



Coastal and Inland subsistence strategies during the Gravettian in the Cantabrian Region (northern Iberian Peninsula)



Angel Blanco-Lapaz ^{a,b,*}, Ana B. Marín-Arroyo ^c, Igor Gutiérrez-Zugasti ^d, Fernando González-Echegaray de Yarto ^c, Manuel R. González-Morales ^d

^a Senckenberg Centre for Human Evolution and Paleoenvironment (SHEP), Hölderlinstrasse 12, 72074, Tübingen, Germany

^b Institute for Archaeological Sciences, University of Tübingen, Hölderlinstrasse 12, 72074, Tübingen, Germany

^c Grupo de I+D+i EVOADAPTA (Evolución Humana y Adaptaciones durante la Prehistoria), Dpto. Ciencias Históricas, Universidad de Cantabria, Av/Los Castros 44, 39005, Santander, Spain

^d Instituto Internacional de Investigaciones Prehistóricas de Cantabria (IIIPC), (Universidad de Cantabria-Gobierno de Cantabria-Santander), Av/Los Castros 52, 39005, Santander, Spain

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ABSTRACT

The Gravettian site of Fuente del Salín Cave is located in the northern Iberian Peninsula (Cantabrian Region, Spain). In 2016, excavations conducted at the site yielded numerous faunal remains, including mammals and fish. Researchers also recovered molluscs remains during the 1990, 1991, and 2000 campaigns. This study presents the results of the archaeozoological and taphonomical analyses of the large mammals and fish remains recovered during these excavations. At Fuente del Salín Cave, a high level of bone fragmentation and the presence of burning damage characterizes the faunal assemblage. Taxonomy of large game shows diverse habitat exploitation, such as coastal valleys and plains (red deer, *Cervus elaphus*; horse, *Equus ferus*) as well as rocky landscapes (Iberian ibex, *Capra pyrenaica*; and chamois, *Rupicapra rupicapa*). Additionally, fish remains show the presence of salmonids (*Salmo* sp.), cyprinids, and haddock (*Melanogrammus aeglefinus*), indicating the exploitation of coastal, demersal, and riverine species. The taphonomic analysis of the mammals revealed burning damage concentrated on axial elements and epiphyses, characterized by temperatures typical of carbonization or calcification. The scarcity of carnivore gnawing marks and the presence of butchering marks prove that humans were the main accumulators at Fuente del Salín Cave. Concerning fish, most remains correspond to spines, branchial spines, ribs, and vertebrae, indicating humans processed fish by removing these elements for consumption. Based on our results, Fuente del Salín Cave provides an essential record of the subsistence strategies of the inhabitants of the Cantabrian Region during the Gravettian.

1. Introduction

At the beginning of the 20th century, Breuil (1912) first described the term Gravettian in his work: "Les subdivisions du Paléolithique supérieur et sa signification" during the International Congress of Prehistoric Anthropology and Archaeology of Genève. Modern research shows that the Gravettian covers an extended period (ca. 28–20 kyr ¹⁴C BP) characterized by widely fluctuating climatic conditions, with long cold phases punctuated by short, milder periods (Dansgaard/Oeschger interstadials) (Heinrich stadials; Rufi et al., 2019), which encompassed the final stage of the stadial Marine Isotopic Stage (MIS) 3 and the entirety of MIS 2. Bicho et al. (2017) observed the permanent occupation

of even Europe's peripheral regions by Anatomically Modern Humans between c.37 and 30 ka ago.

During the Gravettian, rapid climatic fluctuations associated with significant territorial increment led to diverse subsistence strategies extending from the Atlantic coast of the Iberian Peninsula to Siberia (Foucher, 2013). In this context, several authors identified subsistence strategies focused on cold-adapted animals, such as the woolly mammoth (*Mammuthus primigenius*) in eastern Gravettian sites like Yudinovo (Siberia; Vereshchagin and Kuz'mina, 1977) and Předmostí (Czech Republic; Bocherens et al., 2015). Similarly, authors such as Boyle (2017) and Lacarrière (2015) observed a hunting focus on reindeer (*Rangifer tarandus*).

* Corresponding author. Senckenberg Centre for Human Evolution and Paleoenvironment (SHEP), Hölderlinstrasse 12, 72074, Tübingen, Germany.
E-mail address: angel.blanco-lapaz@uni-tuebingen.de (A. Blanco-Lapaz).

Moving to the Iberian Peninsula, particularly in the Cantabrian Region, Marín-Arroyo et al. (2018) conducted a recent review of the regional duration of the Gravettian, suggesting dates between 36,800–35,000 cal BP and 26,000 cal BP. The Gravettian lithic record is characterized by the presence of Noailles burins, La Gravette points, Font Robert points, and scrapers (Rasilla and Straus, 2004; Rasilla-Vives and Santamaría-Álvarez, 2006; Bradtmöller, 2014). Fortea (1992) conducted a systematic study of the Gravettian in the Cantabrian Region, which shows two main phases: one defined by the presence of Noailles burins and the other by more generic industries similar to the Font-Robert point morphotype. Later, Rasilla and colleagues (Rasilla and Straus, 2004) also characterized the Cantabrian Gravettian into two phases, the first dominated by the Noailles burin and the second characterized by a decrease in Noailles burins and an abundance of pedunculated Isturitz type points. The authors also described the presence of similar proportions of blade and bladelet tools and La Gravette points.

The Cantabrian Region (Fig. 1), comprised of Asturias, Cantabria, Basque Country, and the northern Navarre autonomous administrative regions, is located in north of Iberia. The region is nowadays characterized by its Atlantic coastline, which lies only c. 5–12 km south of the Late Glacial shoreline. This relative stability is due to the strait continental shelf and the steep, peaks and massifs of the Cantabrian Cordillera and the Picos de Europa range, which lie parallel to the coast. In this small area of the northern Iberian Peninsula, a wide range of habitats are present, including the shore, coastal zone, low hills, high mountain slopes, and valleys with different orientations, all of which are easily accessible within short distances. Long-distance movements were thus not required to exploit a wide range of resources during different seasons (e.g., Marín-Arroyo et al., 2023). In this context, archaeologists discovered and studied several relevant Paleolithic sites in the Cantabrian Region, yielding rich lithic and faunal assemblages and remarkable artistic manifestations, such as cave paintings and portable art (e.g., Bernaldo de Quirós, 1982; Bicho et al., 2007; Arias and Ontañón, 2013; Bradtmöller, 2014).

For the Cantabrian Gravettian, along with recent sub-regional studies (Rasilla and Straus, 2004; Martínez and Rasilla, 2012; Foucher, 2013) we have some syntheses mainly focused on lithic industries (de la Peña, 2009; Ríos-Garaizar et al., 2011; Arrizabalaga and de la Peña, 2012), plus different site studies that record the variability of Gravettian occupations in the area; general overview appears in the proceedings of the Altamira meeting on the Gravettian in 2011 (de las Heras et al., 2012). The main problem still present is the poor definition of several of them, especially in the case of old excavations; in other situations, the information is biased by the limited surface excavated. The distribution of Gravettian sites is presented in Fig. 1.

From the paleoenvironmental point of view, during the Gravettian (de la Peña, 2009), authors such as Andersen et al. (2006) and Fernández-García et al. (2023) observed an increase in cooler climatic conditions throughout Europe during the Gravettian. This change led to the

migration of hunter-gatherer populations and an increase in the number of sites compared to prior periods. Based on the genetic record, Fu et al. (2016) and Posth et al. (2023) similarly observed that, during the Last Glacial Maximum, human populations retreated to glacial refugia on the southern edge of Europe (Iberian Peninsula and France), coinciding with the development of Solutrean technology. This model of human population continuity between western Gravettian and Solutrean is supported by Villalba-Mouco et al. (2023).

Palynological studies at the Gravettian levels of Aitzbitarte III (31–28 kyr cal BP; Altuna et al., 2011) and Amalda (28 kyr cal BP; Altuna et al., 1990), both sites located in Guipúzcoa, confirm the decreased presence of forests with a dominance of grass taxa in cold contexts. Jones et al. (2018) confirmed, based on isotope analysis (carbon and nitrogen-stable isotopes collected from herbivores consumed by humans), a predominance of steppe taxa at both sites, such as *Pinus*, Cupressaceae, Poaceae, Anthemidae, and Cichorioe (Iriarte-Chiapusso, 2011). Previous archaeozoological studies of several sites in the Cantabrian Region, such as Lezetxiki, Morín, Labeko Koba, Amalda, Aitzbitarte, Cueto de la Mina, El Castillo, and Covalejos, indicate the presence of mammals from cold (such as seals, *Pusa hispida* or *Phoca vitulina*; wolverines, *Gulo*; reindeer, *Rangifer tarandus*; and arctic foxes, *Alopex lagopus*), open (such as red deer, *Cervus elaphus*; aurochs, *Bos primigenius*; and bison, *Bison priscus*), and rocky (Iberian ibex, *Capra pyrenaica*; chamois, *Rupicapra rupicapra*) environments during the Aurignacian-Gravettian (e.g., Álvarez-Lao & García, 2011; Altuna et al., 2013; Sánchez-Romero et al., 2021). Additionally, cold-adapted birds also are present in the Cantabrian Region, such as rock ptarmigan (*Lagopus mutus*) (Altuna et al., 2013).

1.1. Terrestrial resources during the Gravettian

Exhaustive archaeozoological studies from various sites in Cantabria indicate a dominance of red deer (*C. elaphus*) during the Gravettian (Altuna, 1972; Freeman, 1973; Straus, 1977; Bernaldo de Quirós, 1982; Marín-Arroyo and Sanz-Royo, 2021), which characterize the subsistence strategies of this region. This signal differs from that of France, where reindeer (*R. tarandus*) prevailed due to local environmental and geographical conditions (e.g., Quesada López, 1995, 1997a,b,c; Mellars, 2002; Discamps et al., 2011). In the Cantabrian Region, humans also exploited Iberian ibex (*C. pyrenaica*) and other occasional herbivorous such as aurochs (*B. primigenius*), bison (*B. priscus*), horse (*E. ferus*/sp.), chamois (*R. rupicapra*), and exceptionally roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*) during this time. From the Aurignacian onwards, the frequency of horse and large bovid decrease, becoming notable in the Magdalenian. Although, the presence and abundance of some taxa are determined by the environmental conditions (González-Echegaray de Yarto, 2020), humans may have preferred specific resources.

Among the ungulates hunted by Gravettian populations, the acquisition appears more linked to environmental availability. However, the proximity to the coast meant that hunter-gatherer groups were in an advantageous position, by following the migratory movements of animals to obtain resources more effectively. Despite this, and as previously mentioned, the main prey in central and eastern Cantabria is red deer (*C. elaphus*), followed by medium-size caprines (*C. pyrenaica* and *R. rupicapra*) in mountain or mid-mountain areas and large bovids in the eastern part of the Basque Country, as in Aitzbitarte III (e.g., Quesada López, 1997c; Altuna et al., 2011; Altuna et al., 2013; González-Echegaray de Yarto, 2020).

In addition to ungulates, the carnivore taxa in the Cantabrian Region include bears (*Ursus* sp.), large felids (*Panthera* sp.), wolves (*Canis lupus*), red fox (*Vulpes vulpes*), and European badger (*Meles meles*) (Yravedra, 2002; Normand et al., 2012; Iriarte-Chiapusso and Arrizabalaga, 2012; González-Morales and Straus, 2012; Marín-Arroyo and Sanz-Royo, 2021).

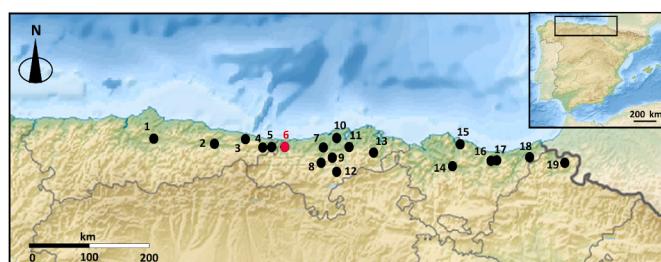


Fig. 1. General location of the Fuente del Salín Cave and the most important Gravettian sites within the Cantabrian Region. In Asturias: 1. La Viña, 2. Sopeña, 3. Cueto de la Mina, 4. Coimbre B, 5. Llonfín; In Cantabria: 6. Fuente del Salín, 7. Altamira cave, 8. Hornos de la Peña, 9. El Castillo, 10. El Pendo, 11. Morín, 12. La Garma A, 13. El Mirón; In the Basque Country: 14. Bolinkoba, 15. Antolíñako, 16. Irakaitz, 17. Amalda, 18. Aitzbitarte III; Navarre: 19. Alkerdi.

1.2. Aquatic resources during the Gravettian

Aquatic resources, especially molluscs, were traditionally considered low-ranked and only consumed during periods of dietary stress (Osborn, 1977; Parmalee and Klipper, 1974). From the perspective of the Broad Spectrum Revolution, these resources were only consumed intensively during the Mesolithic, a sign of diversification and intensification, which occurred as a response to increasing population size and rising pressure on land resources (Binford, 1968; Flannery, 1969). However, in the last two decades, new models have proposed that the use of aquatic resources during the Upper Paleolithic has been underestimated (Bailey and Milner, 2002; Bicho and Haws, 2008; Bailey and Flemming, 2008; Bicho and Esteves, 2022). These models emphasize the bias produced by sea level rise, which covered Upper Paleolithic coastal areas and, therefore, a significant portion of coastal settlements. Despite this underrepresentation, and thanks to intense research efforts, today, there is plenty of evidence of the use of marine resources throughout the Upper Paleolithic across the coastal areas of Atlantic and Mediterranean Europe (Colonese et al., 2011; Gutiérrez-Zugasti et al., 2011). In some regions, such as the Atlantic coast of Portugal, marine productivity was even higher than in the Holocene. Thus, human populations could have benefited from the abundance, predictability, and ease of access to intertidal resources, such as molluscs. Moreover, current evidence suggests that diversification and intensification primarily began during the early Upper Paleolithic (e.g., Bicho and Haws, 2008) as seen, for example, at the Gravettian site of Vale Boi where coastal adaptations have been recently described (Bicho and Esteves, 2022). New investigations (e.g., Zilhão et al., 2020; Nabais et al., 2023) observed that an intensification of marine resources such as fish, molluscs, and crabs, was already incipient during the Middle Paleolithic. In the north of the Iberian Peninsula, the role of aquatic resources as part of human subsistence strategies during the Upper Paleolithic has gained importance in recent years (Freeman, 1973; Straus, 1977; Straus and Clark, 1986; Álvarez-Fernández, 2011a; Gutiérrez-Zugasti et al., 2011). However, even though 12 sites show evidence of aquatic resource exploitation during the Gravettian, only a few have been thoroughly studied, and only Fuente del Salín Cave and La Garma A have essential quantitative and qualitative studies based on malacofauna (Álvarez-Fernández, 2007; Gutiérrez-Zugasti et al., 2012, 2013). These studies show the use

of marine molluscs as food, attested by the collection of edible species, such as the common limpet (*Patella vulgata*), the common periwinkle (*Littorina littorea*), and the mussel (*Mytilus sp.*), but also as ornaments, which is suggested by the presence of pierced flat periwinkle (*L. obtusata*) and cowrie (*Trivia sp.*) shells. Other sites, such as Altamira cave, also show evidence of shell collection for food (de las Heras et al., 2012), while Aitzbitarte III presents a few molluscs from each level (edible and ornamental). Still, they are present across the entire Gravettian sequence of the site (Álvarez-Fernández, 2011b), reflecting a continuous collection throughout the period. At other sites only a few ornamental shells have been recorded, such as at Coímbre cave (Álvarez-Fernández, 2017). Thus, data from these and other sites (Table 1) indicate a significant and stable collection of molluscs on rocky intertidal shores. Finally, the importance of molluscs for Gravettian societies is also evidenced at Fuente del Salín and Altamira caves through the use of marine shells as tools, especially for getting ochre powder likely destined to paint the exceptional rock art present in both caves (Cuenca-Solana, 2013, 2016). Overall, data from northern Iberia also suggest the occurrence of coastal adaptations (or at least a systematic use of marine resources) since the Early Upper Paleolithic.

If we talk about recovered and studied fish remains from Gravettian sites in the Cantabrian Region, few pieces of evidence are described in detail. At Aitzbitarte III, Roselló-Izquierdo and Morales-Muñiz (2011) defined the presence of Atlantic species such as the poor cod (*Trisopterus minutus*, an inhabitant of waters close to the coast), the mackerel (*Scomber sp.*, which is common in the Cantabrian Sea during the spring), the blenny (*Blennius sp.*, typical from rocky areas close to the coast), and the European flounder (*Platichthys flesus*, present in sandy soils). Also, the authors documented the presence of remains from salmonids (*Salmo sp.*) and anguillids. The last two families are also recorded at La Garma A (Dr. Sónia Gabriel, Directorate-General for Cultural Heritage (DGPC), Lisboa, Portugal, com. pers.). Ongoing excavations at both sites will provide more comprehensive information about the role of fish in the human diet. At Coímbre B (Asturias), Gabriel (2017) observed the presence of two brown trout (*Salmo cf. trutta*) remains from the Gravettian layer Co. B.6.

Marine mammals are less frequent in the Gravettian-Solutrean record of the Cantabrian Region. Evidence corresponds to a seal (*P. hispida* or *P. vitulina*) canine from level E and a dolphin (*Tursiops truncatus*) tooth

Table 1
Sites presenting Gravettian layers from the Cantabrian Region with malacofauna lists. Modified from Castaños and Álvarez-Fernández (2012).

Taxa	Gravettian Cantabrian archaeological sites											
	C.Mina	F.Salín	Pendo	Altamira	Morín	Garma A	Castillo	Bolinkoba	Amalda	Aitz. III	Alkerdi	Coímbre B
<i>P. vulgata</i>	+	+	+	+	+	+	+			+		
<i>P. depressa</i>												
<i>Patella sp.</i>					+							
<i>L. littorea</i>	+	+		+		+	+	+	+	+	+	
<i>Mytilus sp.</i>						+						
<i>P. lineatus</i>						+						
<i>Ostrea sp.</i>					+							
<i>Trivia sp.</i>		+				+			+			
<i>L. obtusata</i>	+	+			+	+		+	+	+	+	
<i>L. fabalis</i>												
<i>L. saxatilis</i>						+						
<i>Littorina sp.</i>						+						
<i>T. reticulata</i>					+	+						
<i>N. lapillus</i>						+						
<i>Turritella sp.</i>							+					
<i>L. lurida</i>												
<i>Colus sp.</i>						+						
<i>S. saburon</i>						+						
Gast. Indet.						+						
<i>Antalis sp.</i>												+
Cardiidae					+	+						
Neritidae						+						
<i>A. islandica</i>						+						
Mol. Indet.									+	+		

from level G of La Garma (the piece exhibits a perforation probably used as an ornament; Álvarez-Fernández, 2011a), a canine tooth belonging to an undetermined seal from Altamira (Breuil and Obermaier, 1935; Álvarez-Fernández and Fernández-García, 2011), and a phalange of *P. vitulina* (Altuna and Straus, 1976) alongside two unidentified seal bones from levels 4 and 7 at La Riera (Altuna and Straus, 1976).

This study aims to provide new and relevant data on the subsistence strategies of the hunter-gatherers of the Cantabrian Region during the Gravettian. We focus, in particular, on the Fuente del Salín Cave as an example of a site between the coast and the mountains. Due to the small number of multi-taxa (large game, fish, and molluscs) and multi-proxy (taphonomy, seasonality, paleoenvironment) studies, we improve our knowledge of subsistence during the Gravettian period in this area. Additionally, this region is particularly interesting for understanding how subsistence strategies evolve and change concerning environment, landscape, and geography.

2. Fuente del Salín Cave

Fuente del Salín is a cave in Muñorodero (Val de Sal Vicente) on the western edge of the Autonomous Region of Cantabria (North Iberia, Fig. 1). The site, discovered in 1985 (González-Morales and Moure-Romanillo, 2000), lies at an altitude of 15 m.a.s.l., ca. 40 m above the base of the Ruao mountain, and is situated around 20 m from the Nansa river. The cave is currently located 3 km from the open shore (Cuenca-Solana, 2013) but less than one from the inner edge of the estuary.

The cave is characterized by a lower and a middle gallery, both with circulating water, which is still active today. Since Fuente del Salín Cave is close to the Nansa River, its geological context presents several fluvial terraces. Several tributaries, located in Peña Labra and Peña Sagra mountains, are the primary source of the Nansa River.

The original entrance is blocked, and the cave is only accessible from the lower galleries (González-Morales and Moure-Romanillo, 2008). The main gallery where the archaeological deposit was found is located on the upper level of the cave, which also exhibits wall paintings (Fig. 2).

Discovered in 1985 by explorers of "Sociedad de Actividades

Espeleológicas de Cantabria (SAEC)" caving group, the site includes an exceptional set of hand stencils painted in red, along with two positive ones and three others in black. These Palaeolithic representations were located close to the cave's original entrance; initial excavations developed in 1990 and 1991 confirmed the presence of a single archaeological layer of the Gravettian. The stratigraphy of the excavated section includes three sedimentary levels. Level 1 comprises three sublevels corresponding to a thin layer of dark clay (sublevel 1.1), which sealed a thin stalagmitic crust underneath (sublevel 1.2). Below sublevel 1.2 is sublevel 1.3, which is characterized by a soft and disintegrated stalagmitic fill. Under this, a virtually sterile stalagmitic package, lies a deposit (Level 2) with dark sediment (Fig. 1). This level corresponded to a large hearth, alternating layers of burnt clay and charcoal beds, abundant mammals and fish remains, and many molluscs. The presence of tools and worked bones were scarce. The excavation stopped at the base of the hearth, wherein an archeologically sterile layer (3) was encountered. The radiocarbon dates place the duration of the occupation (28,080–26,640 cal BP) in the Gravettian (González-Morales and Moure-Romanillo, 2008, Fig. 3, Table 2), in accordance following the characteristics of lithic and bone/antler industries. Seven radiocarbon dates were undertaken to provide a chronology for the Gravettian level 2 located inside the cave. Two dates were made on bone collagen, one in shell and three in charcoal recovered in the hearth. Samples were measured at Geochron laboratories, the University of Groningen, the Oxford Radiocarbon Accelerator Unit (ORAU) the Centre for Applied Isotope Studies (CAIS) at the University of Georgia (USA), and the International Chemical Analysis Inc. (ICA). (Table 2). A Bayesian age model was built for the site using OxCal4.4.2 software (Bronk Ramsey, 2009a), with the INTCAL20 calibration curve (Reimer et al., 2020).

A Delta-R of -577 ± 131 was used for calibration of marine samples. This value was calculated following the method established by Soares et al. (2016) and using the Marine20 calibration curve.

Considering the stratigraphic information of the site, the dates were modelled in a sequence model with the stratigraphic level represented a phase, with a start and end boundaries. All radiocarbon determinations were given a 5 per cent prior likelihood of being an outlier within the General t-type Outlier Model (Bronk Ramsey, 2009b), so that the model

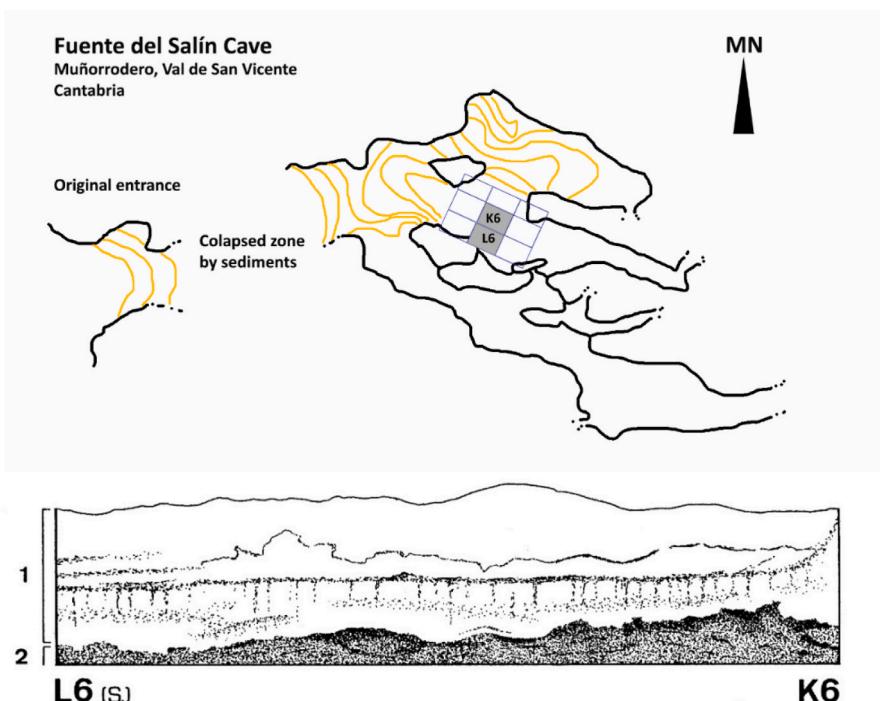


Fig. 2. Plan of the cave with the two excavated squares, the origin of the materials of this study in grey (K6 and L6), and the stratigraphic section below. Modified from González-Morales and Moure-Romanillo (2008).

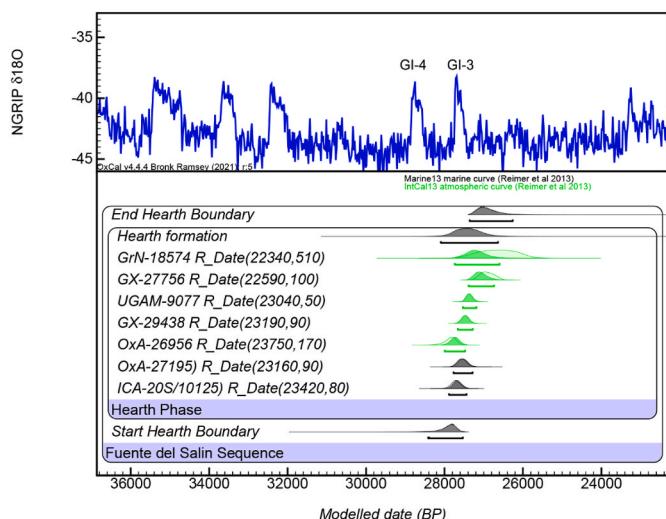


Fig. 3. Radiocarbon dates for the Gravettian assemblages of Fuente del Salín Cave calibrated against IntCal20 in OxCal v.4.4, assuming each sample has a 5% prior probability of being an outlier within the general t-type outlier model. Overall = 85. the duration phase of the hearth is between 28,080 and 26,640 cal BP.

Table 2
Radiocarbon dates from Fuente del Salín Cave.

Sample area	Material	method	14C age BP	\pm	Laboratory reference
Black negative hand	Charcoal	AMS	18,200	70	GX-27757
Hearth surface	Bone	?	23,190	900	GX-29438
Charcoal in the hearth	Charcoal	?	22,340	510/	GrN-18574
				480	
Charcoal in the hearth	Charcoal	AMS	22,580	100	GX-27756
In the hearth	Bone	?	23,040	50	UGAMS-9077
In the hearth	Shell	?	23,160	90	OxA-27195

could test their reliability. Convergence was greater than 95 per cent, and the model agreement index was 87.4 per cent. The results were compared with the Greenland ice-core oxygen isotope record (NGRIP) (Andersen et al., 2006; Svensson et al., 2008), used as a global climatic record to correlate each culture with the different climatic phases.

3. Material and methods

This paper includes fish and macromammal remains collected during the 2016 excavation campaign from a 2 m² area (squares K6, sectors 1–9; and L6, sectors 1–9) (Fig. 2). All fish material belongs to level 2. Although excavators sometimes denoted the sublayer “2-Fondo”, all remains were analyzed together.

While investigating this material, we used a binocular EXACTA OPTECH model LFZ s/n 201030 20 W, LEICA S8 APO stereoscope, and a Dino-Lite Edge Digital Microscope.

3.1. Taxonomy

We analyzed the macromammal material following standard archaeozoological methods. Most specimens were identified to genus/species, whereas fragments with no-diagnostic attributes were assigned to body size categories.

Due to the lack of specific landmarks and high fragmentation, we grouped the taxonomically unidentifiable specimens based on their body size into five categories of mammals: size 1, smaller than rabbit/

hare; size 2, small mammals weighing <20 kg (lagomorphs, rodents, and small carnivores); size 3, medium mammals between 20 and 100 kg (*C. pyrenaica*, *R. rupicapra*, *C. capreolus*, *C. lupus*); size 4, medium/large mammals between 100 and 300 kg (*C. elaphus*, Ursidae); and size 5, large mammals of >300 kg (large bovids).

We quantified the assemblage using the following indices: Number of Remains (NR), Number of Identified Specimens (Grayson, 1984; Lyman, 2008), Minimum Number of Individuals (MNI; Grayson, 1984; Lyman, 1994, 2008), Minimum Number of Skeletal Elements (MNE) and Minimum Animal Units (MAU) following Marín-Arroyo (2009).

We used the osteological comparative collection at the EvoAdapta Laboratory, University of Cantabria.

We conducted anatomical and taxonomical classifications for fish remains using the modern reference collection at the University of Tübingen and several osteological atlases (Conroy et al., 2005; Lepiksaar, 1994; Watt et al., 1997). We employed the taxonomic nomenclature from Cannon (1987) and Wheeler and Jones (2009). However, we considered indeterminate fragments in the taphonomic analysis. Some elements were indeterminate due to poor preservation. For this paper, when osteometric models to estimate the fish size was not available, it was visually estimated through direct comparison (Guillaud et al., 2017, 2020) with specimens of known length data from the modern comparative collection based at the Senckenberg Center for Human Evolution and Palaeoenvironment, University of Tübingen.

3.2. Taphonomy and skeletal representation

We examined bone surface damage in detail to determine the principal accumulation agent and/or modification (carnivores and birds of prey versus humans) and post-depositional processes. We followed Behrensmeyer (1978) and Fisher (1995) to document natural surface damages and weathering, such as flaking, cracks, and exfoliation on bones (González-Echegaray de Yarto, 2020). In addition, we recorded the presence of taphonomical signals such as chemical weathering and root etching. Other indications that we analyzed for each specimen were rodent and carnivore gnawing, epiphyseal fusion, tooth wear, burning, and butchery damage (Stiner, 1994, 2005; Stiner et al., 1995). Additionally, we had to prove that fish accumulation in Fuente del Salín Cave could be attributed to human activities before making inferences about human behavior, such as seasonality and subsistence strategies (Butler, 1990; Russ, 2010a, 2011; Hardy and Moncel, 2011; Guillaud et al., 2018, 2020; Blanco-Lapaz et al., 2021). To do so, it was necessary to consider different aspects of the fish assemblage, such as the biology of the sample (ecology, species diversity, and fish size), diversity, taphonomy (element representation, element fragmentation, bone surface modifications, digestion marks, and spatial distribution), and species seasonality to determine the principal agent responsible for the accumulation of the fish remains.

We analyzed bone surface modifications for the fish remains, such as digestion marks, compression, uniaxial mechanical deformation, and gnawing marks (Guillaud et al., 2018; Frontini et al., 2021). We identified evidence of burning using five stages of thermally-induced discoloration following Cáceres et al. (2002). These are based on heat-induced color alterations described by Shipman et al. (1984) and Stiner et al. (1995) for large mammal bones (see also Lloversas et al., 2009; Medina et al., 2012; Walker et al., 2016 for applications to microvertebrates). The stages correspond to 0 (no discoloration), 1 (yellowish with reddish-brown spots; <100 °C to 300 °C), 2 (dark brown to black; <400 °C to 550 °C), 3 (charred bone: dark black or blue over 50–100% of the surface; 500 °C to <700 °C), 4 (grey-white coloration, partial calcination; 650 °C to <950 °C), and 5 (calcined bone: white coloration over 50–100% of the surface; >700 °C).

3.3. Distribution, capture areas, and seasonality

Determining the seasonal variations in the consumed species helps us

to determine an occupation period and also provide us with data on a particular type of different protein production and use. In addition, species-specific birth periods allow us to identify the duration of occupation of the site.

The birth period of each wild species is constant, so the age at which an animal was hunted provides a date of birth and, therefore, information on the occupational duration of the site.

Ungulate mortality patterns were assessed using dental eruption, wear stage, and bone fusion. For cervids, we followed Mariezkurrena (1983), Azorit et al. (2002), and Tomé and Vigne (2003). For caprids, we used Couturier (1962), Pflieger (1982), and Habermehl (1992). Once we determined the age of death, we grouped individuals into five age groups: Foetal/Neonatal; Juvenile: light wear on deciduous teeth and erupted M1; sub-Adult: moderate wear on deciduous teeth and erupted M2; Adult: all permanent teeth erupted with any wear; Old Adult or Senile: advanced wear. We estimated the ratio between juvenile and adult individuals to measure the pressure on low-return younger prey and the type of exploited prey.

Additionally, we applied a Bayesian method based on a Monte Carlo Markov Chain sampling that uses the available skeletal information to constrain the possible degrees of attrition and carcass processing strategies (Marín-Arroyo and Ocio, 2017). This method considers two parameters, alpha (α) and beta (β), active during the assemblage formation and history. α informs about the transport preference based on butchering efficiency in skeletal elements, and it can take any value between -1 (> axial contribution) and 1 (> appendicular contribution). The degree of attrition (β) follows the definition established by Rogers (2000a,b), which relates the survivorship of bone elements to their maximum bone density. This method aims to overcome the problem of equifinality in skeletal profile interpretations by analyzing the two factors simultaneously (e.g., Marín-Arroyo and Ocio, 2017; R code in Marín-Arroyo et al., 2022).

For fish, to determine the possible capture areas and their proximity to the site, we analyzed the geographical distribution and habitats of the fish species based on modern and ancient reconstructions (Kettle et al., 2010; Lloris, 2015). We also compared our results with other studies based on malacofauna (species, size, and age), the reconstructions of the coastline, and the sea level near Fuente del Salín Cave during the Gravettian (Gutiérrez-Zugasti et al., 2012).

4. Results

4.1. Taxonomy of large mammalian game

A total of 2888 macrofaunal remains were identified, corresponding to 2509 unidentified remains (86.9%) and 379 classified to species/genus level (13.1%). From the classified remains, we taxonomically identified 227 (7.9%) and 152 (5.3%) to size class. Seven taxa are

present in Fuente del Salín Cave assemblage, such as red deer (*C. elaphus*, NISP = 156, 68.7%), Iberian ibex (*C. pyrenaica*, NISP = 51, 22.54%), chamois (*R. rupicapra*, NISP = 9, 3.9%), horse (*E. ferus*, NISP = 5, 2.2%), roe deer (*C. capreolus*, NISP = 4, 1.7%), red fox (*V. vulpes*, NISP = 1, 0.4%), and wild cat (*Felis sylvestris*, NISP = 1, 0.4%) (Table 3).

4.2. Taxonomy of fish

Fig. 4 presents the identified taxa at Fuente del Salín Cave (see Table 5).

We identified 1602 fish remains, 1503 (93.8%) of which were classified as unidentified Teleostei due to their poor preservation and fragmentation level. Eleven remains (0.7%) correspond to the family Cyprinidae, most corresponding to vertebrae. The Salmonidae family (salmon and trout) is present in the assemblage, with 84 specimens (5.2%) belonging to the *Salmo* genus. Due to the fragmentary nature of the material, it was impossible to classify the remains to species level. The only species-level classification in Fuente del Salín Cave corresponds to the haddock (*Melanogrammus aeglefinus*), represented by four remains (0.2%).

Due to the poor preservation, estimating fish size was impossible. Using the modern comparative collection of the University of Tübingen, all remains belonging, for example, to *Salmo* sp. might correspond to large animals with a total length of around 60–70 cm. The Cyprinidae elements correspond to vertebrae, which cannot be attributed to genus or species level due to the high diversity and morphological similarity within this family (Roselló-Izquierdo and Morales-Muñiz, 2005).

Most elements classified as unidentified Teleostei correspond to ribs, vertebrae, and neural and branchial spine fragments showing a high fragmentation level, which makes taxonomic determination impossible.

4.3. Taphonomy and skeletal representation. Large game

4.3.1. Anthropogenic fragmentation

A high fragmentation rate characterizes the macrofauna assemblage at Fuente del Salín Cave, since most remains are smaller than 3 cm (87.4%). Only 1.4% correspond to complete elements, usually phalanges and sesamoids. From the remains smaller than 3 cm, 21.6% corresponds to axial elements, 6% to posterior extremities, 2.9% to anterior extremities, and 3.1% to cranial elements. The abundance of less dense bones indicates a high degree of anthropogenic modification at the site. Overall, specimens exhibiting burning damage are frequent (1103 bones, 50.4%), as well as anthropic breakage for marrow extraction (14.5%). No anthropogenic marks are present on the remains of either carnivore (red fox and wild cat), possibly excluding humans as their agent of accumulation (González-Echegaray de Yarto, 2020, Table 4).

Table 3

Macrofaunal remains of Fuente del Salín. Number of identified specimens (NISP), remains (NR), Minimum Number of Individuals (MNI), and relative proportions (%).

Taxa	NISP/NR	%	MNI	%	MNI	Infantile	Juvenile	Subadult	Adult
Ungulates									
Horse (<i>E. ferus</i>)	5	0,2	1	10			1		
Red deer (<i>C. elaphus</i>)	156	5,4	3	30	1		1		1
Roe deer (<i>C. capreolus</i>)	4	0,1	1	10			1		
Iberian ibex (<i>C. pyrenaica</i>)	51	1,8	2	20	1			1	
Chamois (<i>R. rupicapra</i>)	9	0,3	1	10				1	
Carnivores									
Red fox (<i>V. vulpes</i>)	1	0,0	1	10			1		
Wild cat (<i>F. sylvestris</i>)	1	0,0	1	10					1
Large mammal-size	4	0,1							
Medium mammal-size	122	4,2							
Small mammal-size	26	0,9							
Unidentified	2509	86,9							
Total	2888	100	10	100	2		4	2	2

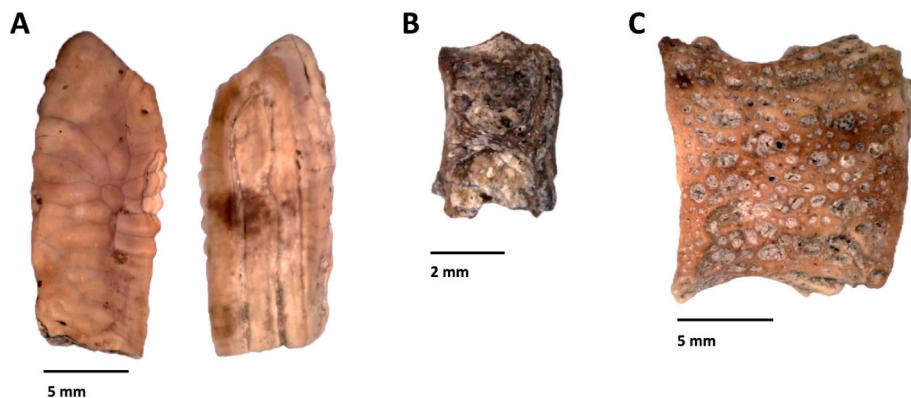


Fig. 4. A. Haddock (*M. aeglefinus*), left otolith (Salín 2016 N.399 L6 Sc.2 UE.2 Tr.1); B. Cyprinidae unidentified, caudal vertebra (Salín 2016 N.405 L6 Sc.1 UE.2 Tr.1); C. Salmonid (*Salmo* sp.), vertebra fragment (Salín 2016 N.393 K6 Sc.7 UE.2 BASE).

Table 4
Taphonomical modifications identified in the macrofaunal assemblage at Fuente del Salín.

	Total	
	NR	%
Biostratinomic alterations		
Fresh breakage	320	14.6
Cut marks	22	1.0
Burning	1103	50.4
Granwing marks	1	0
Rodents		
Trampling	3	0.1
Weathering	16	0.7
Digestion	1	0
Subtotal	1466	67.0
Diagenetic alterations		
Concretions	164	7.5
Iron oxides	241	11.0
Manganese	104	4.8
Water dissolution	203	9.3
Peeling		
Bacteria	9	0.4
Root etching		
Subtotal	721	33.0
Total	2187	100

4.3.2. Burning damage

Most bones showing burning damage (82.5%) endured a firing temperature of between 525 °C and +940 °C (Stages 3–5), which indicates direct exposure to fire. 17.5% of bones show stages 1–2 (185°C–525 °C), indicating a non-direct exposure, probably linked to cooking activities (González-Echegaray de Yarto, 2020). Of the identifiable taxa, we observed black coloration on 79 red deer (*C. elaphus*) bones, indicating temperatures of between 525 °C and 645 °C. No burning damage is recorded on roe deer (*C. capreolus*) or horse bones (González-Echegaray de Yarto, 2020).

4.3.3. Skeletal profiles

For the most commonly identified taxa in the assemblage, the red deer (*C. elaphus*), all anatomical parts appear in different proportions. The extremities (phalanges, metapodials, and sesamoids) are most frequently represented (35.5%), followed by axial bones (23.7%), anterior (12.8%) and posterior (18.6%) long bones, and cranial elements (9%). Therefore, it shows all elements were transported, but there was a preference for those of higher nutritional value, that is, appendicular elements, especially to the detriment of crania. The Bayesian model that gives us information about transport preferences (Fig. 5) indicates a complete transport of animals to the site ($\alpha = 0.13$).

All skeletal parts of the second most abundant species, the Iberian

ibex (*C. pyrenaica*), are present in Fuente del Salín Cave. The extremities (phalanges, metapodials, and sesamoids) are the most represented (49%), followed by long anterior bones (19.6%), axial bones (13.7%), long posterior bones (11.8%), and cranial elements (9%). Anthropogenic marks are present on 37.2% of remains, highlighted by longitudinal fractures. A total of 14 bones show burning damage, indicating temperatures of between 525 °C and 645 °C. The bones of chamois indicate a similar pattern since 66.7% correspond to extremities and 11% to cranial elements. No axial bones are present. All roe deer (*C. capreolus*) elements correspond to extremities. Horse (*E. ferus*) also follow the previous patterns, with the extremities being most represented.

4.4. Taphonomy and skeletal representation. Fish remains

4.4.1. Anthropogenic fragmentation

Taphonomic analysis indicates no mechanical deformation, rounding, or polishing due to compression during digestion (Blanco-Lapaz et al., 2021; Frontini et al., 2021; Morales-Muñiz et al., 2021). The lack of rounded or abraded bones and surface weathering suggest water transport is an unlikely scenario for accumulation at Fuente del Salín Cave. Instead, the bones were deposited at the site and quickly covered by sediment (e.g., Rhodes et al., 2016). Gnaw, crush, and digestive marks are also absent from all fish remains, which means that carnivores or birds of prey can be ruled out (Nicholson, 1993). The lack of carnivore modifications indicates that species, such as red foxes, cats, and birds of prey, infrequently visited the cave (González-Echegaray de Yarto, 2020) and were not the agents of accumulation. This also suggests that the high degree of fragmentation in the fish assemblage corresponds to anthropogenic activity.

4.4.2. Burning damage

The burning analysis of the fish remains revealed 181 remains (11.3%) corresponding to stage 0, 1203 (75.1%) to stage 1, 154 (9.6%) to stage 2, and 54 (3.4%) to stage 3. Only 4 (0.7%) remains correspond to stage 4, and no remains show stage 5 (Table 5, Fig. 6). Based on the thermal discoloration stages, we confirm that most remains (75.1%) indicate a firing temperature between 100 and 300 °C (Stage 1). However, some bones indicate higher temperatures of no more than 700 °C (Shipman et al., 1984).

4.4.3. Skeletal profiles

The recovered fish from Fuente del Salín Cave are characterized by postcranial elements, namely vertebrae, spines, branchial spines, and ribs (NISP = 1578; 98.5%) (Table 6). Cranial bones (NISP = 24; 1.5%) are underrepresented. By taxon/group, unidentified Teleostei make up most of the sample. Vertebrae fragments (NISP = 169; 11.2%), spines (NISP = 970; 64.5%), branchial spines (NISP = 286; 19%), and ribs

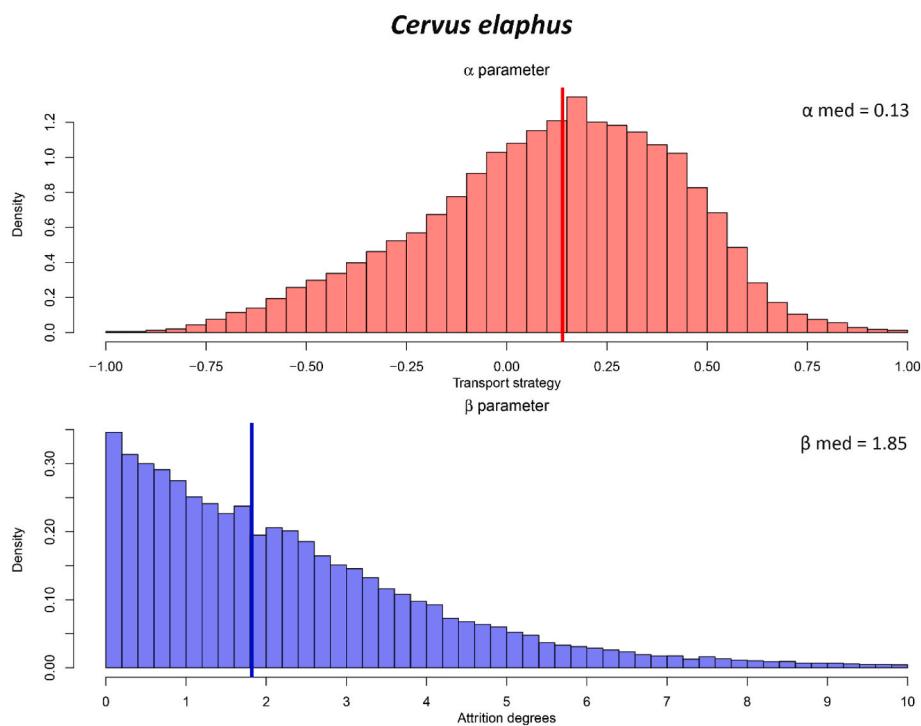


Fig. 5. Results of the Bayesian method to evaluate the model of transport and the degree of attrition in red deer (*C. elaphus*; $\alpha = 0.13$ $\beta = 1.83$). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 5

The number of fish remains and burning stages observed in Fuente del Salín fish remains.

Taxa	Burning stages					Total
	0	1	2	3	4	
Teleostei	162	1161	133	43	4	1503
<i>Salmo</i> sp.	11	47	18	8		84
Cyprinidae	6		2	3		11
<i>M. aeglefinus</i>	2	1	1			4
Total	181 (11,3%)	1209 (75,5%)	154 (9,6%)	54 (3,4%)	4 (0,2%)	1602



Fig. 6. Burning stages observed in Fuente del Salín Cave based on salmonid remains. From stages 0–4 corresponding to Salín 2016 N.397 L6 Sc.7 UE.2 FONDO, stage 4 belongs to Salín 2016 N.399 L6 Sc.2 UE.1 Tr.1.

(NISP = 58; 3.9%) are the most common elements, representing 88.6% of the total. The most common elements belonging to *Salmo* sp. include fragments of vertebrae (NISP = 79; 94%) and just three teeth (3.6%). Vertebrae are the only elements recovered for cyprinids (NISP = 11). Vertebrae (NISP = 3) are the most common elements of the haddock (*M. aeglefinus*), although an otolith is also present (Table 6, Figs. 3 and 7).

5. Discussion

5.1. Taxonomy

The pattern of ungulate exploitation at Fuente del Salín Cave during the Gravettian shows red deer (*C. elaphus*) were the most exploited species at the site, a characteristic of coastal valleys and plains. Martínez-Arroyo and Sanz-Royo (2021) observed the same, since this species is the most exploited in the Vasco-Cantabrian region during the Middle Paleolithic-Upper Paleolithic transition. In Fuente del Salín Cave, this

Table 6

Taxa, number and percentage of the anatomical element recovered in Fuente del Salín Cave. Ce, Cranial element; Cv, Caudal vertebra; Tv, Thoracic vertebra; Fv, Fragment of vertebra; Sp, Spine; Bs, Branchial spine; R, Rib.

Taxa	Skeletal elements							Total
	Ce	Cv	Tv	Fv	Sp	Bs	R	
Teleostei	20 (1,3%)			169 (11,2%)	970 (64,5%)	286 (19%)	58 (3,9%)	1503
<i>Salmo</i> sp.	3 (3,6%)		2 (2,4%)	79 (94%)				84
Cyprinidae		8 (72,7%)		3 (27,3%)				11
<i>M. aeglefinus</i>	1 (25%)	1 (25%)	2 (50%)					4
Total	24 (1,5%)	9 (0,6%)	7 (0,4%)	248 (15,5%)	970 (60,5%)	286 (47,5%)	58 (3,6%)	1602

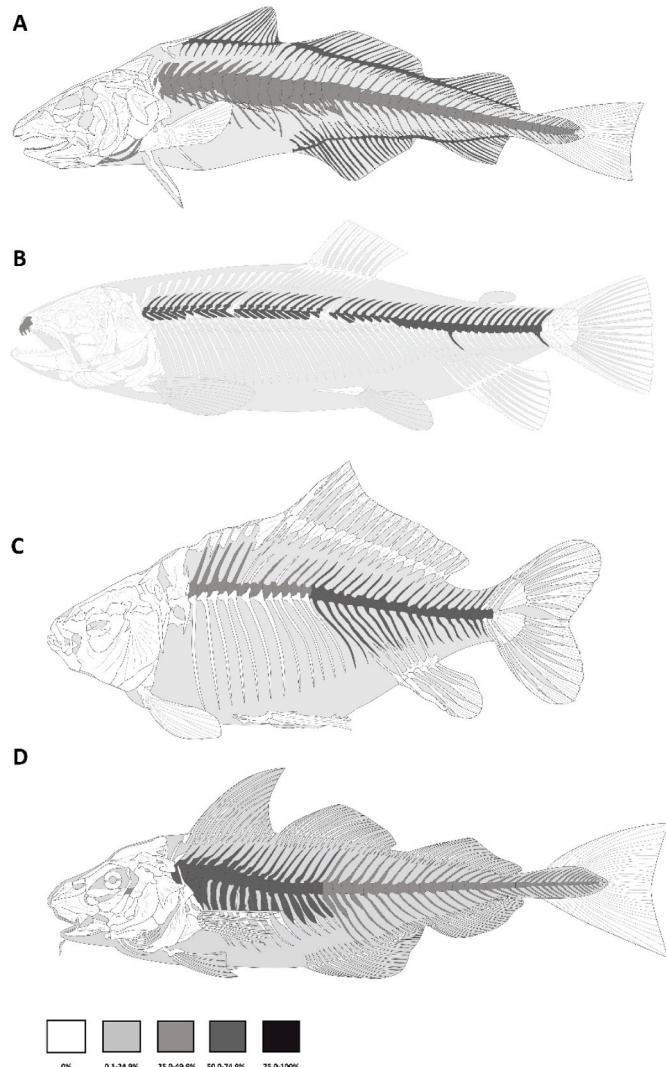


Fig. 7. Percentage of the skeletal element present in Fuente del Salín Cave. A: Cod skeleton representing the Teleostei unidentified remains, B: Atlantic salmon (*Salmo salar*) skeleton representing the *Salmo* sp. remains, C: Carp skeleton (*Cyprinus carpio*) representing the Cyprinidae remains, D: Haddock skeleton (*Melanogrammus aeglefinus*). Modified from Michel Coutureau and Philippe Béarez (collab.), 2017/ArcheoZoo.org (License CC BY NC SA 4.0 International).

species is followed by the Iberian ibex (*C. pyrenaica*) and the chamois (*R. rupicapra*), indicating the exploitation of steep, rocky landscapes. The scarcity of carnivores excludes the alternation between human and animal occupation at Fuente del Salín Cave.

During the Upper Paleolithic in the Cantabrian Region, a diversity of fish species in assemblages is generally rare, represented mostly by

salmonids (*Salmo* sp.) and cyprinids (e.g., Straus, 1983; Straus and Clark, 1986; Russ, 2010b; Roselló-Izquierdo and Morales-Muñiz, 2011; Aura-Tortosa et al., 2019; Blanco-Lapaz et al., 2021; Álvarez-Fernández et al., 2022) (Table 7). The brown trout is the most common salmonid in the Iberian Peninsula (e.g., Russ, 2010b; Aura-Tortosa et al., 2019; Blanco-Lapaz et al., 2021). However, researchers have also described the presence of the Atlantic salmon (*S. salar*) since the Middle-Upper Paleolithic (e.g., Russ, 2010b; Álvarez-Fernández et al., 2022).

In this paper, we described large-sized salmonids at Fuente del Salín Cave. Large-sized animals are more characteristic of the Atlantic salmon (*S. salar*) than the common brown trout (*S. trutta*) in the Iberian Peninsula, which rarely exceeds 60 cm and 10 kg (the maximum for the trout in Central Europe corresponds to 100 cm and around 20 kg; Consuegra et al., 2002; Doadrio et al., 2011). Although this could indicate that all Fuente del Salín Cave salmonid remains correspond to Atlantic salmon (*S. salar*), we cannot confirm this hypothesis due to the fragmentary nature of the assemblage and difficulty in distinguishing Atlantic salmon and trout.

Additionally, we describe the presence of large haddock specimens (>50 cm total length), indicating that the presence of large-sized fishes is probably due to anthropogenic activity (Morales-Muñiz and Roselló-Izquierdo, 1990; Roselló-Izquierdo and Morales-Muñiz, 2005).

5.2. Taphonomy

At Fuente del Salín Cave, archaeologists observed that the cave walls and roof were significantly damaged. This damage is located 2 m high around the large hearth and probably resulted from a significant concentration of high temperatures. The mechanical alteration of the limestone was caused by a temperature between 600 °C and 900 °C (González-Echegaray de Yarto, 2020).

In general, the burning damage on mammal bones is located primarily on axial elements and epiphyses, where the possible use of these remains as combustion material joined with wood cannot be ruled out (Yravedra et al., 2017).

Based on the mammal remains, 82.5% showed burning damage, indicating temperatures typical of carbonization or calcification with black and grey colors. Together with the high degree of fragmentation (more than 70%) and the higher burning frequency on elements rich in fat (epiphyses and axial elements), this evidence suggests bone burning would serve to increase the duration of the fire. This combination at the hearth would offer constant high temperatures either to eliminate organic elements or for use as fuel. Lastly, the alternating layers of clay and coal in the central area of the hearth, together with the location of the deposit, lead us to suggest the everyday use of firewood and bones for a repeatedly lit hearth (González-Morales and Moure-Romanillo, 2000; González-Echegaray de Yarto, 2020).

Our archaeozoological and taphonomical analyses, based on mammal bones from Layer 2 at Fuente del Salín Cave, prove the anthropogenic nature of the site. The scarcity of carnivore gnawing marks and the taphonomic alterations typical of butchery processing indicates that humans were the main accumulators at Fuente del Salín Cave, where the high degree of fragmentation and fresh breakage also indicates an intensive use by its inhabitants.

Table 7

Gravettian sites from the Cantabrian Region with fish remains lists. Aitz. = Aitzbitarte.

Taxa	Cantabrian Region Sites										
	C. Mina	F. Salín	Pendo	Morín	Garma A	Castillo	Bolinkoba	Amalda	Aitz. III	Alkerdi	Coímbre B
<i>Teleostei</i>		+			+				+		
<i>Blennius</i> sp.									+		
<i>Scomber</i> sp.									+		
<i>P. flesus</i>									+		
<i>M. aeglefinus</i>	+										
<i>Salmo</i> sp.	+				+				+		
cf. <i>S. trutta</i>											+
<i>Cyprinidae</i>	+										
<i>Anguillidae</i>				+							

The taphonomic analyses based on fish remains indicate an abundance of spines, branchial spines, ribs, and vertebrae fragments (NISP = 1578; 98,5%), suggesting that humans removed the spines and branchial spines for consumption. Although there is no direct evidence of fishing implements such as hooks, leisters, gorges, harpoons or fishing nets, humans likely used composite tools or fishing traps made of wood or plant fibers, which were not preserved in the cave's wet, humid conditions.

5.3. Marine, estuarine, riverine and terrestrial exploitation

The collection of molluscs for food at Fuente del Salín Cave almost exclusively includes the limpet *P. vulgata*. Oxygen stable isotope analysis indicates these limpets were collected in spring, summer, and late fall-early winter (unpublished data). The study of shell collection areas suggest that the inhabitants of the cave primarily collected the molluscs on the upper intertidal zone of sheltered shores. Although limited, the presence of sea urchins and crab remains shows that other intertidal resources were also collected for food.

During the Gravettian, the distance from Fuente del Salín Cave to the coast was between 9 and 11 km, which is within the limits of an acceptable distance for coastal resource exploitation among hunter-fisher-gatherers (Gutiérrez-Zugasti et al., 2012, 2013). However, the closer areas of the inner estuary could have also been exploited.

Ornamental species, such as *L. obtusata* and *Trivia* sp. (as well as the presence of unmodified *L. saxatilis*), reflect how shells were also used for symbolic purposes. At the same time, prior functional analysis demonstrated that *P. vulgata* were also used as tools (Cuenca-Solana et al., 2013; 2016). Therefore, shells were used for different purposes, indicating that these resources played an important role for Gravettian populations living in coastal areas.

From an environmental point of view, all mollusc species identified at the site indicate cold waters (Gutiérrez-Zugasti, 2009), which is in agreement with environmental conditions reflected by other proxies for this period. In the present study, salmonids (*Salmo* sp.) and the haddock (*M. aeglefinus*), a boreal gadid species, also confirm this finding.

Haddock (*M. aeglefinus*) is a demersal species that prefer cold waters (4–10 °C) and are located at depths between 10 and 450 m, although they live more frequently between 80 and 200 m. Several authors (e.g., Casaretto et al., 2014, 2015) observed that the spawning season of haddock occurs generally between January and June. This species is currently present in Northwest Europe with a southernmost range in the Bay of Biscay (Withehead et al., 1986). Rodrigo (1994) also reported the presence of haddock and salmonids in Nerja cave (Málaga, Southern Spain) during the LGM.

Concerning salmonids, two species are present in the Iberian Peninsula: Atlantic salmon (*S. salar*) and brown trout (*S. trutta*). Atlantic salmon (*S. salar*) reproduce in cold and well-oxygenated waters. Their entrance to the rivers occurs from October to August (Doadrio et al., 2011). In northwestern Europe, the current southernmost range of Atlantic salmon is northern Portugal. However, Kettle et al. (2010) also studied the presence of this species in southern Spain during the LGM

(Nerja cave in particular), indicating that immigrant populations would have passed through the Straits of Gibraltar when temperatures in southern Spain were similar to present day northern Europe. Like the Atlantic salmon, the brown trout (*S. trutta*) also lives in cold and rapid waters. Their reproduction period is between November and January when the water temperature oscillates between 5 and 10 °C (Doadrio et al., 2011).

Cyprinids present in the assemblage would indicate an availability all year round. In general, this family is distributed in most water types (Doadrio et al., 2011), and the presence of salmonids and cyprinids would suggest exploitation of different areas in the Nansa River and, not only in fast-water portion, where salmonids are mostly present (Doadrio et al., 2011). However, we cannot conclude this hypothesis due the difficulty to identify cyprinids to species level based on their vertebrae (Roselló-Izquierdo and Morales-Muñiz, 2005).

Based on the recovered fish remains, salmonids (probably Atlantic salmon, *S. salar*) and cyprinids indicate extensive fish exploitation at Fuente del Salín Cave, since their presence in the fluvial/estuarine system occurs from fall to summer. In addition, the presence of haddock (*M. aeglefinus*) supports this pattern since their spawning season also takes place from winter to summer.

Concerning terrestrial resources, red deer (*C. elaphus*) are the most useful to estimate the period of occupation and seasonality at Fuente del Salín Cave. We observed a predominance of juvenile and infant individuals, mostly indicating a fall-winter hunting period. The first molar of an Iberian ibex (*C. pyrenaica*) also indicates a winter occupation. However, horse remains and a neonatal Iberian ibex (*C. pyrenaica*) indicate a spring component. Unfortunately, we could not determine if the cave was used by humans in a single event or over several occupations. However, the seasonality results and the hearth stratigraphy indicate a short-term occupation. Overall, in Fuente del Salín Cave, we argue that hunting was episodic, but occurred mainly during fall/winter.

Our results based on aquatic (fish and molluscs) and inland (large game) resources indicate that Gravettians exploited large mammals mainly during fall/winter and fish from fall to summer. Limpet shells of *P. vulgata* were collected in spring, summer and late fall-early winter (unpublished data). These results expand our knowledge of seasonal occupation at the site and in the Cantabrian Region during the Upper Paleolithic. Additionally, considering the short-term nature of the occupations, it is important to highlight the high diversity of prey for human subsistence in Fuente del Salín Cave.

6. Conclusions

Fuente del Salín Cave, located on the southwestern slope of a ridge above the spur that enters the mouth of the Nansa River, presents an excellent location for hunting, fishing, and gathering in various biotypes. The site exhibits human subsistence dominance of red deer, which was supplemented by other resources provided by the river and the coast, such as fish and molluscs.

The fish and mollusc remains located in the Gravettian layers of Fuente del Salín Cave prove that aquatic resource exploitation was a

strategy within a diversified human diet during the beginning of the Upper Paleolithic. During the Gravettian, only two other sites point towards fish exploitation in the Cantabrian Region (Aitzbitarte III and La Garma A), with salmonids being most commonly recovered. Our taxonomic, palaeoecological, and taphonomic results indicate that, in Fuente del Salín Cave, humans mainly exploited two fish taxa, salmonids (*Salmo* sp.) and (much less) haddock (*M. aeglefinus*). These taxa indicate capture areas close to the coast and the river mouth, although the presence of haddock could show some fishing far from the coastline.

Red deer (*C. elaphus*) and Iberian ibex (*C. ibex*), together with limpets (*P. vulgata*), salmonids (*Salmo* sp.), cyprinids, and haddock (*M. aeglefinus*), were transported to the site whole and subsequently cooked, as indicated by frequent burning damage, which suggests indirect exposure to fire. Once consumed, their remains were abandoned in the vicinity of the habitation area, perhaps during domestic cleaning tasks.

Our results indicate that fish exploitation complemented the human diet during the summer periods, while humans exploited larger game during the spring and fall-winter periods, and molluscs in all of these seasons. Layer 2 of Fuente del Salín Cave hosts a record of short-term occupations, where humans transported mostly complete ungulate prey to the site, combined with molluscs and fish. The diversity of recovered taxa was likely stimulated by the site's proximity to various coastal and mountainous biotopes, and reflects the topographic characteristics and vegetation cover of the surrounding paleoenvironment.

Studies of fish exploitation in the Cantabrian Region during the Gravettian are limited in comparison with works related to Solutrean and Magdalenian sites, making it hard to reconstruct human fishing activities during this period. Exploring fish assemblages from other sites in the region could help to improve our knowledge of fishing strategies as part of human subsistence practices during the Upper Paleolithic in the North Iberian Peninsula.

Author contributions

A. B.-L. analyzed and studied the fish assemblage. F. G.-E. and A.B. M.-A. analyzed and studied the large game assemblage. I.G-Z previously analyzed the mollusc assemblage. I. G-Z, M.R. G-M., IG-Z, and A.B.M-A. provided archaeological, archaeozoological, and geological contexts. A-B-L. primarily wrote the manuscript, but all authors contributed to all sections. All authors reviewed and approved the manuscript before submission.

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Informed consent statement

Not applicable.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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