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Investigating the diet of Mesolithic groups in the Southern Alps: An attempt using stable carbon and nitrogen isotope analyses

L'alimentation des groupes mésolithiques du Sud des Alpes : nouvelles données par l'étude des compositions isotopiques (carbone, azote) des restes osseux

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Abstract – Stable isotopic data ($\delta^{13}C$; $\delta^{15}N$) were obtained from Mesolithic human and faunal remains from north-eastern Italy in order to document the human diet and provide information on the relationship between landscape use and subsistence strategies. The bone samples were from an adult female individual (Early Mesolithic, Late Sauveterrian) buried at Vatte di Zambana (Trento), an adult male (Late Mesolithic, Castelnovian) buried at Mondeval de Sora (Belluno), and an adult female from Mezzocorona Borgonuovo (Trento). For the latter, the stratigraphic position of the burial pit and evidence of the associated ritual suggest a Mesolithic attribution. Carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) stable isotope compositions of human bone collagen were compared with those of animal remains from different taxa found in stratigraphic association with the burial. The isotopic data and the Bayesian model developed from the latter and from data in the literature indicate a very significant proportion of terrestrial resources in the protein fraction of the human diet, particularly from red deer compared to other ungulates and potentially from freshwater fish and small mammals. These results add to the information provided by zooarchaeological studies and reopen the debate on the role of secondary resources such as chamois, ibex, small mammals and fish, such as pike, in the diet of these mobile human societies. However, as this is a preliminary study based on a very small sample size, interpretations should be considered with caution.

Keywords – Italian Alps, mobility, hunter-gatherer-fishers, bone, collagen

Résumé – Les compositions isotopiques en carbone et en azote ($\delta^{13}C$; $\delta^{15}N$) ont été mesurées sur des restes osseux humains et animaux du Mésolithique dans le nord-est de l'Italie afin de documenter l'alimentation de ces dernières communautés de chasseurs-cueilleurs et les liens entre l'environnement et les stratégies de subsistance. Les restes osseux analysés proviennent d'une femme adulte (Mésolithique ancien, Sauveterrien récent) inhumée à Vatte di Zambana (Trento), d'un homme adulte (Mésolithique récent, Castelnovien) inhumé à Mondeval de Sora (Belluno) et d'une femme adulte du site de Mezzocorona-Borgonuovo (Trento). La position stratigraphique de la sépulture à Mezzocorona-Borgonuovo ainsi que les pratiques funéraires suggèrent une attribution au Mésolithique. Les ratios isotopiques du carbone et de l'azote du collagène osseux des sujets humains ont été comparés avec ceux d'animaux de différentes espèces associés stratigraphiquement aux sépultures. Les résultats isotopiques ainsi qu'un modèle bayésien, réalisé à partir de ces données et celles de la littérature, indiquent une contribution très significative des protéines animales du milieu terrestre, et surtout la consommation importante de cerfs par rapport aux autres ongulés, ainsi qu'un rôle potentiel des poissons d'eau douce et de petits mammifères. Ces données complètent les informations apportées par les études archéozoologiques et relancent la discussion sur le rôle secondaire que peuvent avoir le chamois, l'ibex, les petits mammifères et les ressources aquatiques, comme le brochet, dans la subsistance de ces nomades. Cette étude reste toutefois préliminaire et le faible corpus d'échantillons analysés nous amène à considérer ces interprétations avec prudence.

Mots clés – Alpes italiennes, mobilité, chasseurs-cueilleurs-pêcheurs, os, collagène

Introduction

Subsistence strategies and landscape use are two key and related aspects when reconstructing the life histories of prehistoric populations. Following the stabilisation of climatic conditions at the beginning of the Holocene (ca. 9700 cal BC), a variety of behaviour patterns clearly emerges across Mesolithic Europe with occupation of different landscapes (Crombé and Robinson 2014). North-eastern Italy stands out not only for its particular topography and ecological features, which include both a vast lowland area (the Venetian plain) and the mountainous territory of the south-eastern Alps intersected by valleys, but also for the rich corpus of archaeological data collected in the last 50 years. These studies have helped to delineate the main stages in the process of occupation of this area, from the Late Glacial in the final phases of the Palaeolithic (ca. 17000-9500 cal BC) (Bertola et al., 2007; Montoya et al., 2018) to the gradual and extensive occupation of the area, including the mountainous sector, by Mesolithic hunter-gatherers (9500-5500 cal BC) (Broglio, 1980; 1992; Broglio and Lanzinger, 1996; Kompatscher and Hronzy-Kompatscher, 2007; Fontana, 2011; Fontana et al., 2011; Fontana and Visentin, 2016). At the beginning of the Holocene, the extent of mixed forests increased with rapid warming of the climate and increased rainfall. By the end of the Pre-Boreal (ca. 8250 cal BC), plant cover in the Alps had reached altitudes at least 200 m above today's levels (Soldati et al., 1997; Frisia et al., 2007; Ravazzi et al., 2007; Tinner and Vescovi, 2007; Drescher-Schneider, 2009). Geomorphological studies in the main Alpine valley bottoms, the Adige and the Piave valleys, and in the intra-mountain valleys have identified the presence of lake basins (Bassetti and Borsato, 2005; Carton et al., 2009). The distribution and location of known Mesolithic sites extend from the present-day coast of the Venetian plain to the innermost highland areas, up to ca. 2300 m a.s.l. However, attention has mostly focused on the Alpine area, which has yielded the richest evidence, while the record from the lowland territory is almost exclusively represented by lithic scatters on the surface (Fontana 2011; Fontana and Visentin, 2016).

The subsistence strategies of the groups that occupied north-eastern Italy have been reconstructed primarily through analyses of faunal remains. In particular, the record from the valley-bottom sites in the Alpine area indicates the presence of varied assemblages, with forest ungulates, especially red deer (*Cervus elaphus*), playing an important role at least from the second part of the Pre-Boreal, alongside smaller mammals (Boscato and Sala, 1980; Rowley-Conwy, 1996; Clark, 2000; Bertolini et al., 2016). Moreover, the presence of lakes and marshes along the valley floors favoured the use of wetland species such as fish, beaver and freshwater molluscs (Boscato and Sala, 1980; Cassoli and Tagliacozzo, 1996; Wierer and Boscato, 2006; Wierer et al., 2016). Among the highland sites, only two, Plan de Frea and Mondeval de Sora in the inner Alpine area, have yielded faunal remains. Ungulate species, especially red deer, ibex (*Capra ibex*) and chamois (*Rupicapra rupicapra*), with some small mammals such as hare (*Lepus, cf. timidus*) and marmot (*Marmota marmota*), dominate the assemblages recovered from the Sauveterrian layers of these sites (Angelucci et al., 1998; Fontana et al., 2009a; Thun Hohenstein et al., 2016). Due to poor preservation, there are no data for the lowland areas, but the presence of large forested areas across this territory suggests potential reliance on a wide array of resources, possibly including forest ungulates, small mammals, freshwater and terrestrial molluscs and edible fruit (Fontana et al., 2016b). Moreover, coastal areas offered favourable environments for the use of marine resources but no data are available from the sites located along the present-day coast, except for some possible mollusc remains from sites in the Venice lagoon area, where only surface surveys have been conducted (Broglio et al., 1987; Fontana, 2011; Fontana and Visentin, 2016). Based on assessments of sea-level changes in the late phases of the Pleistocene and during the Holocene, it is also likely that several such sites, and especially those belonging to the earliest phases of the Holocene, are now submerged (Lambeck et al., 2011).

In the 1980s, the main settlement model developed from the rich archaeological evidence in the Alpine area around the river Adige basin and the surrounding highlands focused on mountain areas, which were considered as closed systems. For the Sauveterrian, a model has been proposed based on seasonal mobility from the valley bottoms to the uplands (Early Mesolithic) (Broglio, 1980; Broglio and Improta, 1994-1995; Broglio and Lanzinger, 1996). For the Castelnovian (Late Mesolithic), a gradual decrease in mountain area occupation, with human groups moving towards the lowlands and a trend towards reduced mobility, has been proposed (Bagolini and Broglio, 1985).

In the last twenty years, new data have brought such models into question (Fontana, 2011; Fontana et al., 2011; Fontana and Visentin, 2016). On the one hand, evidence from the pre-Alpine area (e.g. the Cansiglio plateau, Peresani et al., 2009; Visentin et al., 2016a) and the Venetian plain (e.g. the area around the Sile river springs, Fontana et al., 2016b) seems to point to a more complex model of occupation in the Sauveterrian (Fontana et al., 2011). On the other hand, for the Castelnovian, a review of the archaeological record from the upper Piave basin has highlighted intensive occupation in this phase also, potentially signalling more continuity in upland occupation compared to the previous early Mesolithic phase (Visentin et al., 2016b; 2016c). A possible change in the mobility patterns of late Mesolithic groups could thus be related to more organised logistics implying, for example, seasonal migrations to mountain areas of specialised hunting parties instead of family groups (Fontana, 2006). Accordingly, the patterns of occupation by Mesolithic groups in north-eastern Italy should be reconsidered in order to establish whether the Alpine areas and the Venetian plain were part of the same territory or whether they were occupied by different groups (Grimaldi, 2006; Fontana and Visentin, 2016).

In order to obtain new data that could shed light on the relationship between subsistence and landscape use by the last hunter-gatherers of the south-eastern Alps, this study puts forward new points of discussion based on analyses of carbon and nitrogen stable isotope compositions ($\delta^{13}C$ and $\delta^{15}N$). The samples analysed are from three human and eight faunal osteological remains from three sites in the Alpine area: Vatte di Zambana, Mondeval de Sora and Mezzocorona-Borgonuovo (figure 1). Although radiocarbon dates place the latter individual in the transition phase between the Late Mesolithic and Early Neolithic, based on the stratigraphic position of the burial pit and the type of ritual, a Mesolithic attribution has also been proposed (Dalmeri et al., 2002) (table 1). The human sample size is small since only few remains dated to the Mesolithic are known for the Southern Alps. Moreover, we are aware that the selection of animal remains only represents a partial view of the yearly subsistence cycle. The presence of fish remains is also attested at Mondeval de Sora and Mezzocorona-Borgonuovo but these have not yet been the object of a determination study. The present study should therefore be considered as preliminary. Stable isotope analysis will be considered together with other evidence of the subsistence strategies of Mesolithic hunter-gatherers from north-eastern Italy and discussed with respect to the ecosystems assumed to have been occupied by the Mesolithic groups in this region.

The archaeological contexts

Vatte di Zambana (Trento) is a rock-shelter located along the right bank of the Adige valley at an altitude of 220 m a.s.l. The shelter, originally covered by a thick debris cone, is characterised by four anthropic layers (tt. 2-3, 5, 7, 10). Layers 7 and 10 are attributed to the Sauveterrian (early Mesolithic) and layers 2-3 and 5 to the Castelnovian (Late Mesolithic). The female burial was discovered in 1968 in layer 10, close to a recess in the rock-wall (figure 2). The upper part of the body was covered by a mound of 20 stones, with one slab lying on the skull. The individual was in a supine position lying northwest to southeast, with the head turned towards the left. The upper limbs were along the hips, the forearms were flexed and the hands crossed over on the pelvis. No grave goods were identified but some fragments of red ochre were found under the skull (Corrain et al., 1976). The remains belong to a female about 50 years of age. Palaeoanthropological analyses revealed the presence of healed fractures of the right radius and ulna and of the left olecranon, the latter resulting in severe arthrosis of the elbow (Corrain et al., 1976; Villotte, 2008; Sparacello et al., 2018). These health conditions caused a disability in the individual that most probably made her dependent for subsistence on other people in the group. The burial is dated to the final phase of the Sauveterrian (KIA-12442: 7943±46 BP, 7036-

Sampled material	SU	Lab/sample	BP	Δ13 C	Cal BC (95.4%)	Reference
Vatte di Zambana burial, human bone	-	KIA-12442	7943±46	-	7036-6690	Dalmeri et al., 2002
Mondeval de Sora burial, human bone	4	OxA-7468	7425±55	-19.5	6429-6121	Skeates, 1994
Mondeval de Sora burial, charcoal	7II	GX-21793	8260±175	-	7598-6756	Fontana, 1998
Mezzocorona-Borgonuovo burial, human bone	-	ETH-15980	6005±75	-21.0±1.2	5204-4713	Dalmeri et al., 1998; 2002
Mezzocorona-Borgonuovo burial, human bone	-	ETH-15981	6170±70	-22.0±1.2	5301-4947	Dalmeri et al., 1998; 2002
Mezzocorona-Borgonuovo burial, animal bone	151	ETH-15984	64 10±75	-24.2±1.2	5491-5225	Dalmeri et al., 1998; 2002
Mezzocorona-Borgonuovo burial, human bone	-	UtC-7201	6380±50	-23.3	5475-5231	Dalmeri et al., 1998; 2002
Mezzocorona-Borgonuovo burial, human bone	-	UtC-7202	6210±60	-23.8	5304-4999	Dalmeri et al., 1998; 2002
Mezzocorona-Borgonuovo, animal bone	148	KIA-12446	7793-43	-21.11-0.15	6698-6498	Dalmeri et al., 2002

Table 1. Radiocarbon dates for the burial contexts of Vatte di Zambana, Mondeval de Sora and Mezzocorona-Borgonuovo (dates calibrated with OxCal 4.3 – IntCal13) / *Datations par le carbone 14 des contextes sépulcraux des sites de Vatte di Zambana, Mondeval de Sora et Mezzocorona-Borgonuovo (les datations sont calibrées par OxCal 4.3 – IntCal13)*

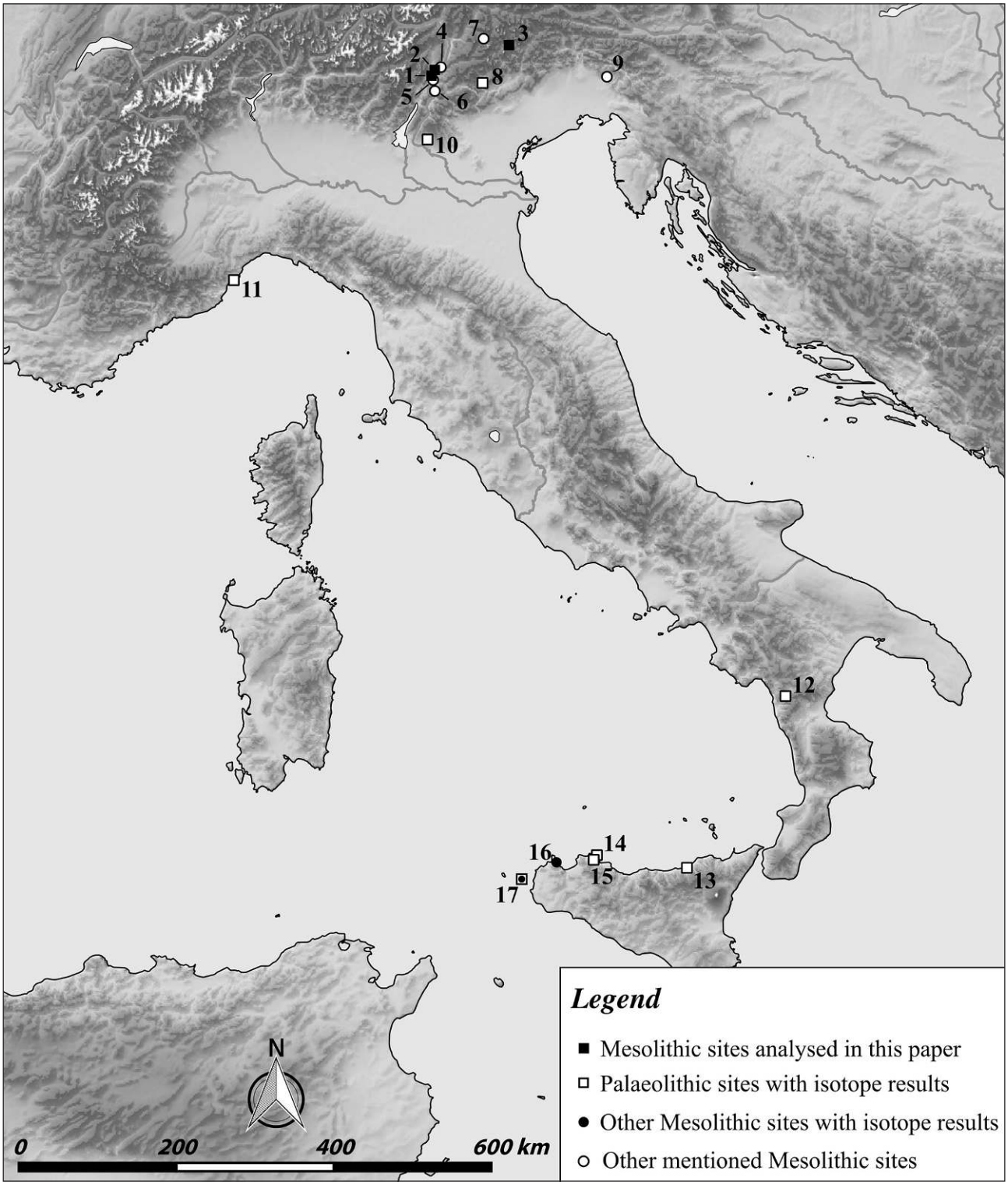

Figure 1. Location of the sites of Vatte di Zambana (1), Mezzocorona-Borgonuovo (2) and Mondeval de Sora (3*) in the Southern Alps (Northern Italy) and of the Italian Upper Palaeolithic and Mesolithic sites mentioned in the text: Galgenbühel (Dos de la Forca) (4), Pradestel (5) - Romagnano Loc III (6), Plan de Frea (7*), Riparo Villabruna (8), Riparo Biarzo (9), Riparo Tagliente (10), Arene Candide (11), Grotta del Romito (12), Grotta San Teodoro (13), Grotta dell'Addaura (14), Grotta Molara (15), Grotta dell'Uzzo (16), Grotta d'Oriente (17). * indicates high altitude sites (around 2000 m a.s.l.) (CAD: D. Visentin) / *Localisation des sites de Vatte di Zambana (1), Mezzocorona-Borgonuovo (2) et Mondeval de Sora (3*) dans les Alpes du sud (Nord de l'Italie) et des sites italiens du Paléolithique supérieur et du Mésolithique mentionnés dans le texte : Galgenbühel (Dos de la Forca) (4), Pradestel (5) - Romagnano Loc III (6), Plan de Frea (7*), Riparo Villabruna (8), Riparo Biarzo (9), Riparo Tagliente (10), Arene Candide (11), Grotta del Romito (12), Grotta San Teodoro (13), Grotta dell'Addaura (14), Grotta Molara (15), Grotta dell'Uzzo (16), Grotta d'Oriente (17). * indique les sites qui se trouvent à haute altitude (DAO : D. Visentin)*

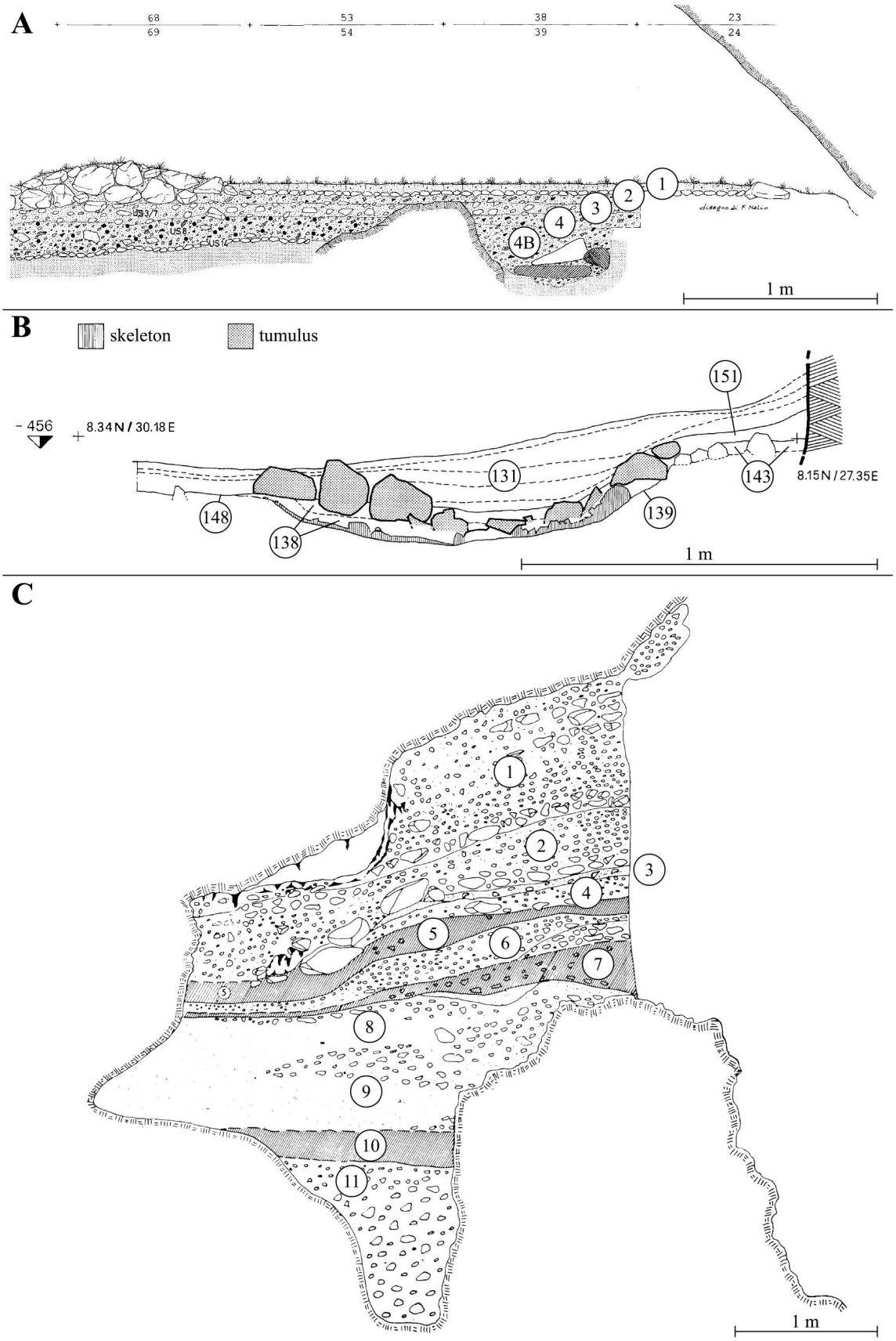

Figure 2. Stratigraphic sections of the sites of the three burials: (a) Mondeval de Sora, sector 1. (b) Mezzocorona-Borgonuovo. (c) Vatte di Zambana / *Coupes stratigraphiques des sites d'où viennent les trois sépultures de cette étude : (a) Mondeval de Sora, secteur 1. (b) Mezzocorona-Borgonuovo. (c) Vatte di Zambana*

6690 cal BC, 95.4%, Dalmeri et al. 2002) (table 1). This result fits in with the burial's stratigraphy and the dates previously obtained from the charcoals in the burial pit (R-491: 8000±110 BP, 7293-6632 cal BC, 95.4%, R-491a: 7740±150 BP, 7050-6269 cal BC, 95.4%) (Corrain et al., 1976). Red deer (*Cervus elaphus)* (NISP=50) is the main species in the layers in stratigraphic association with the burial (layers 11-9). A few remains of chamois (*Rupicapra rupicapra*, NISP=3) and ibex (*Capra ibex*, NISP=4) are also attested along with a few bird remains, but there is no evidence of fish consumption. Two dates are available for layer 10: R-490ȧ 7960±100, 7136-6601 cal BC, 95.4% and R-490, 7860±110, 7047-6499 cal BC, 95.4% (Boscato and Sala, 1980; Clark, 2000). The absence of fish remains in this site represents an exception with respect to the other known Mesolithic valley-bottom sites of the Adige valley and could be related to the technique used in the past when the site was excavated. Vatte di Zambana was in fact the first Italian Mesolithic Alpine site to be investigated at the end of 1960s (Broglio, 2016).

The Mondeval de Sora (Belluno) site is located in the Belluno Dolomites under the overhang of a large erratic dolomite boulder, on a terrace lying 2150 m a.s.l. in the upper valley of the Piave river. Fieldwork carried out between 1986 and 2000 revealed traces of human occupation under three sides of the boulder (Sectors I, II, III). The Castelnovian burial was identified and excavated in 1987 in Sector I, whose stratigraphy spans the Early Mesolithic to the Medieval period (Alciati et al., 1992; Fontana and Vullo, 2000; Fontana and Guerreschi, 2003; Fontana et al., 2009a). The Mesolithic levels, including the burial, have only been preserved in the southern portion of this sector, mostly represented by Early Mesolithic (Sauveterrian) dwelling structures and anthropic layers. The burial lay north to south and parallel to the side of the boulder. The individual had been placed in a supine position with extended limbs (Gerhardinger and Guerreschi, 1989; Guerreschi, 1992; Fontana, 2006; Fontana et al., 2016a). The lower part of the body, from the pelvis downwards, had been covered with stones, apparently collected in the area surrounding the site. A small patch of red ochre was identified near the hand of the individual. Additionally, 60 items had been carefully arranged near different areas of the body. The typology of the objects and their position in relation to the individual point to a role in the funerary ritual (Fontana et al., 2016a; 2020). Seven pierced atrophic canines were recovered in the upper part of the body, while three blades were identified, above each shoulder and below the head respectively. One awl was found on the sternum and another between the knees. Lastly, three groups of various objects (grave assemblages I, II, III) were documented along the left side of the body, possibly indicating they were originally placed inside three separate bags made of organic material (Fontana et al., 2016a). The first assemblage comprised 34 objects: 22 lithic flaked artefacts, three deeply weathered limestone/dolomite pebbles and nine osseous artefacts. The second consisted of three items: a lump of organic substances, mostly resins collected from pines and spruce, and two flint artefacts. The third grave assemblage comprised 11 items: an agglomerate similar to the one found in the second group but mostly made of propolis, a boar tusk and nine lithic artefacts. Paleoanthropological analyses determined that the individual was a robust male about 40 years old and 167 cm tall (Alciati et al., 1992; 2005). Radiographic and histological examinations of the ribs and tibiae suggest a rare form of poliostotic dysplasia also reported as Rosy-Cajal disease, and showed the presence of a healed fracture of the second metacarpal (Alciati et al., 1992; 1997). The dentition displayed an extra-masticatory wear pattern (Alciati et al., 1992; 1995; 1997; 2005). More recent work has focused on the biomechanics of the tibiofibular complex, revealing a certain degree of mobility compatible with seasonal high-altitude hunting, despite the bone abnormality due to systemic disturbances (possibly related to Paget's disease) (Sparacello et al., 2018:386). An AMS radiocarbon date from the individual's remains (OxA-7468) yielded a result of 7425± 55 BP (6429-6121 cal BC, 95.4%) (table 1). Interestingly, the four charcoal samples collected from the burial pit infill (SU 4B) (figure 2) relate to different periods: one (R-1939) is chronologically close (7330±50 BP, 6354-6065 cal BC, 95.3%) to the date obtained for the skeleton, the second (R-1937) is older (8380±70 BP, 7581-7194 cal BC, 95.4%), and two are much more recent (R-1941, 5875±60 BP, 4901-4558 cal BC, 95.5% and R-1936, 4160±55 BP, 2888-2581 cal BC, 95.4%). The occupation layers attributed to the Castelnovian phase (SUs 7, 36 and 100) appear compromised by post-depositional events. One radiocarbon date is available for SU 7II (GX-21793, 8260±175, 7598-6756 cal BC, 95.4%) relating to the final phase of the Sauveterrian. SU 7 in fact lies over SU 8, i.e. the main Sauveterrian occupation layer, and the transition between the two layers was not clear during excavation; moreover, we do not exclude mixing of materials from the two occupation phases, both in the past and as natural post-depositional events. Nevertheless, the species most represented in the presumed Castelnovian layers is red deer (NISP=42), followed by ibex (NISP=18.3) and roe deer (NISP=10.1). Wild boar (*Sus scrofa*) (NISP=3.7) and bear (*Ursus arctos*) (NISP=0.9) are scarce (Govoni, 2006). There are also some fish remains from these layers but they are awaiting analysis. These results are very similar to the species representation for SUs 8 and 31 (Sauveterrian, GX-21788, 9185±240, 9157-7751 cal BC, 95.4%), where chamois is also represented along with a very few remains of *Bos primigenius*, *Canis lupus* and *Vulpes vulpes* (Thun Hohenstein et al., 2016).

The Mezzocorona-Borgonuovo rock-shelter lies at an altitude of 250 m. a.s.l., at the foot of the rocky cliffs of Monte di Mezzocorona (Trento) (Dalmeri et al., 1998; 2002). The shelter is covered by a detritus cone and the stratigraphic sequence spans the period from the Early Mesolithic (Sauveterrian facies) to the Bronze Age. The Mesolithic layers explored in the area where the burial was found were divided into seven "cuts" (I-VII). The burial, which was discovered in 1995, consisted of a shallow pit

about 20 cm deep. The pit cut (SU 139) yielded a layer (SU 148) relating to a recent/final phase of the Early Mesolithic (Sauveterrian) by its lithic assemblage and by radiocarbon dating of an animal bone (KIA-12446, 7793±43 BP, 6698-6498 cal BC, 95.4%) (table 1), and was covered by cut III of SU 131 also attributed to a late phase of the Sauveterrian by its cultural content (figure 2). The top of the burial pit was characterised by a heap of more than forty dolomite stones of various sizes, which were placed directly on the body but mainly on the upper part. They were arranged to form a small burial mound and some of them bore traces of red ochre. A large slab of rock was placed directly on the skull (Dalmeri et al., 1998; 2002). The burial contained the skeletonised remains of a female individual lying east to west in a supine position with the face turned towards the south, the upper limbs slightly bent and the hands placed on the abdomen; the right hand was located on the elbow of the left forearm and the left hand on the pelvis. The lower limbs were extended and parallel. No grave goods were identified, but various small pieces of red ochre were found on different parts of the skeleton and particularly on the thorax. Outside the burial structure, to the east of the skull, an accumulation of chosen faunal remains was identified (SU 151). This consisted of a deer antler and a few deer mandibles with traces of reddish colour, interpreted as probably associated with the burial rite. So far, four ^{14}C dates from the human remains indicate a chronological span from UtC-7201, 6380±50 BP (5475-5231 cal BC, 95.4%) to ETH-15980, 6005±75 BP (5204-4713 cal BC, 95.4%) (table 1), which corresponds to the beginning of the Early Neolithic in the Adige region. One of the animal remains from the accumulation located to the east of the skull (SU 151) yielded an age (ETH-15984, 6410±75 BP, 5491-5225 cal BC, 95.4%) which was very close to one of the dates obtained from the human bones (UtC-7201: 6380±50 BP, 5475-5231 cal BC, 95.4%) (table 1). However, these dates are considered incompatible with the evidence for the early Neolithic levels of the Borgonuovo site because: a) as previously mentioned, the burial was covered by a layer pertaining to the final phase of the Sauveterrian (SU 131-cut III); b) the overlying early Neolithic layers contain a lithic assemblage with technological and typological features associated with a later period of this cultural phase and therefore not compatible with the radiocarbon dates obtained; c) there are several similarities with the burial rite attested at Vatte di Zambana. Moreover, as visible in figure S1 (Annexe 1), consolidating products were used to preserve the human bones and we suspect that some residues, even small ones, could have remained after the different extraction protocols for radiocarbon dating. If so, the radiocarbon date could have been rejuvenated, as chemically demonstrated by Devièse et al. (2019) for Upper Palaeolithic human samples in Mongolia. Following Devièse et al. (2019), the human samples from Mezzocorona-Borgonuovo would benefit from compound-specific radiocarbon dating of collagen amino acid (hydroxyproline) to determine the real chronology and avoid pollution. Pending further analytical possibilities, the burial is considered to be Mesolithic (probably Sauveterrian) in this study. The faunal assemblage coeval with the Mezzocorona burial is very poor and zooarchaeological investigations of the Sauveterrian layers of the site are still in progress. Therefore, only limited preliminary data are currently available. These indicate *Cervus elaphus* as the dominant species, the remains of which appear as very fragmented and badly preserved (A. Fontana pers. com.).

Materials and methods

Stable isotope analysis to reconstruct the diet of past populations

In this study, we applied stable isotope analysis to human and animal bone remains from the Mesolithic levels of the three sites mentioned above. Bone is composed of both inorganic and organic parts from which stable isotope analysis can be performed to infer diet and environment. The organic part of the bone, collagen, is made of amino acids from the protein part of the food consumed (e.g. Ambrose, 2000). The carbon and nitrogen isotopic composition of the collagen ($\delta^{13}C$ and $\delta^{15}N$) mainly allows identification of the relative proportion of animal protein in the diet and the environment used (e.g. Lee-Thorp et al., 1989). As collagen turnover is continuous in bones, for adults it provides information on the proteins consumed over the last ca. 15 years of an individual's life (Valentin, 2003; Hedges et al., 2007). Carbon isotope ratios mainly indicate the environmental origin of proteins (e.g. terrestrial vs. marine) (DeNiro and Epstein, 1978). The $\delta^{13}C$ values from plants depend on their photosynthetic pathway: C_3, C_4 and CAM (Farquhar et al., 1989). As C_4 plants were virtually absent in Pleistocene Europe, the $\delta^{13}C$ values of animal bone collagen make it possible to discriminate between marine/freshwater and terrestrial foods consumed and can yield information about the ecosystem (e.g., open vs. closed environments) (see review in Salazar-García et al., 2018. Nitrogen isotope ratios indicate the trophic level at which the individual was operating (e.g. herbivore vs. carnivore) as there is $\delta^{15}N$ enrichment by ca. 3-5‰ between prey and predator (e.g., Bocherens and Drucker, 2003) and can thus provide environmental information as well (see review in Goude and Fontugne, 2016).

Samples selected for stable isotope analysis

Stable carbon and nitrogen isotope ratio analyses were performed on bone collagen extracted from three human and nine animal bone samples from Vatte di Zambana (n=4), Mezzocorona-Borgonuovo (n=1) and Mondeval de Sora (n=6) (table 2). For each human individual, and for preservation purposes, only a small rib fragment was sampled (table 2): no trace of bone modification and/or pathology was visible on the anatomical part selected (SI 1).

In order to provide comparative data to interpret the human isotope values, nine adult bone samples were selected from the faunal assemblage. The few samples available

Species	Sample	SU/Layer	Collagen yield	Nitrogen Content (%)	$\delta^{15}N_{Air}$ (‰)	Carbon Content (%)	$\delta^{13}C_{V\text{-}PDB}$ (‰)	C/N
Vatte di Zambana								
Homo sapiens	Rib	burial	56.2	12.9	9.1	36.5	-20.2	3.3
Rupicapra rupicapra	Left metatarsal	XX, layer 9	41.6	13.9	3.1	39.4	-20.1	3.3
Cervus elaphus	Metatarsal	Sect. 6, hearth III, layer 10	17.2	13.3	4.0	37.1	-22.2	3.2
Cervus elaphus	I phanx	XX, layer 9	65.7	14.3	4.0	40.5	-22.3	3.3
Mondeval de Sora								
Homo sapiens	Rib	(SU 4)	193.2	12.4	9.1	34.3	-19.9	3.2
Capra ibex	Left radius	Q. 57/8, SU 100	83.9	11.9	1.8	33.3	-19.3	3.3
Capra ibex	I phalanx	Q. 84/7, SU 7	74.2	11.8	2.1	33.8	-19.2	3.3
Capra ibex	Metatarsal	Q. 84/7, SU 7	59.2	11.7	1.9	33.4	-19.6	3.3
Cervus elaphus	I phalanx	Q. 84/7, SU 7	60.8	12.8	4.1	36.2	-21.7	3.3
Cervus elaphus	Left tibia	Q. 100/2, SU 7	48.8	11.6	3.2	32.7	-21.7	3.3
Mezzocorona-Borgonuovo								
Homo sapiens	Rib	(SU 139)	90.3	12.8	9.4	36.2	-19.9	3.3
Cervus elaphus	Mandible	SU 151, cut IV	-	-	-	-	-	-

Table 2. Collagen yield and elemental and stable isotope compositions (C, N) of the bone collagen samples from Vatte di Zambana, Mondeval de Sora and Mezzocorona-Borgonuovo / *Rendement d'extraction et compositions élémentaires et isotopiques (C, N) du collagène osseux des échantillons de Vatte di Zambana, Mondeval de Sora et Mezzocorona-Borgonuovo*

were chosen according to their state of preservation. Fragments of thick and compact bone (diaphysis of long bones and phalanges) were selected to avoid spongy tissue, burnt bones and remains with cut-marks on the surface. These selection criteria and the limited range of omnivores and carnivores in the faunal assemblages restricted the samples to herbivores only (table 2). Three samples – two of red deer (*Cervus elaphus*) and one of chamois (*Rupicapra rupicapra*) – were taken from the Sauveterrian layers (SUs 11-9) of Vatte di Zambana (Clark, 2000). Five adult bone samples – three of ibex (*Capra ibex*) and two of red deer (*Cervus elaphus*) – were selected from the faunal assemblage of Mondeval de Sora SUs 7 and 100. These stratigraphic units correspond to the Castelnovian although they could include some contamination from the Ancient Mesolithic (Sauveterrian). An attempt was made to select the most reliable ones (table 2). One red deer mandible fragment was selected from available remains at Mezzocorona-Borgonuovo that were stratigraphically close to the burial layer (SU 151). No fish remains were sampled since no detailed analysis was yet available.

Collagen extraction and isotope ratio mass spectrometry

Collagen was extracted from the 12 samples following the Longin (1971) and Bocherens et al. (1997) protocols. Each sample was cleaned by abrasion and washed with distilled water. The cleaned samples were ground into a powder (0.7 mm sieve). The bone powder was first demineralised in an HCl solution (1M, 20 min, room temperature). The residue was soaked in an NaOH solution (0.125M, 20h, room temperature), and solubilised in a weak acid solution (HCl, 0.01M, 17h, 100°C). The dissolved collagen solution was filtered and freeze-dried for 48h in preparation for the analyses.

The elemental compositions (C, N) and stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of the extracted collagen were determined with an Elemental Analyser (Europa Scientific) coupled with an Isotope Ratio Mass Spectrometer (Europa Scientific 20-20 EA-IRMS; Iso-Analytical Ltd). The laboratory standards used[1] were calibrated against IAEA international standards for all measurements; the measurement error was 0.1‰ for carbon and nitrogen. Collagen preservation was checked according to the criteria set out by DeNiro (1985), Ambrose (1990) and van Klinken (1999).

Results and discussion

The stable isotope results, collagen quality indicators and other details obtained from the human and faunal samples analysed are presented in table 2. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values for the human and faunal remains are shown in figure 3.

1 IA-R042 bovine liver; IA-R001 wheat flour; IA-R005/IA-R045 mixture of beet sugar and ammonium sulfate.

Bone collagen preservation

Except for one animal sample, all the remains analysed satisfied the standard protocol for the control of collagen quality and quantity (DeNiro 1985; Ambrose 1990; van Klinken 1999). The collagen yield was clearly higher than 10 mg/g as established by Ambrose (1990) with an average value of 71.9±45.0 mg/g (n=11). Following van Klinken (1999), the C and N contents of 32.7% to 40.5% and of 11.6% and 14.3% respectively indicate that collagen was well preserved. The atomic C:N ratio also indicates good preservation according to DeNiro's (1985) recommendations and ranges between 3.2 to 3.3.

Carbon and nitrogen isotope ratios from the herbivore species

Unfortunately, the single animal sample from Mezzocorona-Borgonuovo did not yield sufficient collagen to be included in the following presentation of data. The mean isotope values of the herbivores from Vatte di Zambana (n=3) are -21.5±1.2‰ for $\delta^{13}C$ and 3.7±0.5‰ for $\delta^{15}N$. Those of the herbivores from Mondeval de Sora (n=5) are -20.3±1.3‰ for $\delta^{13}C$ and 2.6±1.0‰ for $\delta^{15}N$. The $\delta^{13}C$ mean value from Vatte di Zambana (21.5±1.2‰, n=3) echoes the general ^{13}C depletion that began at the start of the Bølling-Allerød interstadial and is better observed at the beginning of the Holocene in the bone collagen of herbivores from north-western Europe (ca. 9-8,5 ka BP) (Richards and Hedges, 2003; Gazzoni et al., 2013). For *Cervus elaphus*, the values obtained for the samples from the two sites ($\delta^{13}C$: -22.2±0.3‰) are in the known range for this species in various Pre-Boreal and Boreal sites in the Jura area ($\delta^{13}C$: -23.2±0.6‰), the French northern Alps ($\delta^{13}C$: -21.0±0.8‰) (Drucker et al., 2003; 2008) and the north-western Europe Mesolithic (Richards and Hedges, 2003). The similarity of $\delta^{13}C$ recorded for red deer in the two sites studied could reflect hunting mainly at high altitudes (whole carcasses are represented at Mondeval de Sora; Thun Hohenstein et al., 2016), with portions of the prey brought back down to the valley (mostly limbs are attested in valley-bottom sites; Clark, 2000). Two further points should also be mentioned: 1. in mountain areas, red deer tend to reach higher altitudes in the summer season and make their way down to the forest during the coldest periods of the year (Luccarini et al., 2006; Kropil et al., 2015); 2. the range of values recorded for herbivores in both sites does not fully reflect the variability of data, given the very small sample size available for this study.

The $\delta^{15}N$ values for the faunal remains from Vatte di Zambana (3.7±0.5‰, n=3) fall within the range of values recorded in herbivore bone collagen from north-western Europe between 12.5 and 8.5 ka BP (Richards and Hedges, 2003). Changes in nitrogen ratios after the Late Glacial are better documented and a general increase in ^{15}N is observed in the Holocene (Drucker et al., 2003; Richards and Hedges, 2003). At Mondeval de Sora, the nitrogen values (2.6±1.0‰, n=5) do not show this increase and the values are lower than the mean herbivore values from coeval European samples (*ibid.*). This could be explained by different climatic factors specific to high altitudes (Ambrose and DeNiro, 1986; Ambrose, 1990; Ambrose, 1993; Mariotti et al., 1980; Drucker et al., 2003), but most of all, it underlines the need to increase faunal sampling in the future to better define the variability of isotopic composition for herbivore species feeding across a large territory.

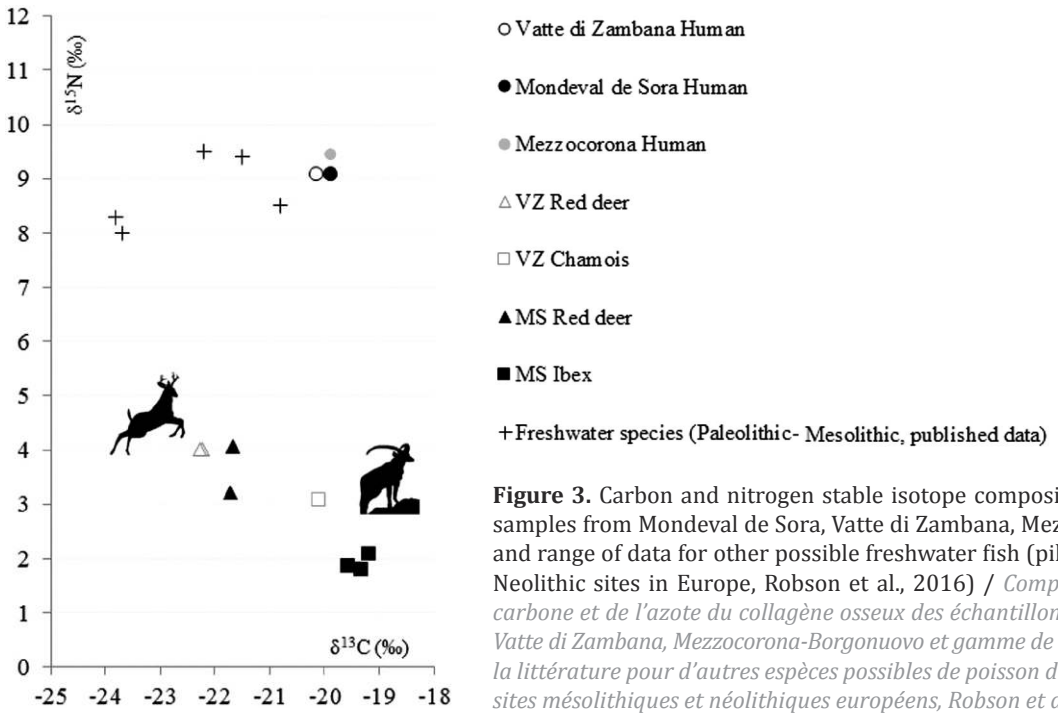

Figure 3. Carbon and nitrogen stable isotope compositions of bone collagen samples from Mondeval de Sora, Vatte di Zambana, Mezzocorona-Borgonuovo and range of data for other possible freshwater fish (pike from Mesolithic and Neolithic sites in Europe, Robson et al., 2016) / *Compositions isotopiques du carbone et de l'azote du collagène osseux des échantillons de Mondeval de Sora, Vatte di Zambana, Mezzocorona-Borgonuovo et gamme de valeurs disponibles dans la littérature pour d'autres espèces possibles de poisson d'eau douce (brochets de sites mésolithiques et néolithiques européens, Robson et al., 2016)*

Both for Mondeval de Sora and Vatte di Zambana, the inter-species difference in values for carbon (Δ 2.3‰ for both sites) and nitrogen (Δ from 0.9 to 1.8‰) distinguish populations that are more related to woodland areas (red deer) from those living mostly in open environments (chamois and ibex, figure 3). This observation could therefore be related to the different ecological areas used and the different dietary preferences of each species (Bocherens et al., 2006; Drucker et al., 2008; Schweiger et al., 2015). Red deer and ibex/chamois probably consumed food of isotopically diverse compositions, i.e. various types of trees or grasses from different habitats as demonstrated by the modern study of Schweiger et al. (2015) indicating low plant biomass for chamois, varied plant biomass for ibex and high plant biomass for red deer foraging areas. Lichens, for example, exhibit more positive $\delta^{13}C$ values than their coeval vascular plants and their consumption affects the isotopic value of the animals that feed on them (Heaton, 1999; Fizet et al., 1995). Ibex in particular, which feed mostly on lichens, display higher $\delta^{13}C$ values than red deer (Mustoni et al., 2005). For red deer, the similar isotopic composition recorded in both sites is consistent with current ecological knowledge on this species.

Carbon and nitrogen isotope ratios from the human remains

The isotope values for the human individuals compared to the related coeval herbivores were higher on average by +1.3‰ in $\delta^{13}C$ and +5.4‰ in $\delta^{15}N$ at Vatte di Zambana, +0.4‰ in $\delta^{13}C$ and +6.5‰ in $\delta^{15}N$ at Mondeval de Sora (table 2). Considering the mobility of humans and their use of different ecosystems according to seasons during the Mesolithic, it is very likely that the faunal remains sampled at each site do not reflect the variety of protein sources accessible during the year to the humans buried at each of the sites. Consequently, and also taking into account the lack of local animal data for Mezzocorona-Borgonuovo, we have considered the isotopic data of Mondeval de Sora and Vatte di Zambana together as a common local baseline for the three human individuals analysed. We also consider that the two females belong to the late phase of the Sauveterrian: their chronology therefore does not diverge too much from that of Mondeval de Sora. Moreover, during the time span that includes the dates of the Vatte di Zambana and Mondeval de Sora burials – i.e. the 7th millennium cal BC – the local environment was covered by dense forests and, as far as we know, there do not appear to have been any major environmental changes in the southern Alpine area. Lastly, we have said that the faunal sample from Mondeval de Sora might be mixed with some Sauveterrian fauna and the date we have for SU 7, from which most of the faunal samples were selected, is indeed very close to that of the Vatte di Zambana burial.

The resulting isotope values for the three human individuals are higher than for the whole herbivore assemblage by ca. +0.8‰ in $\delta^{13}C$ and +6.2‰ in $\delta^{15}N$ on average. These values indicate that the protein fraction of the diet came almost exclusively from animal rather than plant resources. Ungulate meat seems to have provided a significant part of the protein consumed by all the individuals, but other sources from a higher trophic level, such as carnivores, young animals (not weaned) or fish species should be considered for discussion because of the large $\delta^{15}N$ accumulation between prey and predator.

The potential use of aquatic and other mammal resources can be further investigated by using stable isotope information available in the literature. Isotopic measurements performed on bone collagen from Eurasian lacustrine fish by Dufour et al. (1999) exhibit relatively low $\delta^{13}C$ values for freshwater species (<-17‰ for modern samples). For nitrogen isotope ratios, France (1995) asserts that marine fish are higher in ^{15}N compared to freshwater specimens, while estuarine and anadromous fish show intermediate $\delta^{15}N$ values depending on the time spent feeding in either fresh or saltwater (Schoeninger and DeNiro, 1984; France, 1995). Consequently, freshwater fish could be candidates to explain the values for both $\delta^{13}C$ (similar to terrestrial values) and $\delta^{15}N$ (similar to species from aquatic resources) for the three individuals.

Sources of the protein in the human diet

To further test the hypothesis of the potential role of aquatic and terrestrial protein sources in the Mesolithic human diet of the south-eastern Alps we evaluated some of the food items by incorporating them into a Bayesian model (FRUITS; Fernandes et al., 2014). The Bayesian approach proposed by FRUITS (Food Reconstruction Using Isotopic Transferred Signals; https://sourceforge.net/projects/fruits) allows the use of small size samples, multiple isotopic proxies and various source fractions (information provided in SI 2 for our models). Freshwater fish and particularly pike (prehistoric data from Europe, Robson et al., 2016) are compared to three other potential sources of protein from the terrestrial environment: red deer (this study), chamois and ibex (this study) and beaver (modern data corrected, Keenan et al., 2019) (figure 4). It is worth keeping in mind that this approach, as well as other model types (e.g. SIAR Stable Isotope Analysis in R), provides a relative estimation of food sources consumed within the restricted context defined by each study (i.e. relative proportion of a food compared to the other food item chosen to run the model) and cannot be considered as a general pattern (at least in our study where only some selected protein sources are used).

The FRUITS Bayesian models generated by our data (figure 4) show that red deer were the main source of protein for all the individuals. Aquatic sources like pike could have had the same importance as chamois and ibex, or even more. The role of chamois and ibex is not to be neglected, particularly for Mondeval de Sora and Mezzocorona-Borgonuovo. Beaver seems more marginal compared to ungulates and fish, except in the Vatte di Zambana female. This result is not surprising as in some Sauveterrian sequences

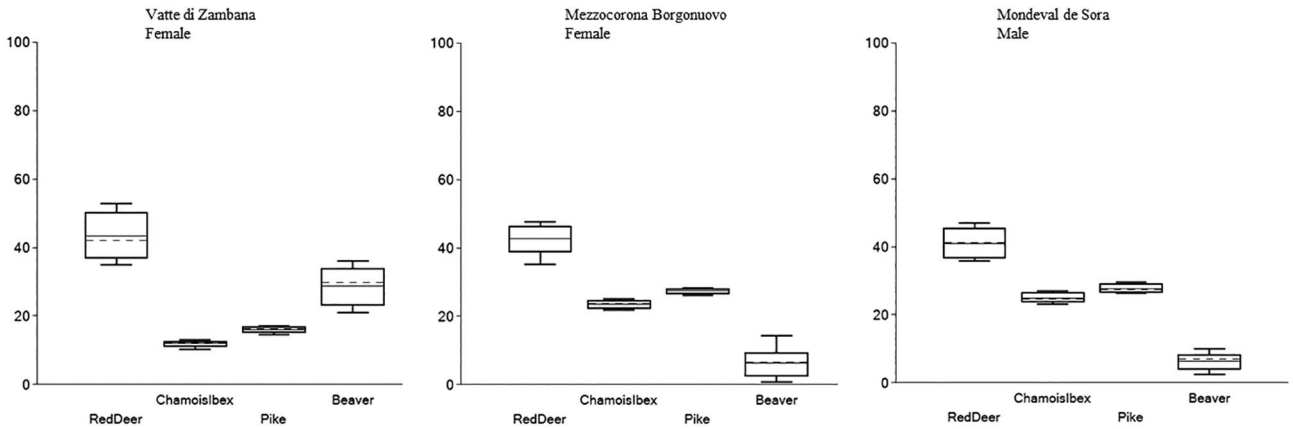

Figure 4. Bayesian model estimate of the proportion of four protein sources in the human diet at Vatte di Zambana and Mondeval de Sora and Mezzocorona-Borgonuovo (FRUITS; Fernandes et al., 2014). Herbivore data are from this study. The archaeological data for pike and beaver are from the literature (pike: Robson et al., 2016; modern bone collagen data for *Castor canadensis* from Keenan et al., 2019, $\delta^{13}C$ corrected by +1.4‰ due to the Suess effect; Marino and McElroy 1991). Details are provided in Tables S1 and S2 (Annexes 2-3). Box plots indicate mean, median and credible intervals at 68 and 95% / *Estimations, évaluées par un modèle bayésien (FRUITS ; Fernandes et al., 2014), des proportions de quatre sources de protéines animales contribuant à l'alimentation humaine à Vatte di Zambana, Mondeval de Sora et Mezzocorona-Borgonuovo. Les données sur les herbivores proviennent de cette étude et celles du brochet et du castor proviennent de la littérature (brochet archéologique : Robson et al., 2016. Collagène osseux actuel de Castor canadensis : Keenan et al., 2019 ; le $\delta^{13}C$ a été corrigé de +1.4 ‰ en raison de l'effet Suess, Marino et McElroy 1991). Le détail de l'utilisation du modèle est présenté dans les tableaux S1 et S2 (Annexes 2-3). Les Box plots indiquent les moyenne, médiane et intervalles de crédibilité à 68 et 95 %*

of the region, beaver is significantly represented in faunal assemblages, for example at Galgenbühel (Wierer et al., 2016). Although the Bayesian model we have discussed does not include marine species, this resource cannot be totally excluded.

At the Mondeval de Sora site, the Late Mesolithic faunal assemblage (SUs 7 and 100) is dominated by ungulate remains, such as red deer, ibex and roe deer, with percentages similar to those from the Sauveterrian layers (Govoni, 2006). The same layers also record the presence of a few bones of omnivores (*Sus scrofa*, 4% of the faunal assemblage, NR=3.7) and carnivores (*Ursus*, 1% of the faunal assemblage, NR=0.9). The list of species attested at Mezzocorona-Borgonuovo is unfortunately not available, while the faunal assemblage of Vatte di Zambana (layers 10-7 or 11-9), particularly in the layers associated with the burial pit (Final Sauveterrian), is dominated by *Cervus elaphus* with a few remains of *Capra ibex* and *Rupicapra rupicapra*. Some remains of *Avies sp*. and *Emys orbicularis* are also attested (Boscato and Sala, 1980; Clark, 2000). To build a wider framework of the animal resources consumed by the Mesolithic hunter-gatherers, it is worth looking into the other sites of the Adige valley that have yielded the richest faunal assemblages. The ibex is the main species only in the most ancient layers (AF and AE) at Romagnano, relating to the earliest Sauveterrian and with few remains. In the subsequent phases of the Sauveterrian, the red deer becomes the most represented taxon, associated with roe deer, ibex and chamois in various proportions. A similar situation is attested at the site of the Pradestel rock-shelter (Boscato and Sala, 1980; Clark, 2000). At Galgenbühel, a rock-shelter dated to the middle Sauveterrian, the main species is the wild boar (*Sus scrofa*) associated with red deer (Wierer and Boscato, 2006; Wierer et al., 2016). A similar situation occurs at the Biarzo rock-shelter in the Natisone valley bottom, further east (Rowley-Conwy, 1996; Bertolini et al., 2016). In the Late Mesolithic (Castelnovian), a considerable decrease of ibex and chamois is recorded in the faunal assemblages of the southern Alpine valley bottom sites. This evidence reflects the establishment and increased density of broadleaved forests during the Boreal and the Atlantic, as also attested by palynological studies (Cattani, 1977; 1994). This environmental change could have favoured the spread of red deer in the Alpine areas and narrowed the open areas that represent ideal environments for the survival of ibex and chamois. Clarks (2000:236) argues that the decrease of chamois and ibex could also be related to "the fact that high-altitude hunting was no longer taking place at the scale previously recorded". However, this hypothesis can be reconsidered in the light of the latest research, based on the considerable presence of Castelnovian sites in the upper Piave valley, although we cannot exclude a change in the mobility patterns of Late Mesolithic groups as they developed more organised logistics (Fontana, 2006; Visentin et al., 2016b). Lastly, the location of the Mondeval de Sora burial at an altitude of 2150 m a.s.l. in the Dolomites and the rich composition of the hunter's grave goods – including a number of items made of red deer antler and bone – confirm the importance of red deer for the subsistence and technology of the last Alpine Mesolithic groups (Fontana

et al., 2016; 2020). Some carnivores are also present in the faunal assemblages of the Adige valley sites, especially those of small size such as pine marten, wolf, wild cat and fox, which are associated with some brown bear remains. One specimen of the latter species from layer AC8-4 at Romagnano shows evidence of processing for bone marrow extraction. Also, Clarks (2000) underlines three main broad trends in the later stages of the Sauveterrian and the Castelnovian at the Pradestel, Romagnano III and Riparo Gaban sites. These trends consist of: a) an increase in species diversity (more use of smaller mammals); b) an increase in younger animal bones, particularly of red deer; c) a general increase in the range of bone types. The contribution of young ungulates, such as red deer, to explain the high $\delta^{15}N$ accumulation between the animal baseline and humans can be proposed, but no isotopic data are available to test this hypothesis. However, this issue should also be considered for future studies.

All Mesolithic layers at Romagnano Loc III, Pradestel and Galgenbühel contain evidence of bird, fish, beaver and freshwater turtle and mollusc remains. At Galgenbühel the beaver is well attested (between 18% to 50% according to the layers) in association with the otter. In this site 12,716 fish remains were also identified. The fish spectrum is dominated by *Cyprinidae*, which are represented by a wide variety of species, and by *Esocidae*, especially pike (*Esox sp.*). This evidence reflects the use of dump areas along the Adige valley and subsistence focusing mostly on valley-bottom resources, which were largely used during the spring and summer (Wierer et al., 2016).

To summarise, carnivores do not seem particularly significant as a resource complementing ungulates in the diet of the last hunter-gatherers of north-eastern Italy. Not only are they rather poorly attested in the sites of the south-eastern Alps, it is also probable that they were rarely consumed and mostly used for their fur (Clark, 2000; Wierer and Boscato, 2006; Bertolini et al., 2016). Therefore, considering the archaeological and geographical contexts and the expected distribution of isotopic values for dietary sources from marine and freshwater ecosystems (fish, shellfish and birds; France, 1995; Fischer et al., 2007), and the results given by the Bayesian model, the consumption of aquatic resources is still a relevant option to explain the $\delta^{15}N$ values of the three human individuals compared to the herbivores. This hypothesis is supported by the presence of fish remains in the Mesolithic levels of Mondeval de Sora and Mezzocorona-Borgonuovo, even though no information about quantities, fish species or their origin – e.g., sea, lake or river – are currently available. Also for Mondeval de Sora, different freshwater ecosystems in the area surrounding the site – including numerous rivers and streams (e.g. the Piave ca. 22 km and its main tributaries such as the Cordevole) and lakes (e.g. Fedaia ca. 16 km, Misurina ca. 17 km), suggest a preference for fishing in a circum-local environment. A habitat of prevailing slack and slow flowing waters, as seen along the Adige valley, possibly also characterised the Piave river valley that provided the best access to the Mondeval de Sora area. Moreover, the results of analyses of lithic raw materials from the burial goods indicate a western (Adige valley) and an eastern provenance (Friulian piedmont) and therefore a pattern of wide-ranging mobility for the Late Mesolithic male individual buried at Mondeval de Sora (Fontana et al., 2016a; Fontana et al., 2020). Pike (*Esox sp.*) and sturgeon (*Acipenseridae*) could be relevant candidates as food sources as they are autochthonous to the Po Valley and are still widespread today in the rivers of north-eastern Italy (Po, Adige, Brenta, Piave, Tagliamento) (Grimaldi and Manzoni, 1990). Pike is best caught between spring and autumn, during its migrations from deep river waters to the coast. A harpoon included in the grave goods of the male individual from Mondeval de Sora strengthens the suggestion that fishing was important among these groups and that this individual probably also fished (Alciati et al., 1992; Guerreschi, 1992; Fontana et al., 2000). Another harpoon comes from the Castelnovian layers of the Romagnano Loc III site in the Adige valley (Trento), and harpoons generally appear in the Late Sauveterrian in the Southern Alps (Cristiani, 2009).

Comparison with the last upper Palaeolithic individuals from Italy

The stable isotope data obtained from north-eastern Italian sites are the first for inland Mesolithic groups in Italy. In this same region, some dietary information comes from stable isotope analyses of human remains from inland Late Pleistocene contexts (table 3), e.g., Riparo Tagliente (Stallavena di Grezzana, Verona) and Riparo Villabruna (Sovramonte, Belluno) (Vercellotti et al., 2008; Gazzoni et al., 2013, Oxilia et al., in press) (figure 1). The Late Epigravettian individual from Riparo Tagliente (OxA-10672: 13190±90 BP; 16634-15286 cal BP) seems to have had a diet combining a large amount of terrestrial mammals with a possibly significant intake of freshwater resources (Gazzoni et al., 2013). For the Villabruna hunter, dated ca. 2000 years later (KIA-27004: 12140±70 BP; 14160-13820 cal BP), the authors propose a diet mainly based on the consumption of terrestrial proteins from herbivores (Vercellotti et al., 2008). However, this site needs further isotope analysis, particularly on animal remains, to confirm this pattern. The estimated distance from the Adriatic coast of the two sites at the time of the burial of the two individuals has been calculated as about 418 km for Riparo Tagliente and 354 km for Villabruna, thus almost equalling the distance to the Tyrrhenian coast (table 3). It should be noted that climatic and environmental conditions were consistently different in the two relevant phases of the Late Epigravettian. At Riparo Tagliente, data from the layers coeval to the burial indicate a dominant open steppe environment (Gazzoni et al., 2013), while the occurrence of some lithic artefacts made on chert form the Umbria-Marche area suggests connections with the mid-Adriatic region (Bertola et al., 2018). The burial of the Villabruna individual corresponds to the initial phase of the Late Glacial interstadial with milder climatic conditions and the spread

of woodland habitats in the Southern Alps (Ravazzi et al., 2007). During the Late Glacial period, there is no evidence of occupation in the Venetian plain although we cannot exclude that the last Palaeolithic hunters settled in this area and that evidence of this occupation has been masked by intense alluvial processes (Fontana et al., 2008). For the Mesolithic, the archaeological record attests occupation from the present-day Adriatic coast to the innermost areas of the Alps (Fontana 2011; Franco, 2011; Fontana and Visentin, 2016). At the time of the burial of the woman at Vatte di Zambana, the distance from the coast had shortened considerably (217 km) while at the beginning of the Atlantic period, the Adriatic Sea was ca. 135 km away as the crow flies from the Mondeval de Sora site (table 3). Its closeness to the sea and the evidence of human occupation in the present-day Venice lagoon area could indicate that the people buried in the Alps had a pattern of mobility spanning an area from the Alps to the Adriatic coast. However, the results of isotope analysis for these individuals, as for those of the Late Palaeolithic, do not point to significant use of marine resources. The main evidence of connections with either the Adriatic or the Tyrrhenian Sea throughout the period from the Late Glacial to the early and first part of the middle Holocene in the south-eastern Alps is represented by the presence of ornamental shell beads. In the Late Palaeolithic/Late Epigravettian, *Tritia neritea* is the main species attested (Bertola et al., 2007), while in the Mesolithic, *Columbella rustica* becomes the main species represented (Cristiani, 2009). One specimen of *Columbella rustica* comes from the Sauveterrian layers of the high-altitude Mondeval de Sora site (unpublished).

Also in southern Italy, at Grotta del Romito on the Tyrrhenian side of the peninsula (figure 1), most individuals from the Late Epigravettian had a similar terrestrial diet with the exception of Romito 9, which is dated to several millennia earlier than the others (LTL-3034A: 13915±70 BP; 17000-16150 cal BP). For this individual, a more varied diet based on freshwater and/or marine fish in addition to terrestrial animals has been suggested (Craig et al., 2010).

Information from stable isotopes on the diet of coastal hunter-gatherers is also available for different Mediterranean sites from the mid-Upper Palaeolithic to the Mesolithic (García Guixé et al., 2006; 2009; Craig et al., 2010; Mannino et al., 2011; 2012; 2015; Fernández-López de Pablo et al., 2013; Fontanals-Coll et al., 2014; Salazar-García et al., 2014; Colonese et al., 2018). A review of the data is available in Salazar-García et al. (2018). Little or no consumption of marine food is attested by the Italian samples, except for the Gravettian individual from Arene Candide known as "Il Principe" (figure 1) (Pettitt et al., 2003). A slight increase in marine food consumption is recorded in Sicily from the Late Pleistocene to the early Holocene (figure 1) (Mannino et al., 2012; 2015; Colonese et al., 2018). Most authors argue that the limited evidence for marine resource consumption in most Mediterranean areas could be a consequence either of the Mediterranean Sea's low productivity compared to the Atlantic Ocean (review in Salazar-García et al., 2018) or of the absence of adequate technology for intensive fishing (Mannino et al., 2011; Mannino and Richards, 2018).

To summarise, compared to the published data for western Europe (Mediterranean, Croatia, France and Belgium) from ca. 10200-7100 cal BP (figure 5; Annexe 2) this study documents the variability of protein intake among the last European hunter-gatherers at the intra- and inter-site levels, including both terrestrial and aquatic (mainly freshwater) resources, and points to the adaptability of human subsistence strategies at the time.

Sampled material	OxCal 4.3 – IntCal13 (cal BC) (95.4%)	cal BP (2σ)	Mean cal age	Coordinates (WGS84)	Palaeo sea level	Palaeocoastline distance, Km
Mondeval de Sora burial	6429-6121	8379-8071	8,225	12.0940; 46.4664	-12,9	**135**
Vatte di Zambana	7036-6690	8986-8640	8,813	11.0694; 46.1481	-18,7	**217**
Riparo Villabruna	12237-11830	14187-13780	13,983,50	11.7650; 46.0843	-81,2	**354**
Riparo Tagliente	14200-13583	16150-15533	15,851,50	11.0056; 45.5406	-102,4	**418**

Table 3. Distance of the Mesolithic sites of Vatte di Zambana and Mondeval de Sora and the Late Epigravettian sites of Riparo Tagliente and Riparo Villabruna from the palaeocoastline at the time when the single individuals were buried. The distances were estimated from the radiocarbon dates (mean radiocarbon age) obtained from the human samples and the sea level was calculated using the model proposed by Lambeck et al. (2011) and applied to the Adriatic seabed without taking into account the thickness of sediments deposited between 15.8 and 8.2 cal BP. For Mezzocorona-Borgonuovo, approximately the same distance to the coastline can be considered as for Vatte di Zambana, as the two sites are close and possibly have a similar chronology / *Distance entre les sites mésolithiques de Vatte di Zambana, Mondeval de Sora et les sites épigravettiens de Riparo Tagliente et Riparo Villabruna et le trait de côte au moment de l'inhumation des individus. Les distances sont estimées à partir des datations par le carbone 14 (moyenne des âges radiométriques réalisée sur les échantillons humains) et le niveau marin calculé par le modèle proposé par Lambeck et al. (2011) et appliqué aux fonds marins adriatiques sans prendre en compte l'épaisseur des sédiments déposés entre 15,8 et 8,2 ka BP cal. Pour Mezzocorona-Borgonuovo, une distance par rapport à la côte similaire à celle considérée pour Vatte di Zambana est proposée compte tenu que les deux sites sont proches et probablement contemporains*

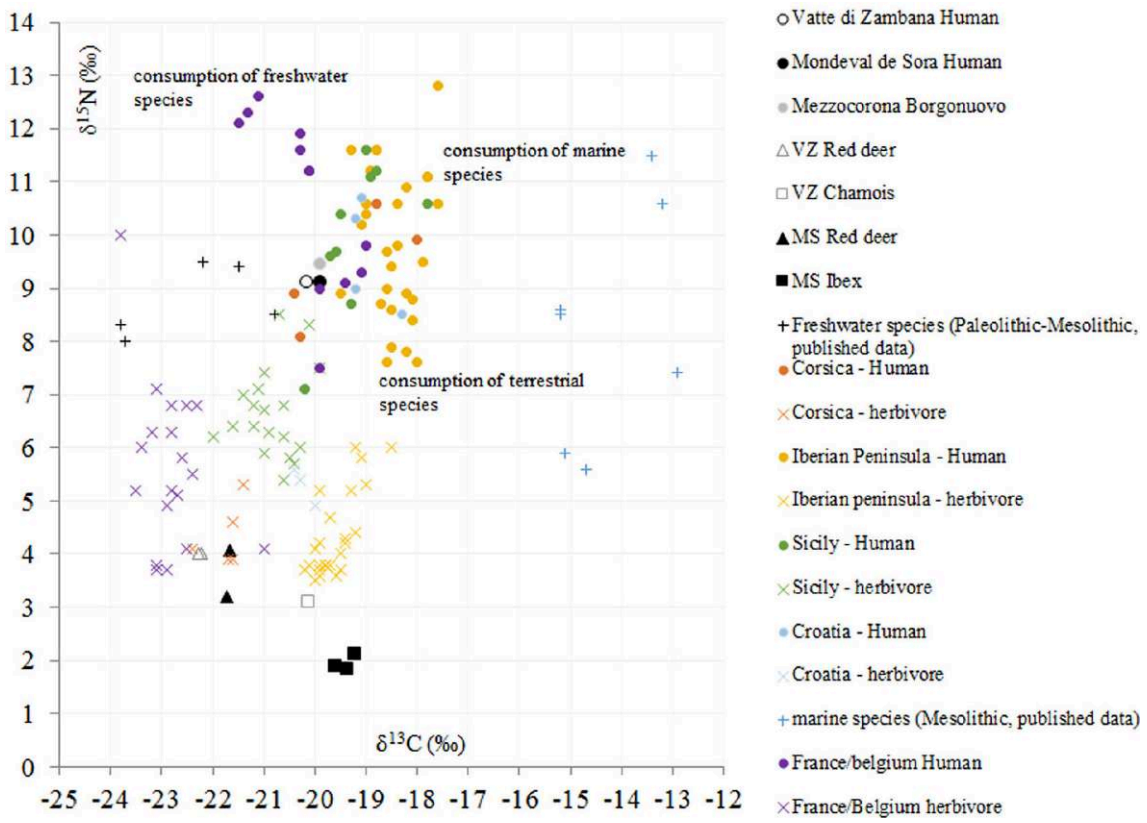

Figure 5. Carbon and nitrogen stable isotope compositions of bone collagen samples from Mesolithic sites (10216-7100 cal BP) in Corsica, the Iberian Peninsula, Sicily, Croatia (García-Guixe et al., 2006; Lightfoot et al., 2011; Mannino et al., 2011; 2012; Fernández-López de Pablo et al., 2013; Salazar-García et al., 2014; review in Goude et al., 2017) and inland in France and Belgium (Drucker et al., 2018; Schulting et al., 2008). Herbivore taxa given in the figure are red deer, roe deer and aurochs (and prolagus only for Corsica) (Annexe 3) / *Compositions isotopiques du carbone et de l'azote du collagène osseux d'échantillons de sites mésolithiques 10216-100 cal BP) de Corse, de la péninsule ibérique, de Sicile et de Croatie (García-Guixe et al., 2006 ; Lightfoot et al., 2011 ; Mannino et al., 2011 ; 2012 ; Fernández-López de Pablo et al., 2013 ; Salazar-García et al., 2014 ; synthèse dans Goude et al., 2017), et de l'intérieur des terres en France et en Belgique (Drucker et al., 2018 ; Schulting et al., 2008). Les espèces herbivores considérées dans la figure sont le cerf, le chevreuil et l'aurochs (et le pika pour la Corse) (Annexe 3)*

Conclusions

This study presents the first isotopic data for Mesolithic humans in the Italian Alps. The very few burials available for this period and the small animal sample size limit interpretations, so that this should be considered as a preliminary study calling for further investigations at different levels (e.g. complete study of fish remains, further CN isotope analysis, S and Sr isotope study to document mobility and ecosystems used). However, our data provide new information at the individual and regional scale. The three alpine individuals had a diet including a large amount of animal protein, mainly from red deer and possibly with slight differences in species ratios according to individuals. The Bayesian model developed by including isotopic data from this study and from the literature supports the hypothesis of an additional intake of freshwater resources and suggests that further consideration should be given to the role of other ungulates (chamois/ibex) and small mammals like the beaver in the diet of some individuals. The potential role of young ungulates and other small mammals deserves further investigation and more in-depth assessments of isotopic data. So far, our results are consistent with archaeological evidence reflecting uses of the highly variable Alpine landscapes between the late phase of the early Mesolithic (final Sauveterrian, ca. 7000-6800 cal BC) and the Late Mesolithic (Castelnovian, 6600-6000 cal BC). Red deer hunting would have been likely in summer with seasonal high-altitude migrations, at a time when the animal has its highest nutritional value. Parts of the carcasses could have been brought to the valley bottom to supplement the winter diet (Clark, 2000; Fontana et al., 2009; Thun Hohenstein, 2016). Valley-bottom sites were especially strategic for the procurement of freshwater resources and other supplies associated with dump environments (Wierer et al., 2016). In both cases, there is evidence for intense exploitation of ecotonal zones by the last hunter-gatherers of north-eastern Italy. Although plant consumption does not appear from our isotope data and so far there is little evidence even from other archaeological records, it may be assumed that these resources

would have represented another complement in the diet of Mesolithic hunter-gatherers (Oxilia et al., in press). Other research questions arising from this preliminary study include those related to gender-based dietary patterns. Given the very limited sample size of our study, it is worth mentioning the possible role of other factors in determining the isotopic composition between male and female individuals, such as potential food restrictions (taboos) linked to gender or social status (Spielmann, 1989) and distinct food acquisition and consumption customs for males and females (Schulting et al., 2008) that could be associated with the mobility and social systems of these human groups (Grünberg, 2017). Concerning the latter aspects, some studies describe possible changes in landscape use linked to a more logistically organised mobility pattern in the Late Mesolithic, which would have involved specialised task groups moving to mountain areas during the summer for hunting, whereas women, babies, children and elderly individuals would have remained in the valley-bottom camps (Fontana, 2006). These hypotheses require appropriate testing of additional CN stable isotope data and the use of additional proxies (e.g. sulphur and strontium isotopes) and analytical procedures (e.g. single compound analysis; cf. Naito et al., 2013); given the few Mesolithic human remains available in Western Europe, this is a challenging issue at present.

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Conflicts of interest

The authors declare that there is no conflict of interest.

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Annexes

Annexe 1

Figure S1. Pictures of the graves and of the samples used for the isotopic analyses (© V. Gazzoni) / *Photos des sépultures et des échantillons prélevés pour les analyses isotopiques (© V. Gazzoni)*

Annexe 2

Target	$\delta^{15}N_{Air}$	±1SD	$\delta^{13}C_{V\text{-}PDB}$	±1SD
Vatte di Zambana Human	9.1		-20.2	
Mondeval de Sora Human	9.1		-19.9	
Mezzocorona-Borgonuovo Human	9.4		-19.9	
Protein sources evaluated				
Red deer	3.8	0.4	-22.0	0.3
Chamois/Ibex	2.2	0.6	-19.6	0.4
Freshwater fish (pike)	9.9	1.7	-17.9	6
Beaver (modern)	4.5	2.2	-23.3	1.1

Table S1. Freshwater fish species (pike remains from Mesolithic and Neolithic sites in Europe) data (mean and ± 1 SD) from Robson et al., 2016. Beaver bone collagen (*Castor canadensis*) data are from Keenan et al. 2019; the $\delta^{13}C$ was corrected by +1.4‰ due to Suess effet (Marino and McElroy, 1991) / *Données isotopiques (moyenne et ± 1 écart-type) d'espèces de poissons d'eau douce (brochets méso-lithiques et néolithiques de sites européens ; d'après Robson et al., 2016). Données isotopiques de collagènes osseux de castors actuels (Castor canadensis) d'après Keenan et al., 2019 ; le $\delta^{13}C$ a été corrigé de + 1,4 ‰ en raison de l'effet Suess (Marino and McElroy, 1991)*

Proxies	Carbone (C) ; Nitrogen (N)
Source fraction	Protein
Offset	0.5‰ (±0.5) for C ; 4‰ (±1) for N
Concentration	100%
Prior info	n/a

Table S2. Bayesian models are performed by using offsets ($\Delta^{13}C$ and $\Delta^{15}N$ between human and animal bone collagen), the means of the isotopic compositions of proxy and their standard deviation and no prior information / *Les modèles sont générés en prenant compte les offsets entre les tissus (collagène osseux humain et animaux ; $\Delta^{13}C$ et $\Delta^{15}N$), les moyennes des données isotopiques des proxies avec leurs écart-types et pas* d'a priori

Annexe 3

Location of Mesolithic sites	(‰) $\Delta^{15}N_{Herbivore\text{-}Human}$	(‰) $\Delta^{13}C_{Herbivore\text{-}Human}$	References
Iberian Peninsula	5.4	1.3	Salazar-García et al. 2014
Sicily coast	4	1.4	Mannino et al. 2011 ; 2012
Adriatic coast	3.6	1.2	Lightfoot et al. 2011
Corsica coast	6.2	3.2	Pouydebat 1997
Corsica inland	4.4	1.2	Goude et al. 2017
France/Belgium inland	6.1	2.2	Drucker et al. 2018
Western France inland	4.8	1.5	Schulting et al. 2008
Vatte di Zambana	6.1	0.6	This study
Mondeval de Sora	6.4	1.1	This study
Mezzocorona-Borgonuovo	6.1	1.1	This study

Table S3. Trophic step between human and animal bone collagen ($\Delta^{13}C$ et $\Delta^{15}N$) recorded in several Mesolithic sites in the western Mediterranean and European areas / *Différences de compositions de isotopiques ($\Delta^{13}C$ et $\Delta^{15}N$) entre le collagène osseux humain et animal enregistrés sur plusieurs sites mésolithiques du nord-ouest de la Méditerranée et de l'Europe*