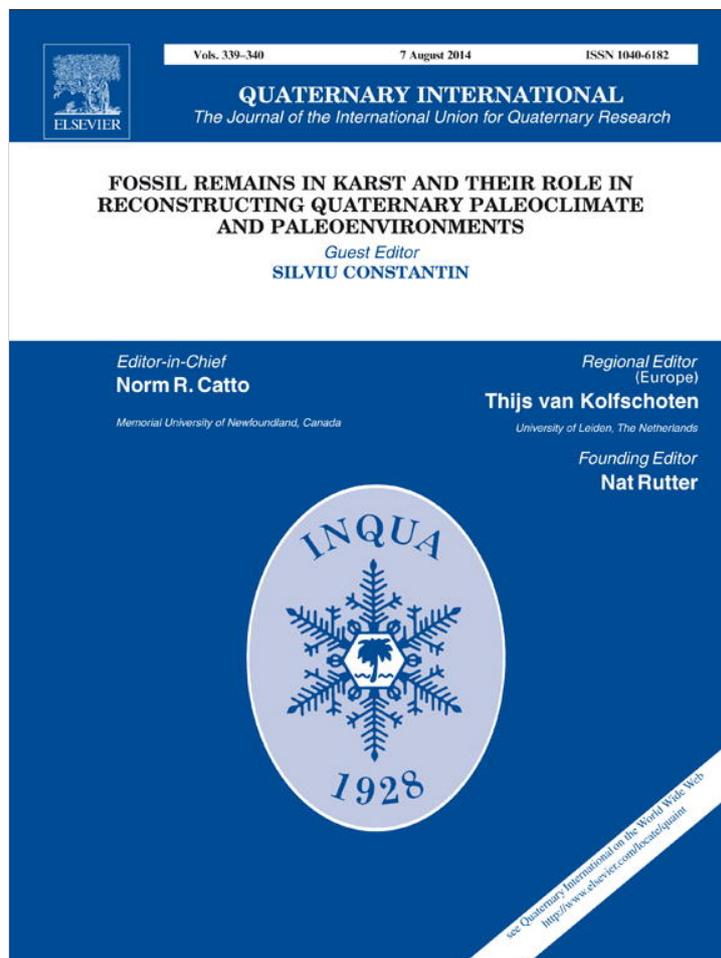


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Were bears or lions involved in salmon accumulation in the Middle Palaeolithic of the Caucasus? An isotopic investigation in Kudaro 3 cave



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ABSTRACT

Bone fragments of large anadromous salmon in the Middle Palaeolithic archaeological layers of Kudaro 3 cave (Caucasus) suggested fish consumption by archaic Hominins, such as Neandertals. However, large carnivores such as Asiatic cave bears (*Ursus kudarensis*) and cave lions (*Panthera spelaea*) were also found in the cave and could have been responsible for such an accumulation. The diet of these carnivores was evaluated using carbon, nitrogen and sulphur isotopes in faunal bone collagen. The results suggest that anadromous fish were neither part of the diet of either cave bear (vegetarian) or cave lion (predators of herbivores from arid areas) and therefore provide indirect support to the idea that Middle Palaeolithic Hominins, probably Neandertals, were able to consume fish when it was available.

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1. Introduction

Reconstructing the diet of predators found in cave fossil assemblages, as well as identifying the type of predators involved in the accumulation of prey skeletal remains, is a difficult task (e.g. Stiner, 1991, 2004; Tappan and Wrangham, 2000; Tappen et al., 2002; Steguweit, 2009). Especially finding which predator(s) may have been responsible for the accumulation of fish remains in cave sites is quite challenging (e.g. Van Neer et al., 2007). When numerous fish remains are found in cave deposits, the possible contribution of cave-dwelling piscivorous species other than hominins needs to be evaluated. Actualistic studies on such mammal and bird species provide information on prey selection (fish species and their sizes) that can be confronted with the archaeozoological data. This usually allows narrowing down the spectrum of potential accumulators and speculating on the role of hominins in the accumulation of fish.

Fish consumption is generally considered to be a recent innovation in hominid evolution. Although some fish remains found in several sites at Olduvai Gorge suggest the possible consumption of fish by early hominins (Stewart, 1994), the consumption of fish and other aquatic resources by hominins is usually considered to have become a common phenomenon with the advent of anatomically

modern humans in the Upper Palaeolithic, as part of the broad spectrum diet hypothesis (e.g. Richards et al., 2001b; Richards, 2009). Archaeological evidence such as fish bones, fishing devices, and stable isotopes in human bones suggest that aquatic resources including fish were regularly consumed during the Upper Palaeolithic, whereas Neandertals focused essentially on terrestrial large mammals as food resources (e.g. Van Neer et al., 2007; Richards, 2009; O'Connor et al., 2011). However, some Neandertal populations have been shown to rely on aquatic resources, especially aquatic molluscs, in the Mediterranean basin (Colonese et al., 2010; Cortés-Sánchez et al., 2011) and freshwater fish consumption is strongly suggested in the Middle Palaeolithic of Belgium (Van Neer and Wouters, 2009). Possible evidence for fish consumption by Neandertals has been documented in several caves from the Caucasus Mountains, where Middle Palaeolithic deposits in Vorontsovskaja, Kudaro 1 and Kudaro 3 caves have yielded large amounts of Black Sea salmon *Salmo labrax* bones (Lioubin and Baryshnikov, 1984). Although the archaeological context of these salmon finds leaves little doubt that these large salmon bones are left-overs of human activity, it is still possible that large carnivores, such as cave bears or cave lions, both represented by bone remains in this cave, may have been involved in the transport and accumulation of salmon remains in these caves (Baryshnikov, 1999; Russ and Jones, 2011). Such terrestrial carnivores are known to consume fish if they are given the opportunity, and could be responsible for the deposition of fish remains in cave sites, either

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through their excrements or by the decomposition of bears that died early during overwintering (e.g. Baryshnikov, 1999; Erlandson and Moss, 2001; Van Neer and Wouters, 2009). For instance, modern populations of brown bears *Ursus arctos* and black bears *Ursus americanus* living along rivers flowing into the Northern Pacific Ocean in Western North America and Eastern Siberia are noted for their dietary use of spawning salmon (e.g. Kistchinski, 1972; Jacoby et al., 1999; Mowat and Heard, 2006). There is no observation of wild modern lions eating fish, but other large felids such as panthers and jaguars are known to consume fish (Erlandson and Moss, 2001). Because the cave lion diet was quite different from that of modern African lions in terms of prey selection (Bocherens et al., 2011a), the possibility that cave lion could have consumed fish cannot be ruled out based on analogy with modern lions.

The question of possible fish consumption by extinct cave bears is more difficult to answer. The raise of molecular palaeontology during the last 20 years has profoundly changed our understanding of the evolutionary ecology of cave bears, an extinct lineage of bears that roamed on the Eurasian landmass until around 24,000 years ago (e.g. Pacher and Stuart, 2009). Palaeogenetic investigations have been crucial to sort out the tremendous morphological diversity of this lineage and suggest a phylogenetical framework with several groups corresponding to possible species (e.g. Hofreiter, 2005; Knapp et al., 2009). In parallel, the use of carbon and nitrogen stable isotopic compositions of fossil bone collagen showed that most if not all cave bears analyzed so far consumed barely any animal proteins, and therefore were much more vegetarian than their brown bear relatives (e.g. Bocherens et al., 1994, 2006a, 2011b). Also interesting is the fact that European cave bears from different lineages, such as *Ursus spelaeus*, *Ursus eremus* and *Ursus ingressus* exhibit similar preferences for plant food (Bocherens et al., 2011b). Only some cave bears of the lineage *U. ingressus* from Romania present isotopic signatures different from the rest of the European cave bears analyzed to date, which have been presented as evidence for possible fish consumption (Richards et al., 2008; Stiller et al., 2010). Alternative explanations are possible that do not include fish consumption, such as the influence of hibernation or the consumption of different plant types (Grandal d'Anglade and Fernández Mosquera, 2008; Bocherens et al., 2011b; Grandal d'Anglade et al., 2011). In any case, the isotopic investigations of cave bear palaeoecology are strongly biased in favour of western and central European populations. Cave bears were also present in the Caucasus Mountains, but they belonged to a different species, *Ursus kudarensis* (Knapp et al., 2009; Rabeder et al., 2009; Baryshnikov and Puzachenko, 2011). As this type of cave bear diverged early from the other cave bear lineages, the possibility that it exhibited different dietary preferences than its European counterparts cannot be ruled out. Only isotopic analyses performed directly on bone material from *U. kudarensis*, can provide a reliable dietary reconstruction and investigate whether these bears have consumed fish such as salmon found in the Caucasian cave of Kudaro 3 cave.

The goal of the present study is to investigate whether large predators such as cave bears and cave lions may have consumed salmon in Kudaro 3 cave and could be responsible for the accumulation of salmon bone instead of the Neandertals that occupied the cave during the same time span. Bone material from different species from the cave, including both carnivores together with potential terrestrial prey such as red deer, wild goat and bison as well as marine salmon from the cave and from other archaeological sites, was analyzed for the stable isotopic composition of carbon, nitrogen and sulphur. This will allow us to determine if the studied carnivores relied on purely terrestrial resources, or if they incorporated some salmon, in which case they would be possible candidates for accumulating salmon bones in the cave, therefore questioning aquatic resource use by Neandertals.

2. Background on dietary determination using carbon, nitrogen and sulphur stable isotopes

Bears are the most abundant carnivores in Kudaro 3 cave. Although bears belong to the mammalian order Carnivora, their diet may include much more than meat. Most extant bear species exhibit an omnivorous diet including plant food as well as animal proteins, which exhibit distinctive carbon and nitrogen isotopic compositions that are recorded in the bear's tissues through digestive assimilation of food with predictable isotopic fractionation (e.g. Hilderbrand et al., 1996; Robbins et al., 2004; Mowat and Heard, 2006). In the case of the lion, a predatory carnivore, the use of stable isotopes can be used to track the kind of prey preferentially consumed, and evaluate the possibility of significant fish consumption, because terrestrial and aquatic resources exhibit different isotopic compositions (e.g. Jacoby et al., 1999; Szepanski et al., 1999; Drucker and Bocherens, 2004; Drucker and Henry-Gambier, 2005; Nehlich et al., 2010; Bocherens et al., 2011c).

In Middle latitude mountainous areas such as the southern Caucasus foreland where Kudaro 3 cave is located, plants use essentially the C3 photosynthetic pathway. The causes of variations of $\delta^{13}\text{C}$ values are water availability, light intensity and altitude (e.g. Heaton, 1999). Plants growing under closed canopy exhibit the most negative $\delta^{13}\text{C}$ values, whereas plants from dry contexts and high altitude present less negative $\delta^{13}\text{C}$ values (e.g. Körner et al., 1991; Diefendorf et al., 2010). During the Middle and Late Pleistocene, short periods of increased C4 plant proportions were detected in paleosol carbonates from NW Caucasus (Kovda et al., 2008), meaning that plants available to herbivores at lower altitude may have included some C4 plants and exhibit more positive $\delta^{13}\text{C}$ values during warm and/or drier periods. There is a slight increase of $\delta^{13}\text{C}$ values of around 1‰ with each trophic level, which leads to carnivores having a slightly more positive collagen $\delta^{13}\text{C}$ value when compared to that of their average prey (Bocherens and Drucker, 2003).

Nitrogen isotopic compositions increase by 3–5‰ between the diet of an animal and its own tissues (e.g. Bocherens and Drucker, 2003). In a rather simplified manner, it is possible to state that the higher the $\delta^{15}\text{N}$ values of an animal, the more carnivorous it is. However, the reality is more complex since different plants exhibit various $\delta^{15}\text{N}$ values as they use nitrogen sources with different isotopic compositions. For instance, graminoids typically present more positive $\delta^{15}\text{N}$ values than shrubs and trees, which obtain their nitrogen from symbiotic mycorrhizal fungi (e.g. Schulze et al., 1994; Michelsen et al., 1998). In addition, environmental factors such as temperature and aridity also affect $\delta^{15}\text{N}$ values of plants (Amundson et al., 2003). Finally, $\delta^{15}\text{N}$ values of plants tend to decrease with increasing altitude (e.g., Sah and Brumme, 2003; Huber et al., 2007). Aquatic food webs usually involve more trophic steps than terrestrial ones, which leads to more positive $\delta^{15}\text{N}$ values for predators consuming aquatic prey than for predators consuming terrestrial prey (e.g. Drucker and Bocherens, 2004; Richards, 2009).

Sulphur isotopic signatures in bone collagen reflect essentially those of the protein fraction of the diet (e.g., Richards et al., 2003). The composition of sulphur isotopes in food webs depends on the characteristics of the geological bedrock and on the microbial processes involved in the biogeochemical cycle of sulphur, which may lead to differences in the isotopic compositions of freshwater and terrestrial food webs in a given locality (e.g. Krouse, 1989; Richards et al., 2001a; Nehlich et al., 2010), although sometimes more complex situations occur (e.g. Privat et al., 2007). In contrast, marine sulphates exhibit a rather constant isotopic composition around +20‰ (Peterson and Fry, 1987). Although the Black Sea is a marine basin with restricted connection with the world ocean, its sulphate exhibits similar $\delta^{34}\text{S}$ values to the rest of the ocean (Sweeney and Kaplan, 1980). The salinity in the Black Sea is known

to have changed during the Late Pleistocene, with a transgression during the early Weichselian (Christova, 2003), but the conditions were more marine during the late Weichselian, as documented by radiocarbon dated molluscs shells (Semenenko et al., 1991; Yanina, 2011). Anadromous fish, such as the Black Sea salmon *S. labrax* thought to have been consumed by Middle Paleolithic humans in Kudaro 3 cave, typically exhibit a marine isotopic composition, reflecting the environment where they grew up even when they are captured in inland rivers (e.g. Szepanski et al., 1999). However, *S. labrax* also has forms with a slower growth rate that stay in the river all year round (Kottelat and Freyhof, 2007) and which would hence have a different isotopic signature more typical of freshwater habitats (e.g. McCarthy and Waldron, 2000). Nowadays, the body length of these resident fish populations in Caucasian rivers of the Black Sea basin does not exceed 30 cm total length (TL) (Barach, 1962), whereas the anadromous form can attain lengths of over 1 m. Although at Kudaro 1 cave both smaller (20–40 cm TL) and larger (50–130 cm TL) salmonids were found (Tsepkin, 1980; Baryshnikov, 1999), the dimensions of the measurable vertebrae from Kudaro 3 cave only indicate the presence of the large, anadromous form with reconstructed fish lengths of between 75 and 95 cm TL.

3. Material and methods

3.1. Material

Kudaro 3 cave is a cave situated in the central part of southern slope of the Greater Caucasus, on the right bank of Djedjori River near Kvaisa City (Southern Ossetia), at around 1600 m asl, and about 260 m above the level of the nearby river. The palaeontological collection of Kudaro 3 cave is kept in the Zoological Institute in St. Petersburg. Layers 3 and 4, from which most fossil bone material used in the present study comes, yielded Mousterian artefacts and their geological age is estimated around 42,000–48,000 years (Baryshnikov, 2011). Two cave bear bones from layer 2 are most probably from layer 3 and were redeposited in the stratigraphically younger layer 2, based on their fossilization aspect.

The studied material consists of cave bear bone fragments, including some samples already investigated for their ancient DNA (Knapp et al., 2009). In addition, bone fragments from herbivorous species, such as *Cervus elaphus* (red deer), *Bison* sp. (bison) and small bovids belonging to *Ovis* (wild sheep) or *Capra* (wild goat) were analyzed for their collagen isotopic signatures to set the baseline of plant isotopic values in the local ecosystems, as well as one cave lion *Panthera spelaea*. Finally, two bones of Black Sea salmon *S. labrax* of large size, as well as three vertebrae from Atlantic salmon *Salmo salar* from the Magdalenian site of Trou du Frontal (Belgium, Van Neer et al., 2007) were included to tentatively provide an isotopic signature for a food resource with a marine provenance in a Late Pleistocene context. Anadromous salmon exhibit marine sulphur isotopic signatures, which are stable worldwide (e.g. Peterson and Fry, 1987; Godbout et al., 2010), but we tried to analyze some ancient marine salmon to verify that this was also the case in the past. Although not an optimal solution,

using fish isotopic values from different sites is sometimes practised to establish a likely end-member for aquatic resources available to prehistoric populations (e.g. Richards et al., 2001b).

3.2. Bone analysis and collagen preparation and isotopic analysis

Bones were sampled for determination of nitrogen content (%N) in whole bones to evaluate the quantity of collagen preserved. Fossil bones with less than 0.4% nitrogen do not usually contain collagen with reliable isotopic compositions (Bocherens et al., 2005a).

Sample preparation was performed as follows. Small pieces of bone were cut from identified remains, sonicated in acetone and then rinsed three times in distilled water. After crushing and sieving to obtain a powder of 0.7 mm grain size, an aliquot of around 5 mg was used to measure the nitrogen, carbon and sulphur content (%N, %C, %S) of the whole bone, in order to screen out samples with excessive collagen loss or extraneous sulphur contamination (Bocherens et al., 2005a, 2011c). The measurements were performed using a Vario EL III elemental analyser using sulfanilic acid from Merck as an internal standard. The mean standard errors were better than of 0.02%, 0.05%, and 0.03% for %C, %N and %S, respectively.

Collagen extraction was performed following Bocherens et al. (1997). The elemental and isotopic measurements were performed at the Geochemical unit of the Geoscience Faculty at the University of Tübingen (Germany), using an elemental analyser NC 2500 connected to a Thermo Quest Delta + XL mass spectrometer. The elemental ratios C/N, C/S and N/S were calculated as atomic ratios. The isotopic ratios are expressed using the “ δ ” (delta) value as follows: $\delta^{13}\text{C} = [^{13}\text{C}/^{12}\text{C}_{\text{sample}}/^{13}\text{C}/^{12}\text{C}_{\text{reference}} - 1] \times 1000$ (‰), $\delta^{15}\text{N} = [^{15}\text{N}/^{14}\text{N}_{\text{sample}}/^{15}\text{N}/^{14}\text{N}_{\text{reference}} - 1] \times 1000$ (‰), and $\delta^{34}\text{S} = [^{34}\text{S}/^{32}\text{S}_{\text{sample}}/^{34}\text{S}/^{32}\text{S}_{\text{reference}} - 1] \times 1000$ (‰), with the international reference being V-PDB for $\delta^{13}\text{C}$ values, atmospheric nitrogen (AIR) for $\delta^{15}\text{N}$ values, and Canyon Diablo Troilite (CDT) for $\delta^{34}\text{S}$ values. Samples were calibrated to $\delta^{13}\text{C}$ values of USGS24 ($\delta^{13}\text{C} = -16.00$ ‰) and to $\delta^{15}\text{N}$ values of IAEA 305A ($\delta^{15}\text{N} = 39.80$ ‰). Samples were calibrated to $\delta^{34}\text{S}$ values relative to CDT of NBS 123 ($\delta^{34}\text{S} = 17.10$ ‰), NBS 127 ($\delta^{34}\text{S} = 20.31$ ‰), IAEA-S-1 ($\delta^{34}\text{S} = -0.30$ ‰) and IAEA-S-3 ($\delta^{34}\text{S} = 21.70$ ‰). The reproducibility was ± 0.1 ‰ for $\delta^{13}\text{C}$ measurements, ± 0.2 ‰ for $\delta^{15}\text{N}$ measurements, and ± 0.4 ‰ for $\delta^{34}\text{S}$ measurements, based on multiple analysis of purified collagen from modern bones.

4. Results and discussion

4.1. Preservation of collagen

All the analyzed mammalian bones from Kudaro 3 cave and the salmon from Trou du Frontal contained more than 0.4% nitrogen, while both salmon samples from Kudaro 3 cave contained much less nitrogen, indicating a complete loss of their original collagen. Therefore, we used isotopic data from Atlantic salmon originating from an archaeological site in Belgium to evaluate the carbon, nitrogen and sulphur isotopic signatures of this food resource (Table 1).

Table 1
List of chemical and isotopic measurements obtained on bones from Kudaro 3 cave and Atlantic salmon from Trou du Frontal. Values in bold indicate results outside the range of acceptable values for collagen. Isotopic values in italics indicate those that were not considered reflecting biological signatures.

Lab-no	Species	Piece	Location	Unit	%N _{bone}	Yield mg g ⁻¹	%C	%N	C/N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	%S	C/S	N/S	$\delta^{34}\text{S}$
SP1009	<i>Ursus deningeri kudarensis</i>	Bone	Kudaro 3 Cave, layer 2, horizon 5	D3	2.89	75.3	38.3	14.0	3.2	-20.2	3.7	0.17	600	188	5.7
SP1010	<i>Ursus deningeri kudarensis</i>	Bone	Kudaro 3 Cave, layer 2, horizon 6	D3	1.71	40.3	34.4	12.5	3.2	-19.6	3.0	0.15	612	191	6.3
SP1013	<i>Ursus deningeri kudarensis</i>	Bone	Kudaro 3 Cave, layer 3, horizon 2, D-5	D3	0.43	0.6	20.9	7.8	3.1	-20.2	0.5	0.37	151	48	10.3

Table 1 (continued)

Lab-no	Species	Piece	Location	Unit	%N _{bone}	Yield mg g ⁻¹	%C	%N	C/N	δ ¹³ C	δ ¹⁵ N	%S	C/S	N/S	δ ³⁴ S
SP1014	<i>Ursus deningeri kudarensis</i>	Bone	Kudaro 3 Cave, layer 3, horizon 2	D3	1.23	7.5	42.1	15.6	3.2	-20.0	2.1	0.25	449	142	8.6
SP1015	<i>Ursus deningeri kudarensis</i>	Bone	Kudaro 3 Cave, layer 3c, horizon 3	D3	0.54	n.d.	36.4	12.9	3.3	-20.4	2.5	0.32	303	92	8.3
SP1016	<i>Ursus deningeri kudarensis</i>	Bone	Kudaro 3 Cave, layer 3d	D3	2.37	38.0	37.8	13.9	3.2	-20.7	1.2	0.14	719	227	3.9
SP1017	<i>Ursus deningeri kudarensis</i>	Bone	Kudaro 3 Cave, layer 3e, horizon 3	D3	1.23	4.8	35.7	12.2	3.4	-20.5	2.3	0.26	366	107	6.1
SP1018	<i>Ursus deningeri kudarensis</i>	Bone	Kudaro 3 Cave, layer 3, horizon 4	D3	1.89	16.2	36.3	12.2	3.5	-19.9	1.7	0.18	537	155	4.4
SP1019	<i>Ursus deningeri kudarensis</i>	Bone	Kudaro 3 Cave, layer 4, horizon 2	D3	1.11	nd	22.6	7.3	3.6	-20.2	1.5	0.33	183	50	7.9
KUD-1	<i>Cervus</i>	Bone	Kudaro 3 Cave, layer 3, horizon 2, 1979		0.49	7.9	11.7	4.1	3.3	-20.1	5.7	n.d.	n.d.	n.d.	n.d.
KUD-2	<i>Cervus</i>	Bone	Kudaro 3, layer 3, horizon 5		1.80	57.8	39.5	14.0	3.3	-20.4	5.3	0.15	702	214	6.9
KUD-3	<i>Capra/Ovis</i>	Bone	Kudaro 3, layer 3c, horizon 2, 1977		2.28	85.6	39.1	14.0	3.2	-20.3	7.2	0.13	790	243	7.6
KUD-4	<i>Capra/Ovis</i>	Bone	Kudaro 3, layer 3, horizon 4, 1959		1.31	19.5	30.8	10.6	3.4	-19.4	7.2	0.08	1001	296	7.5
63 BP.	<i>Bison</i> sp.	Mandible	Kudaro 3, layer 2	D9	2.88	95.3	45.3	16.2	3.3	-19.3	7.3	n.d.	n.d.	n.d.	n.d.
64 BP.	<i>Bison</i> sp.	Mandible	Kudaro 3, layer 3; horizon 2	D3/E3	1.13	13.9	26.2	9.0	3.4	-19.9	4.1	n.d.	n.d.	n.d.	n.d.
65 BP.	<i>Bison</i> sp.	Tibia	Kudaro 3, layer 3; horizon 1	D6	0.61	8.8	11.6	3.5	3.8	-22.6	4.8	n.d.	n.d.	n.d.	n.d.
KUD-5	<i>Panthera leo</i>	Phalanx 1	Kudaro 3 Cave, layer 3, horizon 2, 1959		2.32	64.9	36.6	13.0	3.3	-17.5	9.3	0.18	531	162	5.1
KUD-6	<i>Salmo labrax</i>	Vertebra	Kudaro 3, layer 3, horizon 2, 1974		0.13	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
KUD-7	<i>Salmo labrax</i>	Bone frgts	Kudaro 3, layer 3, horizon 2, 1975		0.18	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Vert-00-107	<i>Salmo salar</i>	Vertebra	Trou du Frontal		2.20	27.5	37.2	13.7	3.2	-14.1	9.5	0.61	163	51	15.6
Vert-00-108	<i>Salmo salar</i>	Vertebra	Trou du Frontal		2.34	32.2	37.2	14.1	3.1	-14.0	10.0	0.61	163	53	15.6
Vert-00-109	<i>Salmo salar</i>	Vertebra	Trou du Frontal		2.74	63.3	40.1	14.8	3.2	-14.2	9.8	0.63	170	54	17.7

For the collagen extracted from mammal bones, all samples except one bison bone (65 BP, as in the table) exhibited C/N ratios ranging from 3.1 to 3.6 (Table 1), which is within the limits of well-preserved collagen (DeNiro, 1985). Besides, one red deer sample (KUD-1) exhibited collagen with %C (11.7%) and %N (4.1%) much lower than those of fresh collagen. Since “collagen” samples with %N < 5% are considered to be possibly altered (Ambrose, 1990), we preferred to discard the isotopic values from this sample from further discussion, and the sulphur isotopic composition was not measured for this specimen. In addition, two “collagen” samples extracted from cave bear samples (SP1013 and SP1019) exhibited around half the proportion of carbon and nitrogen expected for collagen, which casts doubts on their reliability. Therefore, the carbon and nitrogen isotopic composition of the “collagen” extracted from these four mammal bones will not be interpreted in palaeobiological terms. Only extracted collagen samples with %C > 34% and %N > 12% will be further discussed. Interestingly, the C/S and N/S ratios of these two collagen were also outside the accepted range of such values for well-preserved collagen, namely C/S < 300 and N/S < 100 (Nehlich and Richards, 2009; Bocherens et al., 2011c). Moreover, one of the δ³⁴S values measured on one additional cave bear (SP1015) and one ungulate (KUD-4) were also discarded, as their %S were too high or too low, leading to excessively high or low C/S and N/S ratios, although their δ³⁴S value were similar to those measured on other terrestrial specimens with acceptable ratios of the same taxa (Table 1).

The chemical characteristics (%C, %N, C/N, %S, C/S, N/S) of the collagen extracted from the three salmon bones from Trou du Frontal were well within the acceptable values for fish, and also for sulphur (Nehlich and Richards, 2009). The δ³⁴S values of Atlantic

salmons from Trou du Frontal are clearly in the expected range of marine fish and of anadromous salmons from the Northwest Pacific coast (Godbout et al., 2010).

4.2. Isotopic values of faunal collagen

The δ¹³C values of cave bears and ungulates vary in similar ranges, from -20.7 to -19.6‰, and from -20.4 to -19.3‰, respectively (Table 1, Fig. 1). The δ¹⁵N values range from 1.2 to 3.7‰ for cave bears, from 5.3 to 7.3‰ for ungulates (Table 1, Fig. 1). The cave lion presents δ¹³C and δ¹⁵N values of -17.5‰ and 9.3‰, respectively (Table 1, Fig. 1). In contrast, the anadromous salmon

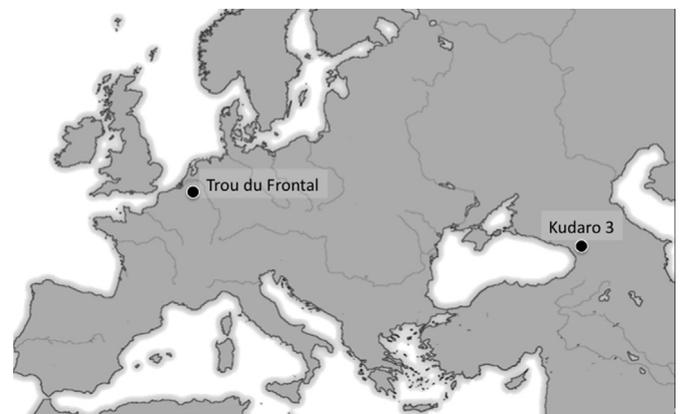


Fig. 1. Map showing the location of the sites discussed in the text.

from European archaeological sites exhibit much less negative $\delta^{13}\text{C}$ values, ranging from -16.1 to -14.0‰ and more positive $\delta^{15}\text{N}$ values, ranging from 9.5 to 12.1‰ (Table 1). The $\delta^{34}\text{S}$ values of ungulates, cave bears and cave lion are clustered between around 0 and 6‰ , very different values from those of salmon from the Belgian Pleistocene sites, which present the expected range of marine values, close to 20‰ .

4.3. Dietary reconstruction of cave bears and cave lion

The distribution of $\delta^{15}\text{N}$ values between the analyzed ungulates and the cave lion is consistent with the expectation of the difference between herbivores and carnivores in a given ecosystem (Fig. 1). However, the lion presents a $\delta^{13}\text{C}$ values that is more than 1.5‰ more positive than that of the potential prey measured in Kudaro 3 cave, pointing to the addition of some food items with less negative $\delta^{13}\text{C}$ values than the potential prey analyzed in this study. In Late Pleistocene sites from western Europe, such a food item is represented by reindeer *Rangifer tarandus* (Bocherens et al., 2011a) but in the Late Pleistocene of the Caucasus, this species is almost completely missing, with only a handful of bones from this species found in Mezmaiskaya Cave in Northern Caucasus (Baryshnikov et al., 1996). Another ungulate with more positive $\delta^{13}\text{C}$ values that could be found in the region is the saiga antelope *Saiga tatarica*, with $\delta^{13}\text{C}$ values estimated for collagen of up to -17.5‰ (Drucker et al., 2005). However, this steppic species also exhibits high $\delta^{15}\text{N}$ values of up to 12‰ (Drucker et al., 2005) and its abundance is limited to the dry plains of Azerbaijan and in the Pleistocene sites of northern Caucasus (Baryshnikov, 2002). Wild ungulates from the steppe regions of Turkmenistan from historical periods also exhibit $\delta^{13}\text{C}$ values ranging from -17 to -15‰ and $\delta^{15}\text{N}$ values ranging from 8 to 13‰ (Bocherens et al., 2006b), showing that preys with enriched $\delta^{13}\text{C}$ values could have been available to the mobile large predator farther north and could explain the isotopic composition of the lion bone collagen. Another explanation is possible: carbon and nitrogen isotopic composition of cave lion collagen could be explained by the consumption of some anadromous salmon, around 25% if we consider the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the Atlantic salmon from Late Pleistocene Belgium as representing the likely end-values of anadromous salmon (Fig. 1). However, the $\delta^{34}\text{S}$ values of the cave lion are in the same range as the ones of terrestrial herbivores and much lower than those measured on salmon (Fig. 2). Therefore, the prey consumed by the analyzed cave lion included only terrestrial animals, possibly from more arid regions than the cave surroundings, but did not include marine resources such as anadromous salmon (Fig. 3).

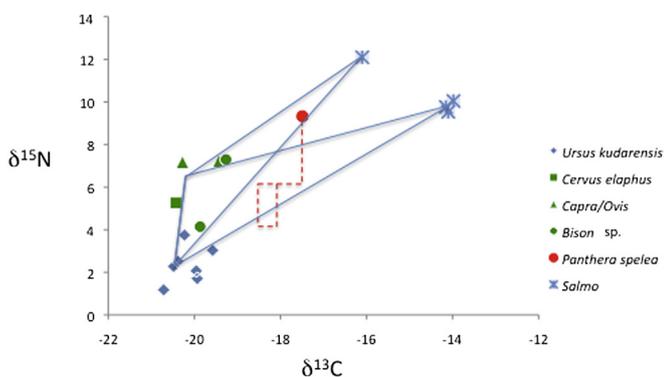


Fig. 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bone collagen from mammals from Kudaro 3 cave, together with Late Pleistocene anadromous salmons (this study and Drucker and Bocherens, 2004). The triangles illustrate the end-points of possible food resources for the lion. The rectangle represents the calculated range of average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the lion prey collagen (based on Bocherens et al., 2005b).

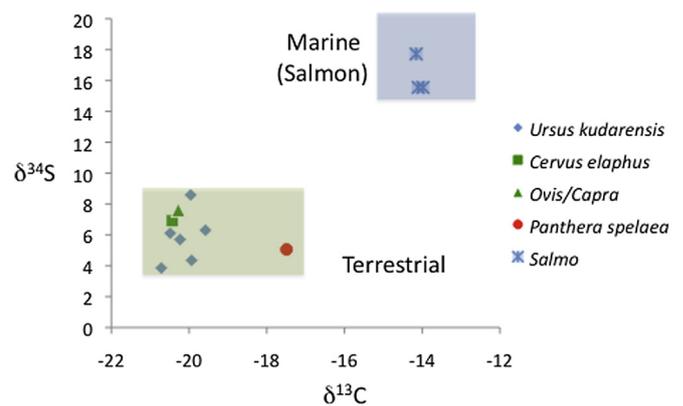


Fig. 3. $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values of bone collagen from mammals from Kudaro 3 cave, together with Late Pleistocene anadromous salmons.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of cave bears *Ursus kudarensis* clearly rule out the consumption of salmon by this species. The cave bear isotopic values are well clustered and lower than those of the ungulates, precluding a carnivorous or omnivorous diet, but pointing instead to an absence of animal proteins and a diet composed of plants. The $\delta^{15}\text{N}$ values of the bears are lower than those of the ungulates from the same site and could indicate either that ungulates consumed preferentially grass and cave bears mainly food sources produced by shrubs and trees, or that cave bears foraged at higher altitude than the ungulates, where plants exhibit lower $\delta^{15}\text{N}$ values (e.g., Sah and Brumme, 2003; Huber et al., 2007). Salmon $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are typically more positive in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than those exhibited by cave bears and terrestrial herbivores in Kudaro 3 cave and cannot explain the distinctive values of the cave bears compared to the ungulates. Moreover, the $\delta^{34}\text{S}$ values of the cave bears are similar to those of the terrestrial herbivores, also ruling out marine food consumption of these bears. Therefore, it is concluded that the Kudaro cave bears were, like other cave bears from western Europe in the Late Pleistocene, essentially vegetarian.

4.4. Implications for salmon consumption in Kudaro 3 cave

The isotopic evidence clearly shows that among the analyzed carnivores, neither cave lion nor cave bears consumed even partly any food resource with a marine signature, as salmon would be. Since salmon consumption would provide a food resource high in nitrogen and sulphur with very distinctive isotopic compositions compared to terrestrial food resource, even a limited amount would have left an imprint on the collagen of these predators. Therefore, the occurrence of large salmon bones in the archaeological layers of Kudaro 3 cave is potentially explained by hominin activity. In the absence of hominid bones that could provide direct isotopic proof that marine food was consumed in Kudaro 3 cave, showing that large carnivores such as cave bears and cave lions did not consume any marine food is the best possible line of evidence that supports the hypothesis that hominins were probably responsible for fish bone accumulation. This suggests that Neandertals were not completely ignoring aquatic food resources when they were available, and that exploitation of aquatic dietary resources is not limited to anatomically modern humans.

5. Conclusions

The carbon, nitrogen and sulphur isotopic composition of cave lion and cave bears in the Middle Paleolithic cave site Kudaro 3 strongly suggests that these large carnivores were not consuming

salmon and therefore were not responsible for the accumulation of salmon bones in the cave. It seems that hominins, in this case most probably Neandertals, were using this food resource. When the environment was providing direct access to abundant aquatic food resources such as anadromous salmon, it seems that Neandertals were not ignoring these resources. This conclusion is in agreement with recent work based on use-wear analyses of lithic artefacts that exhibit a broad-based subsistence for Neanderthals including fish consumption (Hardy and Moncel, 2011). Further isotopic investigations of Neandertal bone using sulphur isotopic composition in addition to carbon and nitrogen may help to document directly and to quantify the consumption of marine food resources in archaic hominins.

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