Surf and turf. Animal resources in the human diet in Cantabrian Spain during the Mesolithic (11.5 – 7.5 Ky cal. BP)

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ABSTRACT

The beginning of the Holocene involved a series of climatic and environmental changes that affected the ways of life of the last hunter-gatherers. In the case of the Spanish Cantabrian region, these changes transformed the material culture and the way human groups interacted with the environment and, therefore, the subsistence strategies of the end of the Upper Pleistocene. In terms of the use of faunal resources, this period was characterised by an increase in the exploitation of coastal resources, mainly molluscs, but also crustaceans and echinoderms, which make up the so-called "shell middens", while at the same time the percentage of macromammals was reduced and animals considered to have a "low energy range" were introduced into the diet. In this paper we assess the role played by each of these animal resources in the subsistence of Mesolithic human groups, determining their nutritional contribution and establishing a prey ranking based on the caloric intake of each resource. For this purpose, we collected archaeofaunal data from 14 sites from recent archaeological excavations with levels dated between *ca.* 11.5 and 7.5 ky cal BP in which the consumption of vertebrates and invertebrates is documented. At each of these sites we analysed diversity, homogeneity and species richness using Simpson's and Shannon's indexes, as well as the effective numbers of species for terrestrial and coastal resources, assessing the relationship between the two. With the palaeoecological and palaeoeconomic data from these archaeological sites (most of them located in caves), we estimate the weight that the different animal resources consumed by the last hunter-gatherer communities of the Cantabrian region had in their diet.

1. Introduction

From an economic point of view, the Mesolithic period in the Spanish Cantabrian region has been characterised as a time in which the exploitation of marine resources intensified, especially molluscs, while at the same time animals considered to have a low energy range were introduced into the diet, and the number of macromammals documented in the sites decreased (Bailey and Craighead, 2003; Álvarez-Fernández, 2005–2006, 2008, 2011 and 2015; Marín, 2008, 2010, 2013; Gutiérrez-Zugasti, 2009; 2011; García-Escárzaga et al., 2015; García-Escárzaga, 2020).

Although in the last decade there have been many studies on faunal resources in the Cantabrian Mesolithic, both in terms of terrestrial (e.g. Altuna and Mariezkurrena, 2012; Andreu, 2013; Marín, 2010; Marín et al., 2020), and marine species (e.g. Gutiérrez-Zugasti, 2011; Álvarez-Fernández, 2012, 2016; Álvarez-Fernández et al., 2013, 2014a; Bello-Alonso et al., 2015; Gutiérrez-Zugasti et al., 2016; García-Escárzaga, 2020), we have few references that establish the specific weight of each

of these animals in the subsistence of human groups in a comparative perspective, with the exception of the works of A.B. Marín (2013) and A. García-Escárzaga and Gutiérrez-Zugasti, 2021). The first of these studies analyses the causes of the change in hunting strategies at the end of the Upper Pleistocene and the energetic contribution of terrestrial versus marine resources based on the Minimum Number of Individuals (MNI), although it does not provide detailed data on the contribution of molluscs to the diet of the different archaeological sequences in the region. The second establishes a methodology for assessing the meat intake of molluscs in the diet, based on an experimental study that is applied to the archaeological sequence of El Mazo cave, providing new data on subsistence strategies and determining a greater weight in the energetic contribution of marine resources in the diet of Mesolithic hunter-gatherers. However, to date we do not have synthesis studies that allow us to assess the role played by each of these resources in the diet of Mesolithic human groups in the Cantabrian region, or that deal with terrestrial and marine resources using the same methodology.

In this research, we evaluate the role played by each of the terrestrial and marine species in different sites from the Spanish Cantabrian region excavated in the last decades. To this end, we apply a new methodological approach that combines palaeoecological analysis based on Simpson's diversity and Shannon's homogeneity indices, with palaeoeconomic studies derived from the meat contribution calculated from the average weight of meat and fat provided by the different animal resources documented in the archaeological sequences, both terrestrial and marine, based on the MNI. Thus, we contribute to the knowledge

about the subsistence strategies of the last hunter-gatherer communities of the Cantabrian region by establishing a prey ranking that includes the energetic supply of calories that each of these species would have provided to the human groups during the Mesolithic (Fig. 1).

2. Methods

To establish the subsistence strategies in the Cantabrian Mesolithic, we selected those archaeological levels of sites with radiocarbon chronologies between *ca.* 11.5 and 7.5 ky cal BP in which the consumption of macromammals and coastal resources is documented, and whose excavations were carried out from the 1970s onwards, when systems based on stratigraphic principles became generalised, while integrating a precise recovery of the material through sieving (Álvarez-Fernández et al., 2014b, 2016; Portero et al., 2019; Portero, 2022). We have also included unpublished information from three sites: La Poza ÍEgua (Lledías, Asturias), Cuevas del Mar III (Nueva, Asturias), and El Alloru (Balmori, Asturias).

The studied contexts have been dated using the radiocarbon method. All dates have been calibrated with OxCal 4.4. program (Bronk Ramsey, 2009) and the IntCal20 calibration curves (Reimer et al., 2020) for terrestrial samples and Marine20 (Heaton et al., 2020) for those of marine origin. In the latter case, the marine reservoir effect for the Cantabrian has been included, which gives a Delta $\pm$ R of -105 ± 21 for the early Holocene (Monge Soares et al., 2016).

To calculate the abundance of the different animal species we use the
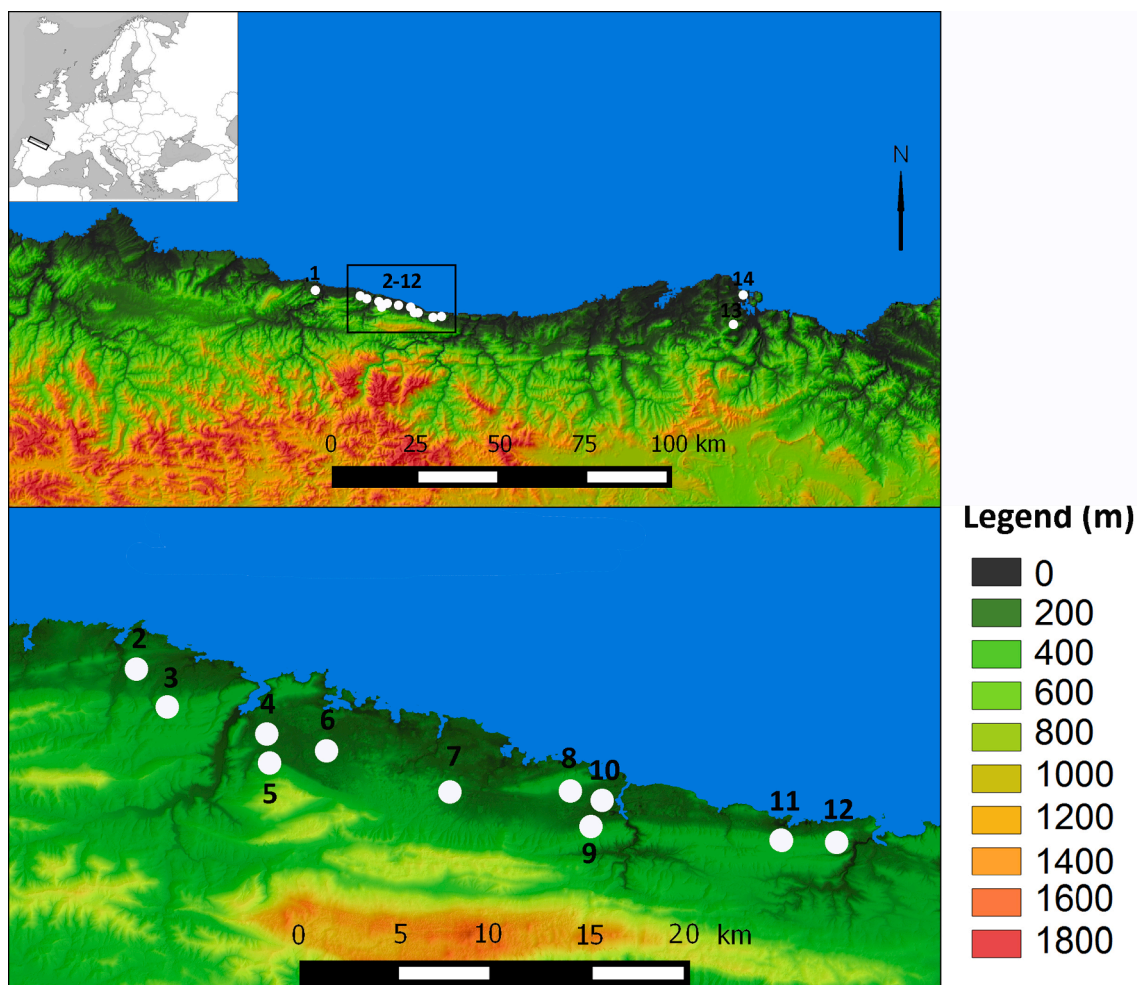
Fig. 1. Topographical map showing the location of the sites included in this paper (Top): 1) El Cierro; 2) Cuevas del Mar III; 3) Colomba; 4) La Riera; 5) La Poza l'Egua; 6) El Alloru; 7) Covajorno; 8) El Toral III; 9) El Águila; 10) Pendueles; 11) El Mazo; 12) Toralete; 13) El Carabión; 14) La Fragua. Extension of the location of the sites of Asturias (bottom) (DEM based on IGN's maps using the software QGIS v.3.22).

MNI (Lyman, 2019), as it is a measure used by all researchers for mammals, molluscs, crustaceans, and echinoderms; unlike other indices such as the Number of Remains (NR), the Number of Identified Specimens (NISP), or the weight of the remains, which do not always appear in the publications. In the sites studied by us, the MNI has been calculated took into account the most represented anatomical part, the laterality of the bone, and the age of the individual (Binford, 1981; Brain, 1981; Lyman, 1994).

2.1. Palaeoecological analysis:

To evaluate the biodiversity of the archaeological levels, we used Simpson's diversity index (**D**), which measures, from a given number of species found in an ecosystem, the relative abundance of each one of them. This index is expressed as follows:

$$D = \sum_{i=1}^{S} \frac{n_i(n_i - 1)}{N(N - 1)}$$

Here S is the number of taxa within the assemblage, n_i the number of individuals of a species i, and N the total number of individuals in the community. This index will indicate the differences or similarities of faunal comparisons without being greatly affected by the amount of the existing remains, as it is an index that can be used in small samples. In this research, we also used Simpson's Reciprocal Index, which consists of dividing 1 by Simpson's index (**1/D**), and which has been frequently used in Palaeolithic research (e.g. Grayson and Delpech, 1998, 2002; Grayson et al., 2001; Jones, 2004; Faith and Du, 2018; Portero, 2022). The value of this index ranges from 1 to the total number of species in the sample; 1 being the value that would represent a community with only one species. Therefore, the higher the value, the greater the diversity of a set.

We also analysed the degree of entropy of the animal communities in each of the selected archaeological levels using Shannon's index (**H'**). This index measures the heterogeneity of a community based on the number of species in the sample and the relative abundance of each of them. Its equation is expressed as follows:

$$H' = - \sum p_i \ln p_i$$

Here p_i is the proportional abundance of i taxon (Grayson and Delpech, 2002; Fontana and Brochier, 2009; Jost, 2010; Faith and Du, 2018; Fontana, 2018). If one individual is very abundant in an ecosystem and the others are poorly represented, we will have a lower degree of uncertainty than if all species were equally abundant. This implies that, in highly taxon-dominated assemblages, the value of **H'** will be close to 0.

From the Shannon index, we calculated the Shannon homogeneity index or *Evenness* (**E**), which allows us to analyse the degree of homogeneity of a faunal assemblage. The calculation is based on the following equation:

$$E = - \sum p_i \ln p_i / \ln(S)$$

Here S is the number of taxa represented in the sample. This index fluctuates between 0 and 1; the closer to 1, the greater the homogeneity (Grayson and Delpech, 2002; Jost, 2010; Faith and Du, 2018).

We also analysed the Effective Number of Species (**^qD**) of the animals in the ecosystem, calculated using the exponential of Shannon's index:

$$qD = exp(- \sum p_i \ln p_i)$$

This configuration allows us to convert diversity indexes into effective numbers, providing an indicator that determines how many species we can consider in our sample, depending on their level of rarity (Jost, 2006). This index measures the diversity that a community composed of i equally common species would have.

The results obtained from Simpson's and Shannon's indexes are shown graphically using scatter diagrams, where the values of Simpson's reciprocity index (1/D) and Shannon's homogeneity index (*Evenness*) are presented on the ordinate axis and the natural and Napierian logarithms of the MNI of each of the levels on the abscissa axis, as proposed by D.K. Grayson and F. Delpech (2002). In addition, to check whether there is a relationship between the indexes and the NISP of the studied levels, we calculated Spearman's rank correlation coefficient between these variables, allowing us to observe the trend and strength of the relationship between both variables, as well as its statistical significance (p-value $< 0{,}05$).

These indexes allowed us to evaluate the specific importance that different species had within an archaeological sequence, observing small variations in the diversity and homogeneity of the assemblages that we cannot see with the naked eye (Magurran, 1988; Quesada, 1997; Grayson and Delpech, 1998, 2002; Jones, 2004; Faith and Du, 2018; Fontana, 2018).

2.2. Palaeoeconomic analysis:

Once we analysed the biodiversity of the documented terrestrial and water species and the specific importance of each one of them in the different archaeological sequences, we estimated the energy input of these animals in the diet of the Mesolithic hunter-gatherers, based on the kilocalories they provided. The method for estimating the caloric energy that we can associate with each species follows these steps (Portero et al., 2019; Portero, 2022):

1) Establishing the mean weight of each taxon from the proportion of males and females of each species, based on current animal populations (Clutton-Brock and Iason, 1986). In the case of mammals, we used the mean weights for males and females of red deer (Carranza, 2017), Iberian ibex (Alados and Escós, 2017), roe deer (Mateos-Quesada, 2017), chamois (Pérez-Barbería et al., 2017) and wild boar (Fernández-Llario, 2017). We are aware that some species such as the red deer were larger at the end of the Upper Pleistocene and the beginning of the Holocene than the present ones. However, we use the studies based on actual populations because we do not have data that allow us to know the body mass by sex of the Mesolithic deer of the Cantabrian region in relation to the sizes of the current red deer. Some studies on body mass indexes have been carried out, but, they have not given results that allow us to calculate the detailed weight for males and females in the different periods of the Upper Pleistocene and early Holocene of the Cantabrian region (Mariezcurrena and Altuna, 1983; Castaños, 2014). Although we know how much males and females could contribute individually to the diet, in this work we use the mean of both sexes because usually in the literature on the Mesolithic fauna of the Cantabrian region it is not specified how many individuals belong to males and females. For molluscs we have used the average weight obtained for *Phorcus lineatus*, *Patella vulgata*, *Patella depressa* and *Patella ulysiponensis* in Langre Beach (García-Escárzaga and Gutiérrez-Zugasti, 2021). We have also taken into account the data for *Gibbula* sp. (López-Benito, 1956), *Mytilus galloprovincialis* (Palmerini and Bianchi, 1994), *Ostrea edulis* (López-Benito, 1956), *Scrobicularia plana* (López-Benito, 1956; EOL, 2018), *Ruditapes decussatus* (Ojea et al., 2004), *Cerastoderma edule* (López-Benito, 1956), *Solen marginatus* (López-Benito, 1956), *Haliotis tuberculata* (Izquierdo López, 2008), *Pollicipes pollicipes* (López-Benito, 1956; Seoane, 2015), *Paracentrotus lividus* (Dincer and Cakli, 2007), *Carcinus maenas* (Naczk et al., 2004), *Pachygrapsus marmoratus* (Aydin et al., 2014), *Eriphia verrucosa* (Kaya et al., 2009), *Cancer pagurus* (Tonk and Rozemeijer, 2019) and *Xantho incisus* (Kaya et al., 2009). Although *Cepaea nemoralis* is common in archaeological sites and may have been used as a food resource, it has been excluded from this research because we do not have contemporary studies that dealt with biometric parameters.

2) Calculation of the weight of meat plus fat for each animal, based on the observations of L.W. Binford (1978) for caribou and sheep, and

applicable in the Cantabrian region to cervids and small bovids. For wild boar, we have taken the data from the nutritional tables of the Food Data Central Database of the US Department of Agriculture (USDA, 2020). In addition, as the contribution of mammals' meat and fat varies significantly depending on the age of the individual, we have established a reduction in the weight of the adult animal of 33 % for juveniles and 66 % for immature individuals, broadly coinciding with the weights established in their life cycles (Portero, 2022). In the case of molluscs, crustaceans, and echinoderms, we have used the fresh meat weights proposed by various authors for the different species above mentioned. In this way, we have obtained the weight of the exploitable part of each of the animals.

3) Once the weight of the usable part had been calculated, we estimated the calories per kilo of meat and fat for each of these animals, based on the data provided by the food tables of the US Department of Agriculture (USDA. 2020) and the Spanish Food Composition Database (BEDCA, 2007). These figures have allowed us to document the total energy provided by each specimen when multiplied by the weight contributed by its meat and fat (Tables 1 and 2).

To ensure that the contribution of the macromammals documented in these sites is due to human activity, we only use those species that show signs of anthropic manipulation indicating that they were contributed to and consumed by human groups. Similarly, in the case of molluscs, crustaceans, and echinoderms, we only use those species that are considered edible.

3. Results

To establish the subsistence strategies during the Mesolithic in the Cantabrian region, we rely on a total of 18 archaeological levels from 14 sites dated between *ca.* 11 and 7.5 ky BP (Table 3). From the MNI marine resources are much more abundant (99.8 %) in proportion to terrestrial resources (0.2 %). In all selected levels molluscs are the most abundant resources, exceeding 90 % representation. Mammals are the worst represented, and only in Carabión 1 do they exceed 2 % of the MNI. Crustaceans except in Cierro B, where they represent 6.8 % of the MNI, in no site do they exceed 1.5 % of the representation. Echinoderms are found in almost all levels, but with percentages that in no case reach 2 % of the MNI (Table 4).

From a taxonomic point of view, *Phorcus lineatus* is the predominant species in seven levels, *Patella* sp. in six, *Patella depressa* in four, and *Scrobicularia plana* in only one site. The predominance of these species is between 30 and 55 %, although in some cases, such as Alloru 2003, Covajorno, and Riera 29, the numbers exceed 60 % of the MNI (Supplementary Material 1).

From a palaeoecological point of view, Simpson's diversity index (1-D) shows values between 0.4 and 0.8 ($\bar{X}$=0.64 ± 0.03) and between 1.8 and 5.5 ($\bar{X}$=3.11 ± 0.27) of the reciprocal index (1/D) for these sites. This indicates that we are dealing with faunal assemblages with a low diversity of species, dominated by a few taxa. This can also be seen in the low Effective Number of Species (^qD), which has a mean of 3.97 ± 0.39; a very low value considering that some levels, such as La Fragua 1, have up to 37 species represented. From the point of view of evenness, these assemblages show a very low degree of uncertainty, according to the data obtained in the Shannon index (*H'*), with mean values of 1.30 ± 0.09. From the homogeneity index (*E*), we document that the archaeological levels show a scarce uniformity in the distribution of species in relation to the MNI ($\bar{X}$=0.28 ± 0.02) (Table 5).

From the scatter graph between log. MNI and Simpson's Reciprocal Index (1/D), we document that Riera 29, Covajorno, and Alloru 2003 are the levels most dominated by a single taxon, while Carabión 1, Cierro B, and Toral IIIB 17 are the most diverse (Fig. 3). From Spearman's correlation coefficient we observe that there is a direct and statistically significant relationship between the values of Simpson's Reciprocal Index and the volume of documented individuals ($\rho = 0.57$; $p < 0.01$). This allows us to appreciate that the higher the MNI of a site, the higher the dominance index it presents. Similarly, from the scatter plot between the LN of the MNI and the Homogeneity Index (*E*), Cuevas del Mar III and Pendueles are the most homogeneous levels, while Fragua 1, Poza l'Egua, and El Mazo 100/101 are the least uniform. In this case, the correlation between the Homogeneity Index and the volume of documented individuals is inverse and statistically significant between both variables ($\rho = -0.64$; $p < 0.01$). This indicates that the higher the MNI of the sites, the less homogeneous they are (Fig. 4). In general, these data agree with the values associated with the percentage of MNI, with one or two taxa generally predominating (*Phorcus lineatus* and *Patella* sp.), the most pronounced values of which are documented in Alloru 2003, Covajorno, and Riera 29.

Regarding the amount of meat and fat, as well as the kilocalories that each of these species would have supplied to the diets of the early Holocene human groups, we have calculated the energy intake that each species could have provided according to its MNI by age. The detailed information on the energy calculations per taxon in each of the selected archaeological levels is presented in Supplementary Material 2. In general terms, terrestrial mammals would have provided the greatest amount of meat resources, with 2145.1 kg of meat and fat, representing 94.5 % of the total calories recorded. In second place are molluscs, with around 5.4 % of the total calories and a contribution of 122.9 kg, while crustaceans and echinoderms represent<1 % of the kcal provided, with around 2.9 kg of meat and fat. Despite this general distribution, there are some cases, such as El Mazo 100/101, El Mazo 105, La Fragua 1, or El

Table 1

Caloric energy provided by taxon and age category of the macromammal species documented in the Mesolithic sites of the Cantabrian region, based on the average weight of both sexes and the proportion of meat and fat provided by each individual per age category (AD = adult; JU = juvenile; IMM = immature).

Species	Age Cat.	Middle weight (Kg)	Meat + grease (Kg)	Energy (Kcal/Kg)	Total Energy (Kcal)	References
Cervus elaphus	AD	93,5	36,7	1.110	40.737	Clutton-Brock and Iason, 1986; Marín, 2010 Carranza, 2017; USDA, 2020
	JU	62,4	24,5	1.110	27.195	
	IMM	31,1	12,2	1.110	13.542	
Capra pyrenaica	AD	51,2	19,4	1.140	22.116	Marín, 2010; Alados and Escós, 2017; USDA, 2020
	JU	34,2	13	1.140	14.820	
	IMM	17	6,4	1.140	7.296	
Rupicapra pyrenaica	AD	26,5	10	1.140	11.400	Marín, 2010; Pérez-Barbería et al., 2017; USDA, 2020
	JU	17,7	6,7	1.140	7.638	
	IMM	8,9	3,3	1.140	3.762	
Capreolus capreolus	AD	24,4	9,5	1.110	10.545	Marín, 2010; Mateos-Quesada, 2017
	JU	16,3	6,3	1.110	6.993	
	IMM	8,1	3,2	1.110	3.552	
Sus scrofa	AD	66	25	1.220	30.500	Fernández-Llario, 2017; USDA, 2020
	JU	44	16,7	1.220	20.374	
	IMM	22	8,3	1.220	10.126	

Table 2
Caloric energy provided per taxon of the species of molluscs, crustaceans, and echinoderms documented in the Mesolithic sites of the Cantabrian region, based on the average weight of both sexes and the proportion of meat provided by each individual.

Species	Middle weight (gr)	Wet Flesh weigh (gr)	Energy (Kcal/gr)	Total Energy (Kcal)	References
MOLLUSCS					
Phorcus lineatus	2.7	0.73	1.05	0.77	BEDCA, 2007; García-Escárzaga and Gutiérrez-Zugasti, 2021
Patella vulgata	5.3	1.98	1.02	2.01	López-Benito, 1956; García-Escárzaga and Gutiérrez-Zugasti, 2021
Patella depressa	5.5	2.02	1.02	2.06	López-Benito, 1956; García-Escárzaga and Gutiérrez-Zugasti, 2021
Patella ulyssiponensis	4.7	2.02	1.02	2.06	García-Escárzaga and Gutiérrez-Zugasti, 2021
Cerastoderma edule	13.8	5.2	0.48	2.5	López-Benito, 1956; BEDCA, 2007
Gibbula cineraria	2.8	0.53	0.95	0.51	López-Benito, 1956; BEDCA, 2007
Mimachlamys varia	75	12.1	0,78	9,44	BEDCA, 2007; EOL, 2018
Mytilus galloprovincialis	5	2.45	0.61	1.49	Palmerini and Bianchi, 1994; BEDCA, 2007
Ostrea edulis	31.4	5,4	0.64	3.5	López-Benito, 1956; BEDCA, 2007
Scrobicularia plana	7.6	3.8	0.67	2.55	López-Benito, 1956
Ruditapes decussatus	24,3	5.4	0.48	2.59	Ojea et al., 2004; BEDCA, 2007
Solen marginatus	32,5	25	1.09	27,25	López-Benito, 1956; BEDCA, 2007
Haliotis tuberculata	84,6	17	0.98	16,66	Izquierdo López, 2008; USDA, 2020
Gibbula umbilicatis	2.8	0.53	0.95	0.51	López-Benito, 1956; BEDCA, 2007
CRUSTACEANS					
Pollicipes pollicipes	8	2,5	0.60	1.5	López-Benito, 1956; BEDCA, 2007; Seoane, 2015
Carcinus maenas	62	15.2	1.24	18,85	Naczk et al., 2004; BEDCA, 2007
Pachygrapsus marmoratus	17,5	13.3	1.24	16,74	BEDCA, 2007; Aydin et al., 2014
Cancer pagurus	814	450	1.24	558	BEDCA, 2007; Tonk and Rozemeijer, 2019
Eriphia verrucosa	155	68.2	1.24	84,57	BEDCA, 2007; Kaya et al., 2009
Xantho incisus	155	68.2	1.24	84,57	BEDCA, 2007; Kaya et al., 2009
ECHINODERMS					
Paracentrotus lividus	40.3	2.5	0.90	2.25	BEDCA, 2007; Dincer and Cakli, 2007

Table 3
Radiocarbon dating and its calibration (cal. BP) to 2σ from the IntCal20 (Reimer et al., 2020) and Marine 20 (Heaton et al., 2020) curves, using OxCal v.4.4 (Ramsey, 2009), of the archaeological levels from Mesolithic sites in the Cantabrian region (C = Charcoal; MB = Mammal bone; HB = Human bone; SH = Shell). SM: Shell midden.

Site	Datation BP	Material	Method	Ref. Lab.	cal. BP 2σ	References
Águila SM	7705 ± 50	C	Conv.	UBAR-795	8590 – 8406	Fano, 2004
Alloru 104	7979 ± 38	MB	AMS	OxA-29115–6	8995 – 8698	Arias et al., 2016
Alloru 401	7714 ± 34	C	AMS	OxA-29082	8588 – 8416	Arias et al., 2016
	7342 ± 32	C	AMS	OxA-29083	8281 – 8027	
Alloru 2003	8360 ± 70	C	Conv.	UBAR-781	9527 – 9139	Fano, 2004
Carabión 1	5750 ± 40	C	AMS	Poz-18732	6656 – 6445	Pérez-Bartolomé et al., 2016
	7800 ± 50	MB	AMS	Poz-32691	8720 – 8425	
	5440 ± 40	HB	AMS	Poz-30592	6307 – 6121	
Cierro B	7470 ± 38	SH	AMS	OxA-31702	7991 – 7689	Álvarez-Fernández et al., 2020
	8575 ± 40	SH	AMS	OxA-31705	9350 – 8977	
Colomba SM	7090 ± 60	HB	Conv.	TO-10223	8018 – 7790	Arias et al., 2007
	7020 ± 90	MB	Conv.	UBAR-833	8007 – 7679	
Covajorno SM	7540 ± 100	SH	Conv.	UBAR-773	8173 – 7676	Fano, 2004
Cuevas del Mar III SM	5610 ± 100	SH	Conv.	UBAR-794	6196 – 5649	Fano, 2004
Fragua 1	6650 ± 120	C	Conv.	GrN-20963	7735 – 7315	González-Morales, 2000
	6860 ± 60	C	Conv.	GrN-20964	7833 – 7582	
	7530 ± 70	C	Conv.	GrN-20965	8446 – 8439	
Mazo 100/101	7105 ± 40	MB	AMS	OxA-28397	8012 – 7845	Gutiérrez-Zugasti et al., 2016Marín et al., 2020
	7310 ± 40	SH	AMS	OxA-30780	7860 – 7546	
	7230 ± 36	MB	AMS	OxA-30806	8170 – 7965	
Mazo 105	7595 ± 40	SH	AMS	OxA-30977	8155 – 7828	Marín et al., 2020
Pendueles SM	7080 ± 80	SH	Conv.	UBAR-793	7670 – 7285	Fano, 2004
Poza l'Egua	8550 ± 80	HB	Conv.	TO-10222	9723 – 9323	Arias et al. 2007
Riera 29	8650 ± 300	C	Conv.	GaK-2909	10,510 – 8994	Straus, 1986
	6500 ± 200	C	Conv.	GaK-3046	7753 – 6946	
Toral III B21	7080 ± 30	MB	AMS	UGAMS-5400	7970 – 7840	Noval, 2013
	6750 ± 30	C	AMS	UGAMS-5401	7670 – 7523	
Toral III B17	6430 ± 30	C	AMS	UGAMS-5403	7424 – 7280	Noval, 2013
Toralete SM	7060 ± 80	SH	Conv.	UBAR-777	7655 – 7269	Fano, 2004

Toral IIIB 21, where marine molluscs are of greater importance, with values ranging between 8 % and 20 % of calories, and between 9 % and 21 % of the meat and fat at the level (Fig. 5).

If we look at the energy intake by species, red deer would have provided the greatest number of calories, with 1,589 out of 1395 kg,

representing *ca.* 62 % of the total calories documented at these sites. Furthermore, this species predominates in energy supply in 17 of the 18 selected archaeological levels. However, only in eight of them does it provide more than 60 % of the total calories. In second place is the wild boar, with 528,626 calories out of 483 kg, which is around 20.5 % of the

Table 4
MNI of macromammals, molluscs, crustaceans, and echinoderms, and their percentages in the selected Mesolithic levels. SM: Shell midden.

Site	Mammals	%	Molluscs	%	Crustaceans	%	Echinoderms	%	Total	References
Águila SM	3	0.35	863	99.53	–	–	1	0.12	**867**	Arias et al. 2007
Alloru 104	3	0.13	2309	99.83	–	–	1	0.04	**2313**	Arias et al., 2016; This work
Alloru 401	3	0.38	793	99.50	–	–	1	0.13	**797**	This work
Alloru 2003	1	0.60	164	98.80	–	–	1	0.60	**166**	Arias et al., 2016
Carabión1	21	2.69	760	97.19	1	0.13	–	–	**782**	Pérez-Bartolomé et al., 2016
Cierro B	7	0.78	824	91.35	61	6.76	10	1.11	**902**	Álvarez-Fernández et al., 2020
Colomba SM	3	0.38	782	99.24	–	–	3	0.38	**788**	Arias et al., 2007
Covajorno SM	2	0.58	340	99.13	–	–	1	0.29	**343**	Arias et al., 2007
Cuevas del Mar III SM	2	1.67	117	97.5	–	–	1	0.83	**120**	Arias et al., 2007; This work
Fragua 1	16	0.13	11,900	98.62	150	1.24	1	0.01	**12,067**	Marín, 2004; Gutiérrez-Zugasti, 2009.
Mazo 100/101	9	0.05	19,296	98.94	137	0.70	60	0.31	**19,502**	Andreu, 2013; García-Escárzaga, 2020
Mazo 105	5	0.03	16,605	98.28	17	0.10	268	1.59	**16,895**	Andreu, 2013; García-Escárzaga, 2020
Pendueles	1	0.87	113	98.26	–	–	1	0.87	**115**	Arias et al. 2007
Poza l'Egua SM	16	0.45	3515	98.43	27	0.76	13	0.36	**3571**	Arias et al. 2007; Álvarez-Fernández, 2015; This work
Riera 29	9	1.36	653	98.64	–	–	–	–	**662**	Altuna, 1986; Ortea, 1986
Toral III B21	10	0.12	8063	99.05	41	0.50	26	0.32	**8140**	Andreu, 2013; Bello-Alonso, 2014
Toral III B17	9	0.29	3073	98.34	42	1.34	1	0.03	**3125**	Andreu, 2013; Bello-Alonso, 2014, Martínez Cuesta, 2016
Toralete SM	3	0.60	494	99.20	–	–	1	0.20	**498**	Arias et al., 2007
Total MNI	**123**	–	**70,664**	–	**476**	–	**390**	–	**71,653**	

Table 5
Palaeoecological data of the selected Mesolithic levels. NTaxa = Number of taxa identified in the level. D = Simpson's index. 1-D = Simpson's diversity index. 1/D = Simpson's reciprocal index. H'=Shannon index. E = Evenness. LN MNI = Napierian Logarithm of MNI. Log. MNI = Natural Logarithm of MNI. %MNI-DT = Percentage of MNI-Dominant taxon (PL = *Phorcus lineatus*, PT = *Patella* sp. SP = *Scrobicularia plana*; PD = *Patella depressa*). ^qD = Effective Number of Species. SM: Shell midden.

Site	MNI	NTaxa	D	1-D	1/D	H'	E	LN MNI	Log. MNI	%MNI-DT	^qD
Águila SM	867	10	0.39	0.61	2.57	1.15	0.32	6.77	2.94	45.2-*PL*	3.24
Alloru 104	2313	10	0.49	0.51	2.04	0.76	0.19	7.75	3.36	50.3-*PT*	2.14
Alloru 401	797	10	0.36	0.64	2.79	1.30	0.37	6.68	2.90	54-*PT*	3.68
Alloru 2003	166	7	0.52	0.48	1.94	0.87	0.34	5.11	2.22	65.7-*PL*	2.39
Carabión 1	782	28	0.18	0.82	5.52	2.07	0.28	6.66	2.89	32.8-*SP*	7.90
Cierro B	902	22	0.21	0.79	4.85	1.91	0.31	6.80	2.96	33–*PT*	6.77
Colomba SM	788	10	0.39	0.61	2.58	1.13	0.31	6.67	2.90	51.3-*PT*	3.14
Covajorno SM	343	9	0.54	0.46	1.84	0.82	0.25	5.84	2.54	68.8-*PL*	2.28
C. del Mar III SM	120	8	0.33	0.67	3.03	1.31	0.46	4.79	2.08	44.2-*PT*	3.69
Fragua 1	12,067	37	0.28	0.72	3.64	1.63	0.14	9.40	4.08	45.4-*PD*	5.09
Mazo 100/101	19,502	24	0.27	0.73	3.69	1.53	0.19	9.88	4.29	42.7-*PL*	4.62
Mazo 105	16,895	22	0.26	0.74	3.83	1.52	0.21	9.73	4.23	33.1-*PL*	4.57
Penduelles SM	115	6	0.44	0.56	2.30	0.98	0.39	4.75	2.06	54.8-*PL*	2.76
Poza l'Egua SM	3571	25	0.33	0.67	3.03	1.45	0.17	8.18	3.55	52.6-*PT*	3.68
Riera 29	662	9	0.57	0.43	1.76	0.82	0.25	6.50	2.82	72.5-*PD*	2.28
Toral IIIB 21	8140	15	0.30	0.70	3.34	1.47	0.29	9.00	3.91	47.8-*PD*	4.36
Toral IIIB 17	3125	20	0.20	0.80	4.97	1.77	0.29	8.05	3.49	31.6-*PD*	5.86
Toralete SM	498	10	0.44	0.56	2.25	0.99	0.27	6.21	2.70	55.2-*PL*	2.70

total calories documented, although it is only dominant from an energetic point of view in Covajorno. Iberian ibex and roe deer are in third and fourth place respectively, with 147,744 and 119,320 calories from 129.6 and 107.5 kg of meat and fat, making up 5.7 % and 4.6 % of the total calories recorded. They are followed by chamois, which would contribute 1.8 % of the total calories, with around 45,600 calories from 30 kg of meat and fat. This last species is only recorded as being consumed at La Poza l'Egua and Riera 29. Among the marine resources, limpets have contributed the greatest amount of energy, with *Patella depressa* contributing the most, with 1.3 % of the total calories and around 33 kg of meat and fat; although the whole group of limpets could have provided around 4 % of the total calories documented, contributing around 98 kg of meat, and thus surpassing the energy intake of the chamois. Furthermore, these limpets would have been important at sites such as El Toral III 21, La Fragua 1, El Mazo 100/101, and El Mazo 105, in the latter case having contributed more than 15.4 % of the calories of the level and around 17 kg of meat. The remaining marine molluscs documented in no case reach 1 % of the total calories recorded. However, *Phorcus lineatus* reached values of around 4.3 % of calories in El Mazo 105 and El Mazo 100/101, and mussels exceeded 3.5 % of calories

in El Carabión 1. Crustaceans have made a very marginal supply (<1% of the total calories), with the largest contribution coming from the individuals of *Cancer pagurus* documented in Toral IIIB 17. Finally, echinoderms are the ones that would have provided the least number of calories to the Mesolithic human groups of the Cantabrian region, being below 0.1 %, with the highest contribution in El Mazo 105, with 0.4 % of the calories of the level (Fig. 6).

4. Discussion

Regarding the role played by terrestrial and marine resources in the diets of Mesolithic hunter-gatherers in the Cantabrian region, we have been able to determine their importance in the different sites studied by combining ecological analyses, the representation of species, and the amount of meat and fat contributed by each individual. Although from the MNI we have seen how marine molluscs are the most represented in Mesolithic sites, with values greater than 90 %, in terms of energy intake, terrestrial mammals would have contributed the greatest amount of meat and fat to the diet of hunter-gatherer groups, with values always greater than 78 %.
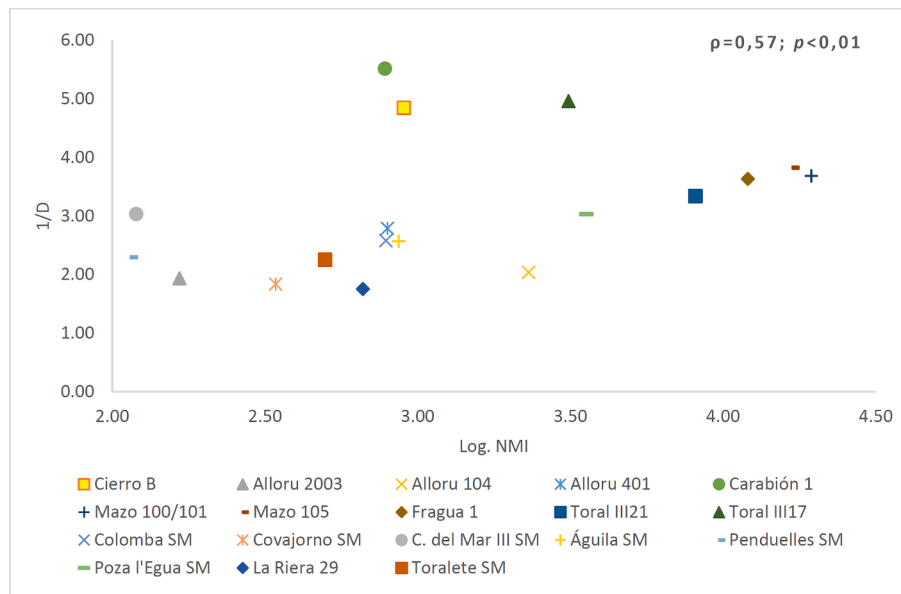
Fig. 3. Graph showing the relationship (Spearman's ρ) between taxonomic representation (Log. of MNI) and Simpson's reciprocal index (1/D) at the different Mesolithic levels.
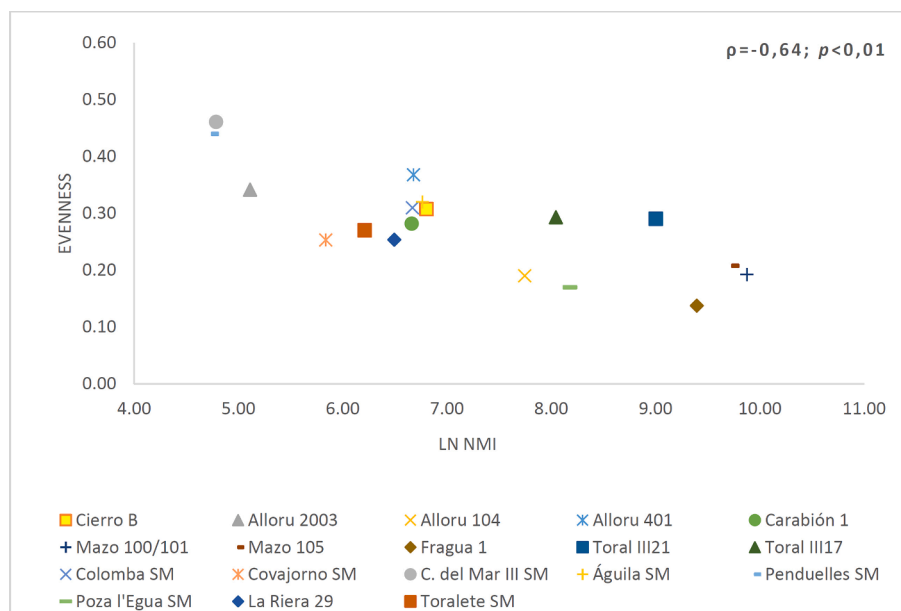

Fig. 4. Graph showing the relationship (Spearman's ρ) between taxonomic representation (LN of MNI) and Shannon homogeneity (*Evenness*) values at the different Mesolithic levels.

As far as the representation of marine molluscs is concerned, limpets, *Phorcus lineatus*, and *Scrobicularia plana* are the most abundant in all levels, being the predominant species in the Mesolithic sites from the MNI; although in most cases they represent<60 %. This is consistent with the data obtained in the biodiversity analyses, which indicate that the effective number of species is around 3.98 ± 0.39, being the most represented species in the selected sites.

If we take into account the meat contribution of marine molluscs, some previous studies carried out in the Cantabrian region have considered the weight of the species documented in archaeological sites, to assess the yield of their meat (García-Escárzaga, 2020; García-Escárzaga and Gutiérrez-Zugasti, 2021). In the case of El Mazo, for example, a 20 % dependence on these resources in the meat diet of its inhabitants has been shown (García-Escárzaga and Gutiérrez-Zugasti,

2021). Although with a different methodology, these same percentages have been obtained in our study for the same site, also highlighting the importance of malacofauna in the sites of La Fragua and El Toral IIIB, where these resources provided between 8 % and 10.5 % of the calories calculated. It should be noted that it is precisely in these contexts where we found less homogeneity in the representation of species, as we have shown from the Shannon index. Nevertheless, and despite the importance of these resources in some sites, the result on the overall energy intake indicates that terrestrial resources were, in all cases, the ones that would have provided a greater amount of meat and fat to the Mesolithic human groups. In this sense, some studies have indicated the high yield of meat from macromammals compared to molluscs at the end of the Upper Pleistocene, despite a clear decrease in the representation of the former compared to earlier times (Marín, 2010; 2013). Among the
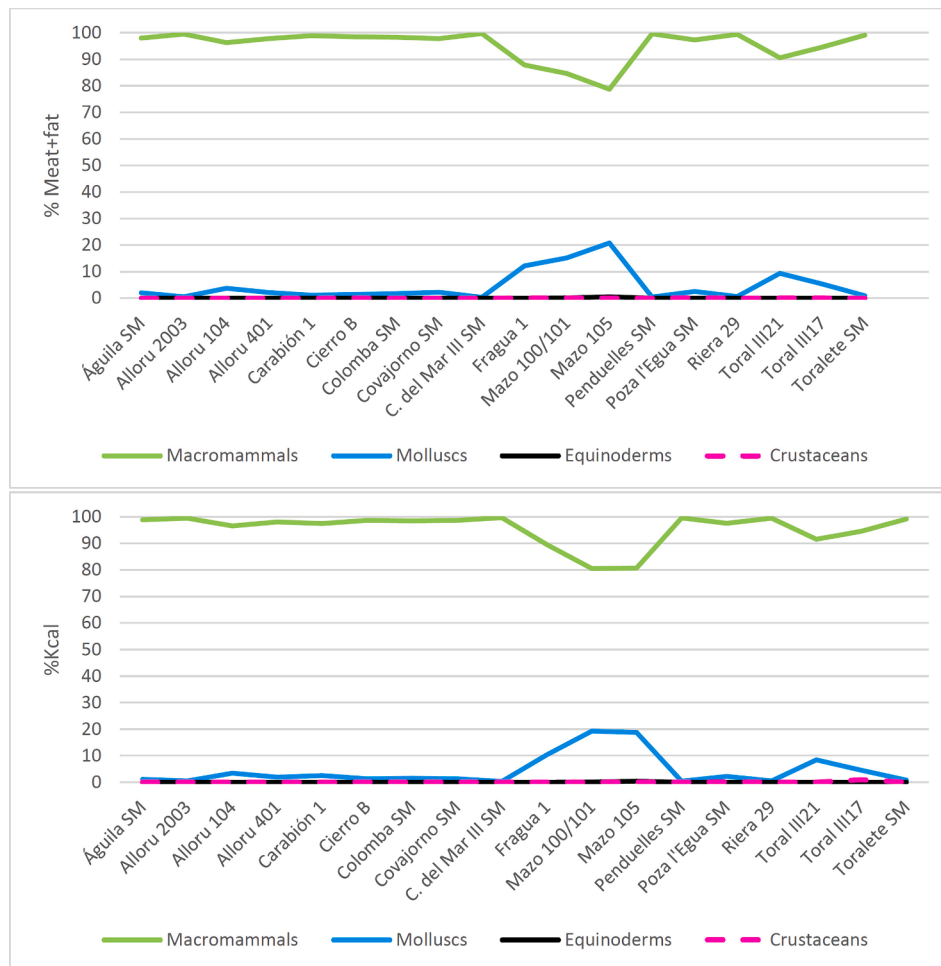
Fig. 5. Percentage of meat and fat (top) and calories (bottom) provided by the different faunal resources in the Mesolithic levels of the Cantabrian region based on their MNI.

macromammals, red deer has been the species that has provided the greatest amount of meat and fat, with slightly more than 60 % of the same, predominating in most of the sites selected for this work. This indicates that the importance of this ungulate in the diet that was observed for the Cantabrian region at different times in the Upper Paleolithic is maintained (Marín, 2009, 2010; Portero, 2022; Portero et al., 2019). However, its presence is much lower than in previous periods and, in most sites, it shares its energetic importance with wild boar, which is the second species in the Mesolithic energetic ranking, providing *ca.* 20 % of the total calories. Iberian Ibex and roe deer have a similar weight in the diet, ranking third and fourth respectively, while chamois is the mammal that would have contributed the least number of calories.

In the case of crustaceans and echinoderms, some studies have highlighted their importance as food resources in the Spanish Cantabrian region (Gutiérrez-Zugasti, 2009; 2011; Álvarez-Fernández, 2011, 2015). However, in no case do they exceed 7 % of the MNI (Gutiérrez-Zugasti, 2011), something that we have also been able to verify in our study. Moreover, their contribution to the diet has been very low in all the sites analysed, providing < 1 % of the total calories. In the case of crustaceans, it is worth highlighting the contribution of *Cancer pagurus* at El Toral IIIB 17, whose individuals would have provided around 900 g of meat and fat. As far as echinoderms are concerned, the most outstanding case is documented at El Mazo 105, where *Paracentrotus lividus* would have supplied *ca.* 670 g of meat and fat.

5. Conclusion

In the Spanish Cantabrian region, compared to earlier periods, the collection and consumption of marine resources intensified during the Mesolithic (e.g., Álvarez-Fernández, 2011). It is in this period when there are many sites where large accumulations, known as "shell middens", have been recorded. These resources, which have a smaller energetic range but greater stability, become a complementary resource to the hunting of ungulates, which at this time is reduced compared to the end of the Upper Pleistocene. However, as far as animal energy supply is concerned, macromammals continue to provide the greatest amount of it.

Throughout this paper, we have analysed the importance that different terrestrial and marine animal resources played in the diet of the Mesolithic populations of the Spanish Cantabrian region. To this end, we have applied a methodology that combines ecological analyses, the average weight of meat and fat of individuals of each species, and the calculation of the calories associated with these resources, allowing us to assess the role played by the different species in human subsistence and generating a prey ranking based on their energy contribution.

It has been shown that, despite being under-represented in the MNI, terrestrial resources would have been the main source of food of animal origin for the Mesolithic Cantabrian people, red deer being the species that would have contributed the most. In contrast, molluscs, which are the most abundant resources according to the MNI, would have provided a smaller contribution to the diet, with *ca.* 4.5 % of the total calories recorded. In the case of crustaceans and echinoderms, these figures are
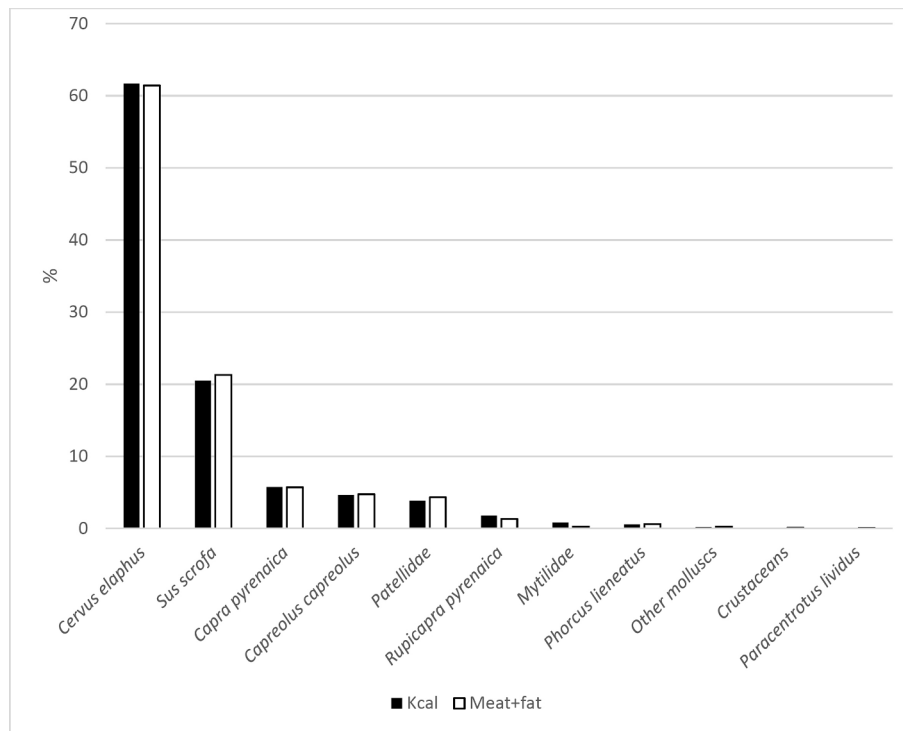
Fig. 6. Prey Ranking based on the percentage of calories and the quantity of meat and fat provided by the faunal resources documented in the Mesolithic of the Cantabrian region.

even lower, and their contribution would have been very low compared to the rest of the resources analysed.

CRediT authorship contribution statement

Rodrigo Portero: Conceptualization, Formal analysis, Data curation, Writing – original draft, Writing – review & editing. **Marián Cueto:** Formal analysis, Data curation, Writing – review & editing. **María J. Fernández-Gómez:** Formal analysis, Data curation, Writing – review & editing. **Esteban Álvarez-Fernández:** Formal analysis, Data curation, Writing – review & editing.

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

No data was used for the research described in the article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2022.103635.

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