-pine woodland later replaced by broad-leaved forest) (e.g., Feurdean et al. 2014). This landscape development offered new opportunities for human subsistence through edible plants' elements, such as nuts and fruits; terrestrial preys such as red deer, roe deer, aurochs, wild boar, and elk; and productive aquatic ecosystems (e.g., Jarman 1972; Clarke 1976; Price 1987; Bridault 1994). Indeed, several zooarchaeology and stable isotope studies have revealed the importance of aquatic resources not only in coastal environments (Boethius et al. 2017) but also in inland contexts (Bazanella et al. 2007; Terberger et al. 2012, 2018; Drucker et al. 2016; Frontin 2017; Meadows et al. 2018). The estimation of the contribution of plants has been more elusive when considering bulk collagen, since plants provide far less protein than meat. Moreover, isotopic composition of vegetal dietary resources is not easy to reconstruct, since herbivorous animals reflect the consumption of other types of plants than those consumed by human individuals (see discussion in Bocherens 2009).

In this paper, we aim at documenting the impact of the climatic oscillations of the Late Glacial to the early Holocene on the habitat of large ungulates in northern France, and more specifically the red deer (*Cervus elaphus*), through the relative carbon-13 and nitrogen-15 abundances of their bone collagen. Such an investigation is also crucial to decipher the local isotopic baseline at the onset of the Holocene that will serve to interpret the isotopic composition of three human individuals from northern France. Direct dating of the animal specimens as well as the human individuals was also conducted to establish the chronological context. Finally, we applied sulfur-34 measurements to potentially gain more information on the diet and environment of the studied humans.

Material and methods

To reconstruct the local isotopic baseline in northern France over time, we identified and selected mature animal specimens. In a given site, when possible, the same anatomical part was preferred to avoid multiple sampling of the same individual (e.g., right metacarpus of aurochs from Belloy-sur-Somme). Organic preservation in the bone remains of the Somme Basin proved to be relatively poor, and only half of the initially selected samples provided collagen of required quantity and quality for the isotopic analyses. Altogether, we could retain 24 faunal samples, including red deer (*Cervus elaphus*, n = 13), wild boar (*Sus scrofa*, n = 4), roe deer (*Capreolus capreolus*, n = 3), aurochs (*Bos primigenius*, n = 2), large bovid (*Bos* or *Bison*, n = 1), and elk (*Alces alces*, n = 1) from archaeological sites located in the Thérain valley a tributary of the Oise river (Warluis) and in the Somme Basin (Hangest-sur-Somme, Belloy-sur-Somme, Conty, Saleux, Pont-de-Metz, and Blangy; Table 1, Fig. 1). All these 24 remains were directly dated in addition to the zooarchaeological analysis and stable isotope investigation. To document further the Preboreal chronozone at the onset of the early Holocene, we have also included previously published data of red deer (n = 1), wild boars (n = 4, 2 of them directly dated), and aurochs (n = 1, directly dated) from Henry-Farman, a Mesolithic site located in the Paris Basin (Leduc et al. 2013) in order to complete the terrestrial isotopic background. Remains of fish are very rare in northern France and generally post-date the Preboreal period, which could be due to the poor conditions of collagen preservation as observed on the mammal remains. In northern France, fish remains come mainly from Northern pike (*Esox lucius*) and European eel (*Anguilla anguilla*), as well as European perch (*Perca fluviatilis*) and cyprinids (*Cyprinidae*) (Marinval-Vigne et al. 1989; Ducrocq 2014). The fluviatile environment is dominated by peat deposit, and the aquatic ecosystem is highly influenced by terrestrial input and shows relatively low productivity. We thus used the

Table 1 List of the studied archaeological sites from northern France with number of human and animal specimens directly dated. * samples more specifically identified as aurochs

Town	Locality	District	Culture	N° lab	Human	Red deer	Wild boar	Roe deer	Large bovid	Elk
La Chaussée-Tirancourt	Le Petit Marais	Somme	Mesolithic	CTpm-	1	5				
Belloy-sur-Somme	La Plaisance	Somme	Mesolithic	BEL-		1			2*	
Saleux	La Vierge Catherine	Somme	Federmesser & Mesolithic	SA-		1		1		
Hangest-sur-Somme	Gravière I/II nord	Somme	Mesolithic	HI-/HII-		2				
Conty	Le Marais	Somme	Federmesser & Mesolithic	CTY-		2				
Blangy-Tronville	La Petite Tête	Somme	Mesolithic	BLA-			1			
Pont-de-Metz	Rue du Petit Saint-Jean	Somme	Mesolithic	PMZ					1	
Warluis	Merlemont	Oise	Mesolithic	WRL-		2	3	2		1
Val-de-Reuil	Les Varennes	Eure	Mesolithic	VAL-	2					
Paris	62 rue Henry-Farman	Paris	Mesolithic	PHF-			2		1*	

Mesolithic river fishes from Abri du Pape in Belgium (Drucker et al. 2018) and Friesack 4 in northern Germany (Meadows et al. 2018; Robson pers. comm. 2019) as proxies for the freshwater resources, since they correspond to the same Preboreal to Boreal chronology and aquatic environment (same fish species and ecological productivity) as for our studied context.

We investigated two human individuals from Val-de-Reuil "Les Varennes" and one from La Chaussée-Tirancourt "Le Petit Marais" (Fig. 1). The two individuals of Val-de-Reuil were excavated from two separate levels of the same burial pit. One (sujet A, sample 2050, VLR-1), a male adult, was found with its skeleton in articulation in context of a primary deposit (Billard et al. 2001). A second individual (sujet B, sample 2010, VLR-2) along with a third individual (sujet C) were present in the pit as scattered bones, resulting from previous inhumations manipulations. Sujet B (sample 2010, VLR-2) was also a mature adult, probably a man, while sujet C was a young adult or an adolescent of unidentified sex. Sujet B and sujet C were previously buried before their bones were

Fig. 1 Geographical location of the archaeological sites with faunal and human remains analyzed for this work
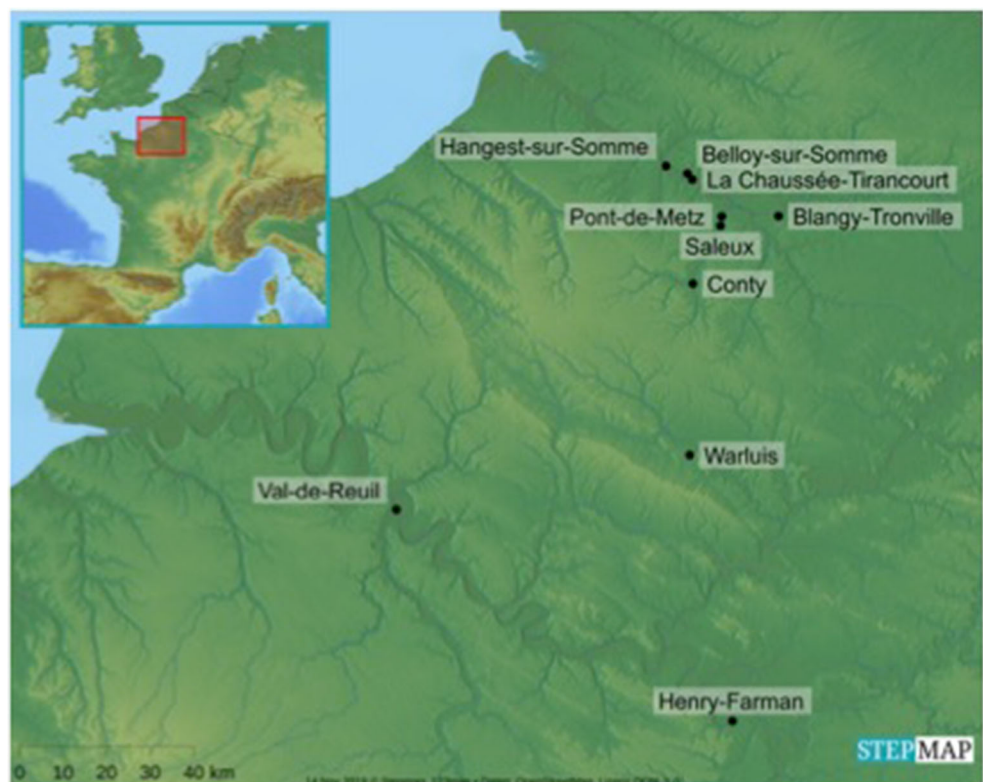
re-arranged to allow some space for the deposition of sujet A. A first dating attempt was conducted on a set of long bones from sujet A (8715 ± 310 BP Ly-6239; Billard et al. 2001). We present here the results of a new AMS radiocarbon dating on this individual and of sujet B. At La Chaussée-Tirancourt, the selected human corresponds to a male adult aged between 50 and 60 years old (Valentin 1995; Ducrocq et al. 1996) whose almost complete skeleton was deposited in a small pit (F4 structure) after some manipulation that resulted in a compact and sorted pile of the bones following a secondary burial process (Ducrocq et al. 1996). The individual was dated to 9020 ± 100 BP (GifA-95523) before a second AMS radiocarbon result of 9240 ± 45 BP was obtained from the same femur (SacA-23956; Ducrocq 2017).

At both Val-de-Reuil and La Chaussée-Tirancourt, animal remains were excavated. The faunal specimens at Val-de-Reuil were subjected to fire, and none of the attempts to retrieve collagen was successful due to destruction of the organic matter. At La Chaussée-Tirancourt, the animal bones were systematically dated to a later chronological phase, mainly Boreal, than the individual from structure F4 (Ducrocq 2017, this work). Thus, we could not retain the faunal remains coming directly from the sites to document the isotopic baseline for the human diet reconstruction.

Collagen extraction was conducted at the Department of Geosciences of Tübingen University following the protocol of Longin (1971) as 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, N) and isotopic measurements (δ^{13}C, δ^{15}N) were performed at the Institut des Sciences de l'Evolution of Montpellier 2 University in France on a CHN-elemental analyzer (Eurovector) coupled to a VG-Optima continuous-flow ratio mass spectrometer for one set of faunal specimens (WRL-1, CTpm-1 to CTpm-9, BEL-1, CTY2, SA-1, HI-1), and at the geochemical unit of the Geoscience Faculty at the University of Tübingen (Germany) using an elemental analyzer NC 2500 connected to a ThermoQuest Delta+XL mass spectrometer for the human individuals and another set of animal samples (WRL-6 to WRL-19, CTpm-10 to CTpm-17, BEL-3 and BEL-4, CTY4, SA-2, HII-2, PMZ-1, BLA-1). The isotopic ratios are expressed using the "δ" (delta) value as follows: $\delta^{13}C = [(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard} - 1] \times 1000‰$ and $\delta^{15}N = [(^{15}N/^{14}N)_{sample}/(^{15}N/^{14}N)_{standard} - 1] \times 1000‰$. The measurements were calibrated in reference to the international standards (V-PDB for carbon and AIR for nitrogen) using cane sucrose ($\delta^{13}C = -11.0‰$) and urea ($\delta^{15}N = -0.33‰$), USGS-24 ($\delta^{13}C = -16.0‰$), IAEA 305A ($\delta^{15}N = +39.8‰$), and in-house reference materials (modern collagen of camel and elk). Analytical precision, based on within-run replicate measurements of laboratory standards (egg albumin, keratin,

alanine amino acid, modern collagen), was ± 0.1‰ for δ^{13}C and ± 0.2‰ for δ^{15}N. The biochemical reliability of the collagen was estimated by considering the chemical composition, with C/N atomic ratio (C:N) ranging from 2.9 to 3.6 (DeNiro 1985) and percentages of C and N above 8% and 3%, respectively (Ambrose 1990). For radiocarbon dating, a C content equal or above 30% is recommended (van Klinken 1999).

Elemental and isotopic analysis of sulfur (S and δ^{34}S) were conducted at the Department of Geosciences of Tübingen University using a NC2500 CHN-elemental analyzer coupled to a ThermoQuest Delta + XL mass spectrometer. Samples were calibrated to δ^{34}S values relative to V-CDT using NBS 123 (δ^{34}S = 17.1‰), NBS 127 (δ^{34}S = 20.3‰), IAEA-S-1 (δ^{34}S = −0.3‰), and IAEA-S-3 (δ^{34}S = − 32.3‰). The reproducibility is ± 0.4‰ for δ^{34}S measurements, and the error on S measurement is 5 %. We retained δ^{34}S values of samples whose atomic C:S and N:S fit into the range of 300–900 and 100–300, respectively (Nehlich and Richards 2009), and whose percentage of S ranged from 0.14 to 0.26 %, as provided by modern mammalian collagen (Aldrich collagen, modern elk and modern camel) measured in the same sets. In the case of fish remains, the preservation criteria are different with C:S and N:S (C/S and N/S atomic ratios) that should fit into the range of 125–225 and 40–80, respectively, since their S content is higher than in mammalian collagen (ca. 0.40 to 0.85%) (Nehlich and Richards 2009).

To group the dietary resources in this study, we applied a multivariate cluster analysis to the δ^{13}C and δ^{15}N isotopic values, using the Ward's minimum variance method in JMP 14. This method is quite common for group formation in paleoecological stable isotope research (e.g., Bocherens et al. 2015; Wißing et al. 2019; Baumann et al. 2020). As a result, we obtained three different clusters of terrestrial resources and one of freshwater resources. We used the R package SIBER (Stable Isotope Bayesian Ellipses in R) following the protocol of Jackson et al. (2011) to check that the niches of the calculated diet resource groups do not overlap. On the one hand, we calculated the complete niche (convex hull; Layman et al. 2007) that includes all specimens of a source group and, on the other hand, we calculated the standard ellipse area (SEA) by using a most likelihood estimation. SEA explains 40% of the data and is recommended by Jackson et al. (2011) to decipher the core niche, which is still informative even with smaller sample sizes.

We simulated the possible proportions of different prey group in the protein fraction of the human diet using MixSIAR (Bayesian Mixing Models in R, Stock and Semmens 2016). The calculations of this package are based on a Bayesian statistical approach, which is quite robust for small sample sizes ($n < 20$) (Inger et al. 2010). To get a robust statistical analysis, we set the MCMC (Markov Chain Monte Carlo, see Stock and Semmens (2016) chain length to 1,000,000 with a burn-in of 500,000 in 3 chains. We verified

the model convergence with Gelman-Rubin and Geweke tests. The Gelman-Rubin test shows model convergence if the values are near 1. In most analyses, values below 1.1 are acceptable (Gelman et al. 2014). Additionally, the Geweke test compares the mean of the first part of each chain with the mean of the second part, using a two-sided z-test. If both means are the same, the model is convergent (Stock and Semmens 2016). MixSIAR allowed us to reconstruct the most likely diet of the different human individuals based on the bone collagen δ^{13}C and δ^{15}N values. The stable carbon and nitrogen isotope composition of a consumer is enriched from those of its prey in a predictable manner (e.g., Bocherens and Drucker 2003). Here, TEF values reflect the enrichment in ^{13}C and ^{15}N abundances in the collagen of the consumer compared with those of the collagen of the preys. For this study, we applied TEF of + 1.1 ± 0.2‰ and + 3.8 ± 1.1‰ for δ^{13}C and δ^{15}N values, respectively, as published in Bocherens et al. (2015).

Results and discussion

δ^{13}C and δ^{15}N values of the red deer over time in northern France

The δ^{13}C and δ^{15}N values of the bone collagen of the red deer ranged from − 23.7‰ to − 20.5‰ and from + 2.8 to + 6.4‰, respectively, during the early Holocene (Table 2). No specimens could be attributed to the last cold spell before the general warming of the Holocene, the so-called Younger Dryas or GS-1, leading to a gap in the chronological isotopic record (Table 2, Fig. 2), a situation that we also experienced with the red deer of the French Jura and western Alps (Drucker et al. 2011). A hiatus in the archaeological record in northern France is indeed demonstrated during this period and could reflect a lack of human occupation in the context of intensified flow frequency (Antoine et al. 2015).

The δ^{13}C values of the red deer could be separated in two non-overlapping groups between the Late Glacial and Preboreal on the one hand (− 21.0‰ to − 20.5‰) and the successive Boreal and early Atlantic periods on the other hand (− 23.7‰ to − 22.5‰; Fig. 2). The significantly lower values of the Boreal and early Atlantic most likely corresponded to a change of habitat from open or lightly forested landscape to closed and densely forested habitat (Drucker et al. 2008, 2011). Palynological studies indeed point to such a closure effect of the landscape, with an increase of tree formations dominated by pine (Pinus) and birch (Betula) during the Preboreal. These boreal-like landscapes were gradually replaced by temperate forests dominated by hazel trees (Corylus) over the Preboreal to Boreal transition (Pastre et al. 2003; Coutard et al. 2010; Antoine et al. 2014). The malacological record evidences the increase of thermophilous

species over the early Holocene, especially those associated with the dense forest which expanded at the end of the Preboreal (Coutard et al. 2010; Antoine et al. 2014). A change from deer and aurochs to wild boar predation is illustrated at Warluis over the Preboreal to Boreal transition (Coutard et al. 2010). The change in the atmospheric δ^{13}C values of ca. + 0.3‰ (Schmitt et al. 2012), at the Late Glacial to early Holocene transition, could not account for the decrease of more than 2‰ observed in the red deer collagen. A possible impact of the change in atmospheric CO_2 concentration on the δ^{13}C values of plants is still highly debated (e.g., Kohn 2016). Even in the case of atmospheric CO_2 concentration dependence, namely, lower plant δ^{13}C values due to increasing CO_2 concentration, we should observe decreasing δ^{13}C values between ca. 11,000 and 13,000 cal BP when the atmospheric CO_2 increased about 40 ppm (Schmitt et al. 2012). However, such a pattern appears clearly after that time in our studied red deer. We thus interpret the decrease in δ^{13}C values of the red deer as a shift to more closed dense habitat.
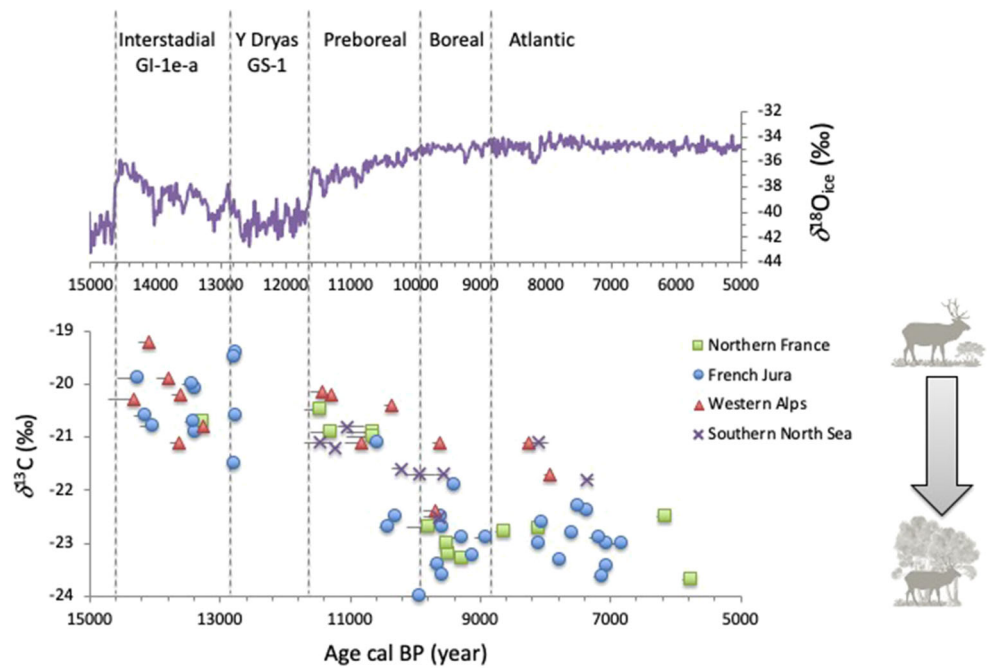
The pattern of ^{13}C variation in the red deer from northern France fits the one observed in the French Jura. In contrast, in the western Alps and the southern North Sea, also called Doggerland (Van der Plicht et al. 2016), red deer gave δ^{13}C values equal or above − 22.5‰ over the early Holocene (Fig. 2). In both cases, the red deer seemed to have persisted in an open habitat, either through a move to higher altitude for the specimens in the Alps (Drucker et al. 2011) or a lack of a dense canopy in the territories of the specimen of the southern North Sea. Ecological studies of offshore locations along the south coast of England showed the occurrence of mixed woodland dominated by pine (Pinus) and hazel (Corylus) during the early Holocene (Gearey et al. 2017). The pollen record of two cores drilled in the center of the North Sea revealed an open birch (Betula) forest that included pine trees during the Preboreal, followed by a large expansion of hazel, replacing birch, at the onset of the Boreal (Krüger et al. 2017). Then, during the course of the Boreal, pine tree occurrence increased and became dominant over the deciduous woodland of oak (Quercus) and elm (Ulmus) formations (Krüger et al. 2017). The pine-dominated vegetation during the Boreal in the Doggerland differs from the hazel-dominated forest over the same period in eastern France (e.g., De Beaulieu et al. 1994) and northern France (e.g., Antoine et al. 2000; Coutard et al. 2010). This forest composition difference and the possibly higher frequency of open patches in the Doggerland could explain the relatively higher δ^{13}C values of the red deer after the Preboreal.

The δ^{15}N values of the red deer from northern France showed an increasing tendency over the Late-Glacial and early Holocene (Fig. 3). The unique specimen dated to the Late Glacial interstadial (GI-1e to GI-1a) displayed the lowest δ^{15}N of all (+ 2.8‰), while one specimen of the Boreal provided the highest value (+ 6.4‰). Like for the δ^{13}C values, the

Table 2 Results of collagen extraction yield (yield), elemental (C, N, C:N), isotopic (δ^{13}C, δ^{15}N), and radiocarbon (^{14}C) analyses on bone collagen of Late Glacial and early Holocene red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), aurochs (*Bos primigenius*), large bovid (*Bos/Bison*), and elk (*Alces alces*) from northern France. All stable isotope data are from this work, except for the site of Henry-Farman (PHF-, Leduc et al. 2013). L stands for left and R for right. Radiocarbon calibrations are given with 2 sigma based on IntCal13 dataset (Reimer et al. 2013) and OxCal 4.3.2 software (Bronk Ramsey 2017). 1, Coutard et al. 2010; 2, Leduc et al. 2013

| N° lab	Species	Sample	N° excavation	Sector/level	Yield (%)	C (%)	N (%)	C:N	δ^{13}C (‰)	δ^{15}N(‰)	^{14}C date BP	^{14}C date cal BP	^{14}C source
CTpm-9	Red deer	Ulna L	CTpm 11 D4 NE7	/ssn	1.2	38.5	14.0	3.2	-23.7	5.8	4985 ± 40 GrA-25179	5890–5600	This work
CTpm-8	Red deer	Humerus L	CTpm 4Y 25 NW	/bsn	2.5	41.8	15.0	3.3	-22.5	4.7	5350 ± 45 GrA-25058	6280–5990	This work
WRL-19	Red deer	Femur	BG59 SE #5254	VIIIa/lb	3.1	35.4	11.7	3.5	-22.7	5.2	7290 ± 40 ETH-70749	8180–8010	This work
CTpm-17	Red deer	Tibia	10 Y10 SW 9156	/lbs	8.9	43.0	14.7	3.4	-22.8	4.4	7845 ± 40 ETH-70748	8770–8540	This work
CTpm-6	Red deer	Phalanx 2	CTpm 10 V1 SE 8	/upper lb	2.0	37.9	13.8	3.2	-23.3	3.7	8290 ± 50 GrA-25178	9440–9120	This work
CTpm-11	Red deer	Metacarpus L	10 N11 NW 7883	/lbs	2.3	34.5	11.8	3.4	-23.2	3.9	8450 ± 60 Erl-9390	9550–9300	This work
WRL-1	Red deer	Metacarpus	AY 17 base tourbe	/base tourbe	7.8	42.0	15.3	3.2	-23.0	6.4	8490 ± 60 GrA-23552	9560–9330	1
HI-1	Red deer	Radius L	none		3.8	38.7	14.4	3.1	-22.7	4.6	8780 ± 50 GrA-25057	10,130–9560	This work
BEL-1	Red deer	Radius R	B150 H5 5657		1.1	40.2	14.5	3.2	-20.9	4.9	9400 ± 60 GrA-25055	11,060–10,430	This work
HII-2	Red deer	Talus L	Hangest II Nord		8.0	40.7	15.0	3.2	-21.0	3.4	9410 ± 65 Erl-9393	11,070–10,430	1
CTY4	Red deer	Femur	O17 base ToLi Rel 2		5.8	39.8	14.0	3.3	-20.9	5.0	9880 ± 70 Erl-9394	11,610–11,180	This work
SA-1	Red deer	Metapodial	Sa 114 Q5 2818	/LGVG	3.1	38.6	13.9	3.2	-20.5	4.0	9990 ± 50 GrA-25195	11,710–11,260	This work
CTY2	Red deer	Metacarpus R	Conty 27 2758	/inferior	1.9	37.3	14.2	3.1	-20.7	2.8	11,420 ± 100 GrA-21523	13,450–13,080	This work
WRL-7	Roe deer	Humerus	BB 16 NW 623	IIIb/	2.7	40.9	14.5	3.3	-23.3	7.0	8766 ± 65 Erl-9384	10,140–9550	1
SA-2	Roe deer	Tibia	Sa 114 R6 1557	/upper LGVG	12.0	37.5	13.4	3.3	-21.8	4.5	9380 ± 65 Erl-9391	10,780–10,390	This work
WRL-9	Roe deer	Metatarsus	Y62 NW 270	IIIa/	3.8	37.4	14.0	3.1	-21.5	5.4	9778 ± 68 Erl-9386	11,350–10,870	1
WRL-11	Wild boar	Humerus	E96 NE 75	IIb/Lb	3.8	42.1	14.8	3.3	-19.8	7.1	8830 ± 60 GrA-23550	10,170–9680	1
BLA-1	Wild boar	Skull			5.4	40.0	14.6	3.2	-20.1	4.1	8895 ± 45 GrA-59509	10,200–9790	This work
WRL-12	Wild boar	Femur	ZA 66 SE 1948	IIc/Lb	8.0	42.7	15.1	3.3	-20.5	8.5	9090 ± 70 GrA-23542	10,500–9960	1
WRL-16	Wild boar	Humerus		Va1/base Lb	4.8	40.4	14.4	3.3	-21.0	3.6	9500 ± 40 ETH-64389	11,080–10,600	This work
PHF-9	Wild boar	Humerus R	Décap.sud iso822	Locus 4	1.4	29.5	9.9	3.5	-20.9	5.3	8805 ± 40 GrA-45017	10,150–9670	2
PHF-31	Wild boar	Radius L	Est iso1291	Locus 6	1.4	39.5	14.2	3.3	-20.0	5.6	8930 ± 55 GrA-50908	10,230–9880	2
BEL-4	Aurochs	Metacarpus R	B 150 E5 5119		3.4	33.5	11.1	3.5	-23.2	5.9	8760 ± 65 Erl-9388	10,140–9540	This work
BEL-3	Aurochs	Metacarpus R	B 150 H6 5394		3.4	33.5	11.3	3.5	-20.4	5.2	9810 ± 70 Erl-9387	11,410–10,880	This work
PMZ-1	large bovid	Mandible	Sondage 2/2bis	Limon brun org.	1.8	31.8	10.8	3.4	-20.6	5.3	9900 ± 40 ETH-64390	11,410–11,210	This work
PHF-11	Aurochs	Metatarsus R	Décap. sud iso895	Locus 4	2.9	39.2	14.5	3.2	-20.8	6.5	9285 ± 40 GrA-45018	10,590–10,290	2
WRL-18	Elk	Metacarpus	Natural input LT/T	Sond. 538 3e tran.	6.1	40.3	14.2	3.3	-22.7	4.5	9240 ± 50 Ly-4843	10,560–10,250	1

Fig. 2 $\delta^{13}C$ values of bone collagen of red deer (*Cervus elaphus*) from northern France (this work), French Jura (Drucker et al. 2011), western Alps (Drucker et al. 2011), and southern North Sea (van der Plicht et al. 2016) over time during the Late Glacial and early Holocene

pattern of variation for $\delta^{15}N$ values of the red deer from northern France was more comparable with the one found for the red deer in the French Jura than in the western Alps or southern North Sea. Especially during the early Holocene, the red deer from northern France showed equivalent values to those of the French Jura, both being higher than those of the red deer from the western Alps. The increase in $\delta^{15}N$ values of this herbivore could indirectly reflect the rise in temperature through the intensification of soil activities, which can lead

to an increase in the $\delta^{15}N$ values of plants (e.g., Hobbie et al. 2005; Drucker et al. 2011). In a warming context, microbial soil activity and thus N mineralization rates are enhanced leading to higher N supply to plants, which is reflected by higher $\delta^{15}N$ values in foliage (Craine et al. 2009, 2015). A shift to a higher altitude, as could take place in the mountainous regions such as the Jura and the Alps, would result in attenuating this effect, since the $\delta^{15}N$ values of soils and plants decrease when altitude increases, which thus may

Fig. 3 $\delta^{15}N$ values of bone collagen of red deer (*Cervus elaphus*) from northern France (this work), French Jura (Drucker et al. 2011), western Alps (Drucker et al. 2011), and southern North Sea (van der Plicht et al. 2016) over time during the Late Glacial and early Holocene
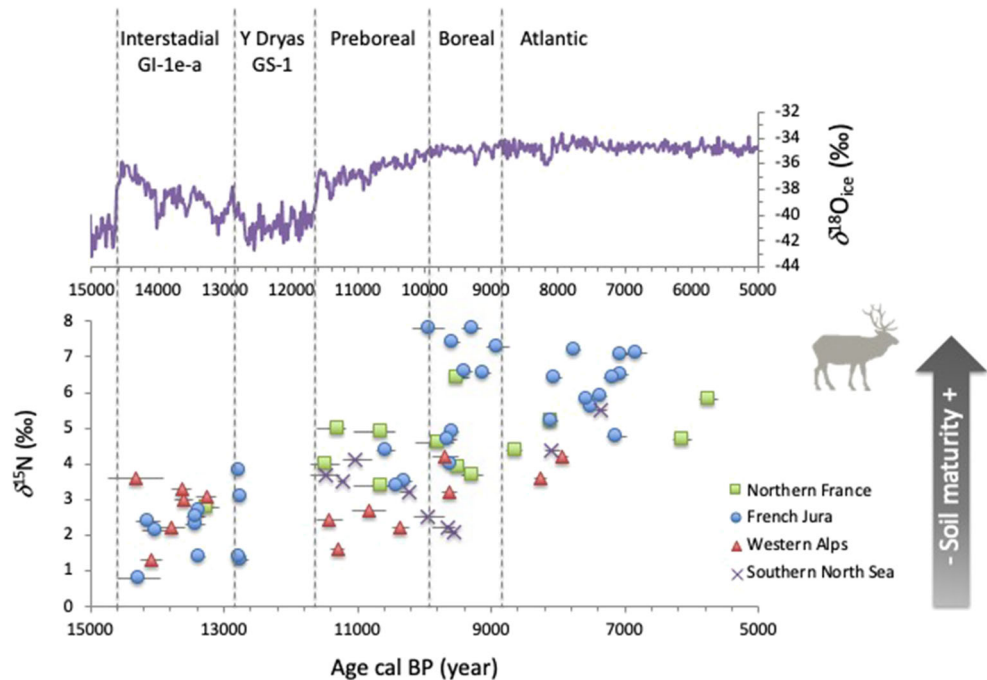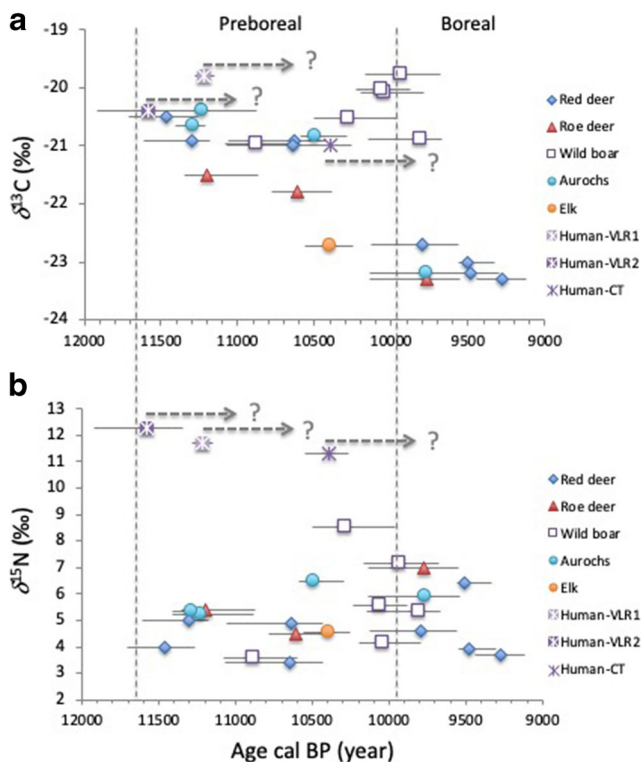
counterbalance the effect of global warming on δ^{15}N values (e.g., Männel et al. 2007; Drucker et al. 2011). The red deer for the North Sea provided a quite different pattern, with an apparent decrease in ^{15}N abundances over the Preboreal and start of the Boreal. This could be due to an additional location effect, in other words a wider geographical origin than reflected by the location of the collection site of the bones. Since the North Sea specimens have been collected opportunistically from net fishing or sand dredging activities, their exact former location is unfortunately not possible to pinpoint (Van der Plicht et al. 2016). As a matter of fact, a large range of δ^{15}N values characterized the red deer specimens of French Jura and northern France during the Boreal, showing that higher ^{15}N contrast according to location may be expected at that time. Nevertheless, higher red deer δ^{15}N values in the North Sea were finally found in the early Atlantic compared with the Preboreal and Boreal periods, as observed in the other regions. All in all, the observed contrasts in δ^{15}N values of red deer over time and space underline the importance of the isotopic investigation at a constrained spatial and chronological scale to most accurately reconstruct the trophic web.

Fig. 4 Results of δ^{13}C (a) and δ^{15}N (b) values on red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), Aurochs (*Bos primigenius*), elk (*Alces alces*), and human individuals from Val-de-Reuil (VLR) and La Chaussée-Tirancourt (CT) over time. The dotted arrows indicate possible reservoir effect on the radiocarbon dating of the human individuals.

δ^{13}C and δ^{15}N of large herbivore species during the early Holocene in northern France

We considered not only red deer but also other species in northern France during the early Holocene (Table 2, Fig. 4). The wild boar δ^{13}C and δ^{15}N values varied from − 21.0‰ to − 19.8‰ and + 3.6 to + 8.5‰, respectively. The roe deer and the aurochs displayed the comparable range of δ^{13}C (− 23.3 ‰ to − 21.5‰ and − 23.2 to − 20.4‰, respectively) and δ^{15}N values (+ 4.5 to + 7.0‰ and + 5.2 to + 6.5‰, respectively). We observed a difference in the variation pattern according to species: a decrease in δ^{13}C values for the aurochs and roe deer that appeared quite similar to the pattern provided by the red deer. The wild boar, in contrast, showed no δ^{13}C values below − 21‰, likely because their feeding habits prevent them to reflect any canopy effect (consumption of fruits and underground tubers; Schley and Roper 2003; Baubet et al. 2004). This difference in the δ^{13}C chronological tendencies between wild boar and other species or for the same species, such as the red deer, between different geographical locations implies a local effect in contrast to the result of a global change in carbon isotopic composition and/or concentration in the atmosphere (see also Drucker et al. 2008). The δ^{15}N values of the large herbivores did not reveal a spectacular change throughout the Preboreal period. However, the highest δ^{15}N values of the wild boar appeared by the end of the Preboreal. This pattern appears consistent with the rising ^{15}N abundances in soils and plants triggered by increasing temperature through enhanced N-cycling by microorganisms (Craine et al. 2009; Hobbie and Högberg 2012). Finally, the elk specimen dated to the end of the Preboreal gave a δ^{13}C value of − 22.7‰, which pointed to a more closed habitat than for the coeval red deer, while the elk δ^{15}N value of +4.5‰ was in line with those of the other deer species. Thus, the Preboreal appears as a key period of change toward more forested habitat for the deer species in a context of increasing soil productivity.

δ^{13}C, δ^{15}N, and δ^{34}S values of the human individuals over the Preboreal

The human individuals were all directly dated and the results are reported in Table 3. The results pointed to a Preboreal age during which early Mesolithic culture developed. A possible consumption of aquatic food items could lead to a reservoir effect. As a result, the human individuals' chronological ages could be in fact younger, to up to several hundred years, than the apparent age given by the ^{14}C results, as found in Mesolithic contexts by Meadows et al. (2018) and Boethius et al. (2017). A review by Fernandes et al. (2016) showed a reservoir effect that accounted for a shift of up to 500 years older in radiocarbon ages for Mesolithic and Neolithic human individuals in Europe. Thus, the chronological difference between the two individuals from Val-de-Reuil may

Table 3 Results of collagen extraction yield (yield), elemental (C, N, C:N), isotopic (δ^{13}C, δ^{15}N), and radiocarbon (^{14}C) analyses on human individuals from Val-de-Reuil and La Chaussée-Tirancourt. L stands for left and R for right. Radiocarbon calibrations are given with 2 sigma based on IntCal13 dataset (Reimer et al. 2013) and OxCal 4.3.2 software (Bronk Ramsey 2017)

| N° lab	Sample	N° excavation	Yield (%)	C (%)	N (%)	C:N	δ^{13}C (‰)	δ^{15}N (‰)	^{14}C date BP	^{14}C date cal BP	^{14}C source
VLR-1	Ulna L	Sujet A 2050	8.6	43.2	15.1	3.3	-19.8	11.7	9800 ± 45 GrA-40464	11,280–11,150	This work
VLR-2	Ulna R	Sujet B 2010	4.9	42.8	15.3	3.3	-20.4	12.3	10,065 ± 45 GrA-40483	11,920–11,340	This work
CTpm-12	Femur L	IIa lb F4 6075	3.1	42.7	13.8	3.6	-21.0	11.3	9240 ± 45 SacA-23956	10,550–10,260	Ducrocq 2017

overestimate the time span between the burial depositions in the case of a difference in diet, namely, in the intake of aquatic resources. The ca. 360 years of difference between the calibrated dates of the two individuals from Val-de-Reuil would indeed imply that the memory of the exact location of the burial could be maintained over several centuries. Alternatively, it could point to a dietary reservoir effect generated by the consumption of aquatic resources, which would

have been stronger for the individual VLR-2 (sujet B) than for the individual VLR-1 (sujet A).

To reconstruct the trophic baseline, we selected not only the fauna from the Preboreal period but also fauna dated to the transition to the Boreal in order to account for the potential chronological uncertainty of the human ^{14}C ages (Table 4, Fig. 5, and Fig. SD1). The δ^{13}C values of the Val-de-Reuil individuals, VLR-1 and VLR-2, were − 19.8‰ and − 20.4‰,

Table 4 Results of collagen extraction yield (yield), elemental (C, N, C:N, C:S, N:S), and isotopic (δ^{13}C, δ^{15}N, δ^{34}S) analyses on fauna selected for the comparison with human individuals from Val-de-Reuil and La Chaussée-Tirancourt. All isotope data are from this work, except δ^{13}C and δ^{15}N values of specimens from the site of Henry-Farman (PHF-, Leduc et al. 2013). L stands for left and R for right

N° lab	Species	Sample	N° excavation	Yield (%)	C (%)	N (%)	C:N	δ^{13}C (‰)	δ^{15}N (‰)	S (%)	δ^{34}S (‰)	C:S	N:S
CTpm-12	Human	Femur L	IIa lb F4 6075	3.1	42.7	13.8	3.6	− 21.0	11.3	0.20	7.8	569	158
VLR-1	Human	Ulna L	sujet A 2050	8.6	43.2	15.1	3.3	− 19.8	11.7	0.16	8.7	736	220
VLR-2	Human	Ulna R	sujet B 2010	4.9	42.8	15.3	3.3	− 20.4	12.3	0.17	6.9	659	202
PHF-24	Red deer	Radius R	1/4 A iso2319 166/971	1.3	36.4	12.9	3.3	− 20.1	4.3				
HI-1	Red deer	Radius L	none	3.8	38.7	14.4	3.1	− 22.7	4.6				
HII-2	Red deer	Talus L	none	8.0	40.7	15.0	3.2	− 21.0	3.4	0.14	6.8	754	238
BEL-1	Red deer	Radius R	B150 H5 5657	1.1	40.2	14.5	3.2	− 20.9	4.9				
SA-1	Red deer	Metacarpus	Sa 114 Q5 2818 LGVG	3.1	38.6	13.9	3.2	− 20.5	4.0	0.16	6.8	631	195
CTY4	Red deer	Femur	Conty O17 base ToLi Rel 2	5.8	39.8	14.0	3.3	− 20.9	5.0	0.18	8.5	586	177
PHF-22	Wild boar	Humerus R	B 165/964 n°14	1.3	30.9	10.6	3.4	− 19.8	8.3				
PHF-9	Wild boar	Humerus R	décap.sud iso822	1.4	29.5	9.9	3.5	− 20.9	5.3				
PHF-10	Wild boar	Humerus R	décap. sud iso876	1.9	35.1	12.2	3.4	− 20.1	5.9	0.16	10.3	600	179
PHF-31	Wild boar	Radius L	est iso1291	1.4	39.5	14.2	3.3	− 20.0	5.6	0.18	9.5	595	183
WRL-11	Wild boar	Humerus	E96 NE 75	3.8	42.1	14.8	3.3	− 19.8	7.1	0.19	− 0.8	596	180
WRL-12	Wild boar	Femur	ZA 66 SE 1948	8.0	42.7	15.1	3.3	− 20.5	8.5	0.19	4.3	594	180
WRL-16	Wild boar	Humerus		4.8	40.4	14.4	3.3	− 21.0	3.6	0.18	− 1.5	609	186
PHF-11	Aurochs	Metatarsus R	décap. sud iso895	2.9	39.2	14.5	3.2	− 20.8	6.5	0.16	11.6	672	213
BEL-4	Aurochs	Metacarpus R	B 150 E5 5119	3.4	33.5	11.1	3.5	− 23.2	5.9				
BEL-3	Aurochs	Metacarpus R	B 150 H6 5394	3.4	33.5	11.3	3.5	− 20.4	5.2	0.14	11.2	625	181
PMZ-1	large bovid	Mandible	sondage 2/2bis	1.8	31.8	10.8	3.4	− 20.6	5.3				
WRL-7	Roe deer	Humerus	BB 16 NW 623	2.7	40.9	14.5	3.3	− 23.3	7.0				
SA-2	Roe deer	Tibia	Sa 114 R6 1557 sommet LGVG	12.0	37.5	13.4	3.3	− 21.8	4.5	0.15	8.3	680	208
WRL-9	Roe deer	Metatarsus	Y62 NW 270	3.8	37.4	14.0	3.1	− 21.5	5.4				
WRL-18	Elk	Metacarpus		6.1	40.3	14.2	3.3	− 22.7	4.5				
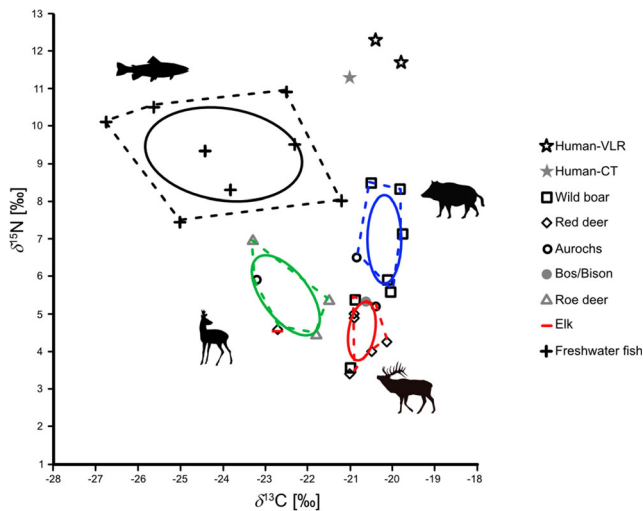
Fig. 5 $\delta^{13}C$ and $\delta^{15}N$ values of red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), Aurochs (*Bos primigenius*), elk (*Alces alces*) from the Preboreal and Preboreal/Boreal transition, and human individuals from Val-de-Reuil (VLR) and La Chaussée-Tirancourt (CT). Results of the diet resources calculated with SIBER (Jackson et al. 2011) are reported in dashed and solid line areas. Dashed line shows the convex hull, the smallest possible surface that encompasses all individuals of one group (Layman et al. 2007). Solid line shows the Bayesian-based Standard Ellipse Area (SEA), which reflects the core niche (Jackson et al. 2011)

respectively, which corresponds to an average diet in terms of collagen value of ca. – 20.8‰ and – 21.4‰. This last range would correspond to the values observed in the open habitat deer and aurochs and/or some of the wild boar (Fig. 4a). With a $\delta^{13}C$ value of – 21.0‰, the individual of La Chaussée-Tirancourt could reflect the consumption of forest-dwelling terrestrial preys (Fig. 4a). The $\delta^{15}N$ values of the humans from Val-de-Reuil were + 12.3‰ for VLR-1 and + 11.7‰ for VLR-2, which were more than + 5‰ higher than most of the Preboreal herbivores, except for two wild boars at the end of the Preboreal and start of the Boreal. These high ^{15}N wild boars were 1000 years younger than the individuals of Val-de-Reuil in apparent calibrated age and indeed in line with the result of the warming effect over the Preboreal. The contribution of freshwater resources, with their higher $\delta^{15}N$ values (+ 7.5 to +10.9‰; Table 5) than the terrestrial fauna with an overlapping range of $\delta^{13}C$ values (– 26.8‰ to – 21.2‰; Table 5), is thus more likely. An aquatic contribution to the diet of the individual of La Chaussée-Tirancourt is more speculative since the high ^{15}N wild boar and aurochs of the end of the Preboreal could account for the human $\delta^{15}N$ value of +11.3‰. The freshwater resources were nevertheless tested for this individual as well in the application of the model calculations.

We applied ^{34}S measurements on the human and fauna of northern France to explore a possible additional tracker of dietary resources (Tables 4 and 5). The $\delta^{34}S$ values of the terrestrial fauna varied between – 1.5 and + 11.6‰. Most of the herbivores clustered between + 6.8 and + 11.6‰, with the aurochs exhibiting the highest values (+ 11.2‰ and + 11.6‰) and the red deer among the lowest values (+ 6.8 and + 8.5‰) (Fig. 6). However, the wild boar was the species displaying the greatest range of values from – 1.5‰ to + 10.3‰. As a matter of fact, all the wild boars displaying lower $\delta^{34}S$ values than the rest of the fauna originated from the site of Warluis and were the only

Table 5 Results of collagen extraction yield (yield), elemental (C, N, C:N, C:S, N:S), and isotopic ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) analyses on fish from early Mesolithic site of Friesack 4 in north Germany (Meadows et al. 2018; Robson pers. comm. 2019), early to late Mesolithic site of Grotte du Paper in Belgium (Drucker et al. 2018), and late Mesolithic site of Noyen-sur-Seine (Drucker et al. 2018). nd stands for not determined

Site	N° lab	Species	Sample	Yield (%)	C (%)	N (%)	C:N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	S (%)	$\delta^{34}S$ (‰)	C:S	N:S
Friesack 4	F4-4-6a + b	Eel	Cleithrum	2.9	38.2	12.5	3.6	– 24.4	9.3				
Friesack 4	F4-3-5a	Perch	Precaudal vertebra	6.6	38.7	14.3	3.2	– 25.0	7.5				
Friesack 4	F4-3-6a	Perch	Posttemporal	10.3	42.7	14.3	3.5	– 26.8	10.1				
Friesack 4	F4-4-1a + b	Perch	Ceratohyal	6.7	39.8	12.9	3.6	– 25.6	10.5				
Abri du Pape	BP-16	Pike	Vertebra	4.2	40.3	14.3	3.3	– 22.5	10.9				
Abri du Pape	BP-20	Cyprinidae	Vertebra	2.6	34.8	12.5	3.2	– 21.2	8.0	0.59	4.0	156	48
Abri du Pape	BP-21	Cyprinidae	Epihyal	1.8	30.5	11.1	3.2	– 22.3	9.5				
Noyen-sur-Seine	NO7600	Eel	Vertebra	nd	40.7	14.5	3.3	– 23.8	8.3				
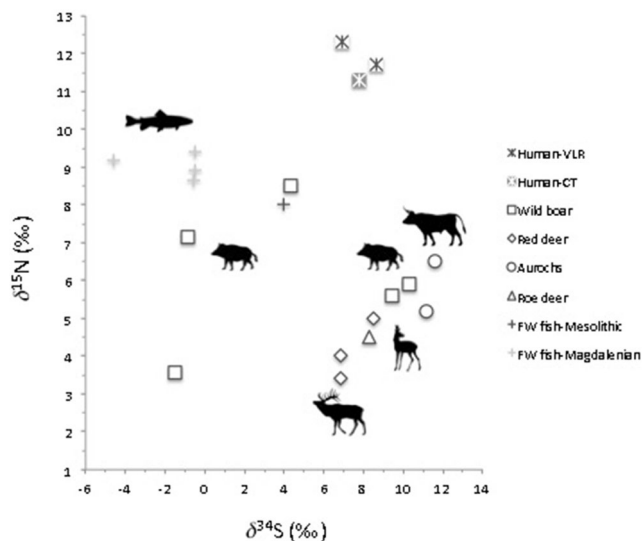
Fig. 6 $\delta^{34}S$ and $\delta^{15}N$ values of red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), Aurochs (*Bos primigenius*), elk (*Alces alces*) from the Preboreal and Preboreal/Boreal transition, and human individuals from Val-de-Reuil (VLR) and La Chaussée-Tirancourt (CT)

specimens from this site with ^{34}S results. Warluis is situated in the alluvial plain of Thérain, a tributary of the Oise river, at the limit of the Cretaceous bedrock, the later characterizing the surroundings of the other sites along the Somme river, along with the Paleogene context of Henry-Farman in Paris and some Jurassic formation west to Beauvais (Ducrocq 2017). This particular geological situation could be the origin of the relatively low $\delta^{34}S$ values of the wild boar from Warluis.

The $\delta^{34}S$ value of one Mesolithic Cyprinid from Grotte du Pape in Belgium was + 4.0‰ and thus is comparable with the values of the wild boar from Warluis (Table 5, Fig. 6). Moreover, reporting from the previously published $\delta^{34}S$ from the Magdalenian fishes from Belgium (− 4.6‰ to − 0.5‰) confirmed a possible overlap between freshwater and terrestrial resources during the early Holocene. As a result, the ^{34}S abundances seem to better reflect the geographical origin of some terrestrial resources rather than serve to disentangle the contribution of the freshwater from the high ^{15}N terrestrial fauna. The $\delta^{34}S$ values of the human individuals ranged from + 6.9 to + 8.7‰ with VLR-2 showing the lowest value, VLR-1 the highest value, and the individual of La Chaussée-Tirancourt the intermediate one (+ 7.8‰). These values were consistent with those of the fauna, when excluding the wild boar from Warluis. Since the $\delta^{34}S$ values do not seem discriminant enough between aquatic and terrestrial ecosystems and may depend significantly on the mobility pattern, we did not use them further for dietary interpretation.

Diet reconstruction based on MixSIAR

A cluster analysis applied on the $\delta^{13}C$ and $\delta^{15}N$ values of the terrestrial fauna revealed three groups named from the dominant species they included (Figure SD2). The group "red deer" ($n = 9$) corresponded to the herbivores with relatively high $\delta^{13}C$ (− 21.0‰ to − 20.1‰) and the lowest $\delta^{15}N$ values (+ 3.4‰ to + 5.3‰), while the group "wild boar" ($n = 6$) encompassed the herbivores with a comparable range of $\delta^{13}C$ (− 20.8 to − 19.8‰) but higher $\delta^{15}N$ values (+ 5.8 to + 8.5‰). Finally, the remaining herbivores with the lowest $\delta^{13}C$ values (− 23.3 to − 21.5‰) and intermediate $\delta^{15}N$ values (+ 4.5 to + 7.0‰) clustered in the "roe deer" group ($n = 5$). For this last group, we did not include the elk specimen in the calculation of the isotopic average since it was of natural origin and not associated to human subsistence activity (see also Bridault 1992). The fish specimens ($n = 8$) were considered as a separate group from the terrestrial ones with their relatively low $\delta^{13}C$ (− 26.8‰ to − 21.2‰) and high $\delta^{15}N$ values (+ 7.5‰ to + 10.9‰). The niche reconstruction provided by the SIBER analysis validated the terrestrial and aquatic grouping described above since it confirmed that the defined prey groups belong to different core niches (Fig. 5).

The results of the simulation provided a rather similar pattern for the two individuals of Val-de-Reuil(Fig. 7). Both freshwater and wild boar clusters may have contributed substantially to their diet, with means of 24.4 ± 19.5% (median 18.9%) and 40.6 ± 24.9% (median 40.4%), respectively, for VLR-1, and of 31.0 ± 21.5% (median 27.9%) and 35.3 ± 23.5% (median 33.5%), respectively, for VLR-2. These two resource groups showed a negative correlation in their posterior distribution, meaning that a higher proportion of one involves a lower proportion of the other, without further possible discrimination between the different scenarios based on the model. So far, the chronological evidence of high $\delta^{15}N$ wild boar apparently post-dated the chronological position of the individuals of Val-de-Reuil, even in the hypothesis of a reservoir effect correction. Interestingly, the increasing presence of the wild boar among the hunted preys seems to start only at the Preboreal to Boreal transition (Bridault 1997; Coutard et al. 2010; Ducrocq et al. 2014). If we favor the hypothesis of a higher contribution of the freshwater resources over the wild boar, we find the expected higher aquatic product consumption in VLR-2 rather than in VLR-1, which would be consistent with a reservoir effect biased gap between the radiocarbon ages of the two individuals. In any case, the potential intake of roe deer and red deer groups as prey appeared minor for the human individuals from Val-de-Reuil, at least not exceeding 25% of the protein part of the diet (Fig. 7).

The combinations of prey groups tested for the human of La Chaussée-Tirancourt showed a possible main input of the freshwater and wild boar clusters (Fig. 7). The freshwater group could have contributed to 29.7 ± 15.3% of the dietary protein on
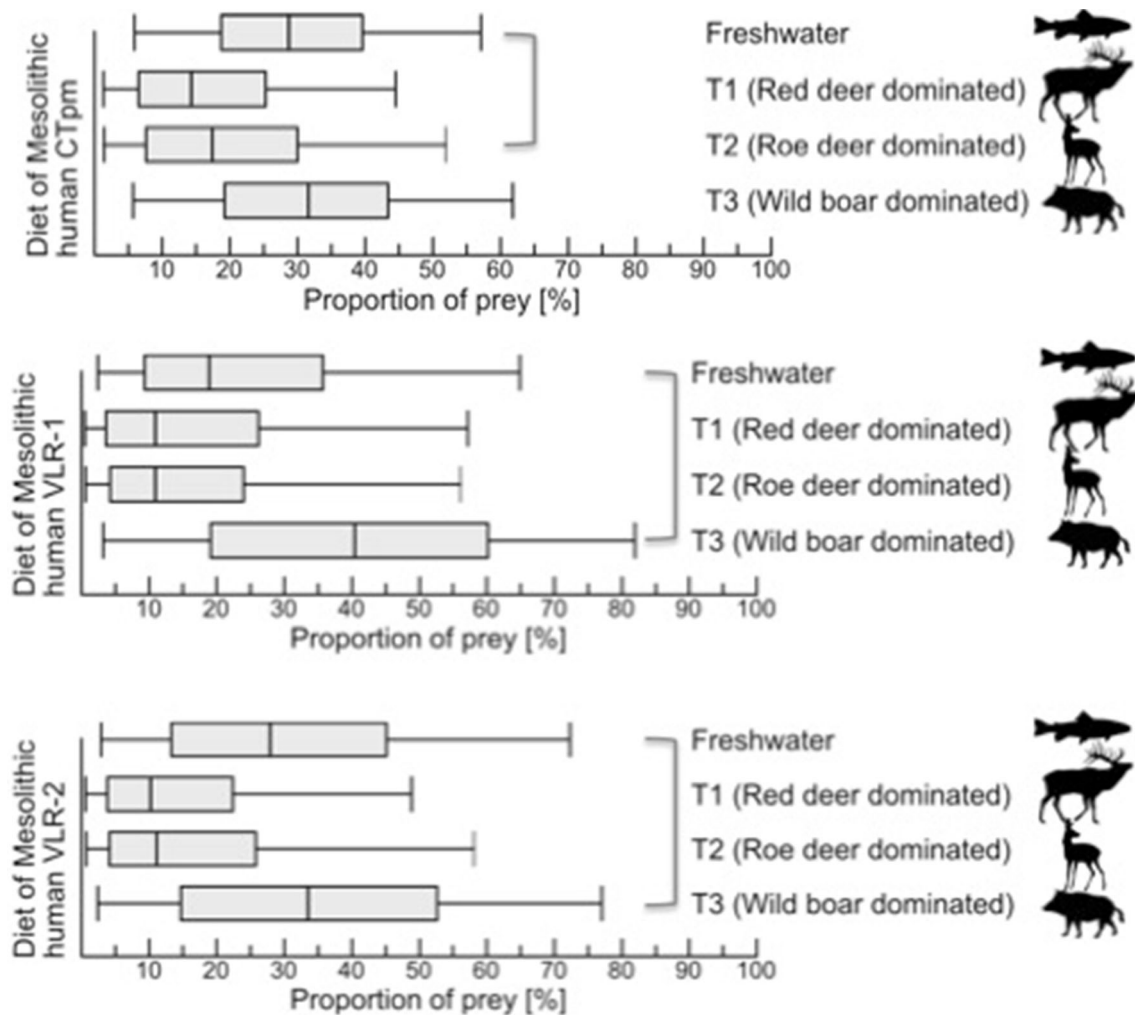
Fig. 7 Results of the MixSIAR model simulation of the relative contribution of the different prey groups. The brackets connect the resources with a significant negative correlation in their posterior distribution

average (median value of 28.7%), while the wild boar group could have provided 32.2 ± 17.0% on average (median value of 31.6%). However, a negative correlation could be noticed between the freshwater group and the roe deer group. This last cluster, corresponding mainly to forest-dwelling prey, could represent a mean of 20.5 ± 15.9% (17.4% as median value), which was comparable with the red deer group whose input could be 17.5 ± 13.8% (median value of 14.3%). So far, no consumption of aquatic resources could be attested for through zooarchaeological evidence from the early Mesolithic in northern France, where remains of fish have not been found before the end of the Boreal occupation (Ducrocq et al. 2008; Ducrocq 2014). Thus, the roe deer group could be a convincing alternative to aquatic resources when dealing with human diet by the end of the Preboreal, which would be consistent with the increasing role

of the forested areas in the subsistence of the Mesolithic hunter-gatherers over the early Holocene (Coutard et al. 2010). Although archaeofauna dated to the Preboreal are still poorly documented in northern France, it is interesting to note that roe deer is the second preyed upon species at Warluis IIIb (Bridault unpublished) and the first one at Les Closeaux IV (Bridault unpublished) and Warluis IIIa (Bridault unpublished) in the Paris Basin. A contribution of roe deer in the human diet during the Preboreal is thus consistent with the archaeozoological observations to date.

Fig. 8 $\delta^{13}C$ and $\delta^{15}N$ values of human (individual data) and fauna (averages and standard deviations) from northern France (this work), western France (Schulting et al. 2008), Belgium (Bocherens et al. 2007), southern North Sea (van der Plicht et al. 2016), and northern Germany (Meadows et al. 2018) during the Preboreal.
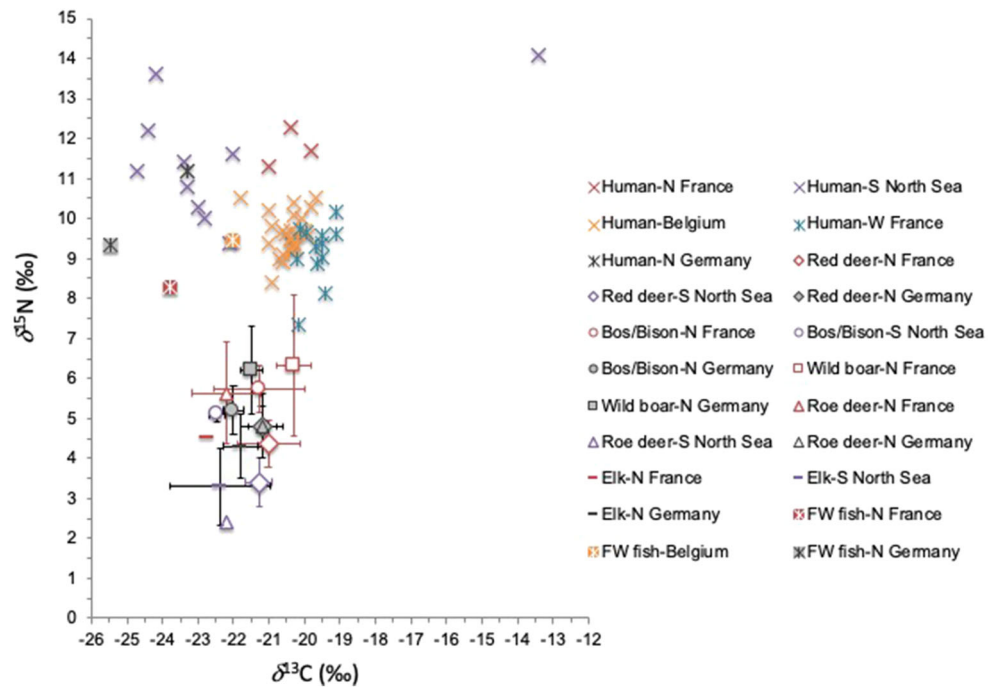
Diet reconstruction in the context of the early Holocene

Investigation into early Mesolithic human diet based on collagen stable isotopes has been conducted in other inland contexts, such as the Doggerland (currently North Sea), the Meuse Basin in Belgium, the site of La Vergne in western France, and Friesack in north Germany (Bocherens et al. 2007; Schulting et al. 2008, van der Plicht et al. 2016, Meadows et al. 2018; Fig. 8). When possible, we have reported the results of the associated fauna in addition to those of human individuals to take into consideration possible biases linked to a difference in the local baseline. We have not observed significant contrasts in the $\delta^{13}C$ and $\delta^{15}N$ values according to location. The only notable exception would be the roe deer with a difference of ca. 3‰ between northern France and the North Sea, but the comparison may be biased since only one specimen was analyzed in the North Sea. We can thus consider a direct comparison for the human individuals. Remains from animal and human bones from the North Sea were directly dated, and a number of them were found to belong to the Preboreal period, from ca. 10,000 to 8900 BP (ca. 11,500–10,000 cal BP). Most of them delivered higher $\delta^{15}N$ values than those expected for the consumption of the chronologically associated fauna for comparable or lower $\delta^{13}C$ values, pointing to significant consumption of freshwater resources (van der Plicht et al. 2016). For the same time range, one individual provided remarkably high $\delta^{13}C$ and $\delta^{15}N$ values revealing an additional contribution of the marine resources in the diet. In Belgium, the region of the Meuse Basin is rich in Mesolithic human remains belonging to the early phases of the Mesolithic, and a terrestrial-based diet

was inferred from the relative abundances of ^{13}C and ^{15}N in their collagen (Bocherens et al. 2007). Their $\delta^{13}C$ and $\delta^{15}N$ values were indeed significantly lower than those of the individuals consuming freshwater food from the North Sea. The same conclusion applies to the western French site of La Vergne where several early Mesolithic individuals, all directly dated, could be analyzed (Schulting et al. 2008). Their $\delta^{15}N$ values were comparable to those of the Meuse Basin, while their $\delta^{13}C$ values were slightly higher which could indicate a more open habitat for the consumed terrestrial prey. Finally, the early Mesolithic adult from Friesack 4 showed ^{13}C and ^{15}N relative abundances fitting in the range of the freshwater resources consumers of the North Sea, which is consistent with the conclusion of large freshwater ecosystem contribution drawn from the study of Meadows et al. (2018).

The humans from northern France provided higher $\delta^{15}N$ values than the individuals from the Meuse Basin and western France, which is consistent with a contribution of freshwater resources and/or high ^{15}N terrestrial prey. Their $\delta^{13}C$ values were higher than those of the North Sea, which should again be interpreted as a contribution of more terrestrial prey but also could be attributed to the high variability in ^{13}C of the freshwater resources as illustrated by the fish data reported in Fig. 8. An alternative scenario would be the occurrence of additional marine resources in the diet. However, the measured $\delta^{34}S$ values do not support such a hypothesis, since those of the human individuals were comparable with those of most of the terrestrial fauna and were not shifted toward higher values. We thus consider the consumption of freshwater resources as being a possible scenario for the humans from

northern France, especially for the individuals from Val-de-Reuil.

Conclusions and perspectives

The Preboreal proves to be a key period for the change in herbivore habitat. In northern France, the δ^{13}C and δ^{15}N values of the large deer species clearly reflect a transition to dense forest and more productive vegetation sustained by developing soils. The rapid change at the scale of the radiocarbon dating results in a complex baseline with terrestrial resources potentially difficult to distinguish from the aquatic resources. The δ^{34}S values may not be a helpful tracker in this context, since they seem to depend more on the location of the prey than on the ecosystem (terrestrial *versus* aquatic) they belong to. However, if such geographic contrast in ^{34}S relative abundances could be confirmed, such as on other species than wild boar at the site of Warluis, they could represent a promising tool for reconstructing the mobility of the animals and their predators, including human groups. If the MixSIAR calculations do not rule out or confirm the consumption of aquatic resources, they may point to the increasing influence of the forest ecosystem on the human subsistence. Besides, the different possible scenarios are consistent with a diversified diet in terms of source of meat protein. If the consumption of aquatic resources can be suspected, especially in the case of the individuals of Val-de-Reuil, the use of other meat resources was not otherwise disregarded. The whole range of opportunities to access animal protein may have been exploited.

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