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Long-term dietary change in Atlantic and Mediterranean Iberia with the introduction of agriculture: a stable isotope perspective

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Abstract

The Neolithic expansion in the Iberian Peninsula is marked by the introduction of livestock and domesticated crops which modified subsistence strategies in an unprecedented manner. Bulk collagen stable carbon and nitrogen isotope analysis has been essential to track these changes, which have largely been discussed in relation to particular geographic areas or single case studies. This paper reviews the available isotope literature to provide a regional, long-term synthesis of dietary changes associated with the expansion of the Neolithic and the establishment of farming economy in the Iberian Peninsula. Bulk collagen stable carbon and nitrogen isotope values of 763 human individuals and 283 faunal remains from the Mesolithic to the Late Neolithic period in Iberia (*ca.* 8000–3000 cal BC) were collated and analysed using a Bayesian mixing model. The results show that Mesolithic diets were isotopically diverse in both the Atlantic and Mediterranean regions of the Iberian Peninsula, and that a significant decrease in variability happened with the Neolithisation, culminating with the establishment of farming economies and reliance on terrestrial resources in the Late Neolithic.

Keywords Bulk collagen · Stable carbon and nitrogen isotopes · Palaeodietary reconstructions · Neolithic · Iberian Peninsula

Introduction

The spread of agriculture in Europe during the Early to Middle Holocene constitutes one of the most transformative and controversial socio-cultural processes in Prehistory. Coastal zones and immediate inland areas of the Iberian Peninsula offer attractive

geographic contexts to investigate the magnitude and dietary implications of this process. First, the Peninsula was one of the most densely populated regions in Europe during the Mesolithic, especially along the Atlantic coast (Arias 1999). Second, its geographic diversity has demanded distinct adaptive strategies by prehistoric populations, in particular by those living along the Atlantic and the Mediterranean, coastal areas marked by contrasting biological productivity and resource predictability.

Archaeological evidence shows that early farmers from the Near East migrated across the Mediterranean Sea following a coastal route from the Aegean to the Iberian Peninsula, bringing with them pottery, ground stone tools and domesticated plants and animals, which marked the beginning of the Neolithic in these regions (Guilaine 2017). Ancient human DNA has shown a clear Anatolian ancestry of early European farmers (Mathieson et al. 2015; Omrak et al. 2016), as well as strong genetic differentiation between hunter-gatherers and early farmers (Skoglund et al. 2014; Lazaridis et al. 2014), supporting the archaeological model of a maritime colonisation of Iberia in the 6th millennium cal BC (Zilhão 2001; Isem et al. 2014; Martins et al. 2015).

The introduction of farming, however, was not uniform across Iberia. The first domesticates are known for the Mediterranean region of the Peninsula, consisting of cereals and livestock, and

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have been radiocarbon dated to the mid-6th millennium cal BC (Saña 2013; Martins et al. 2015; Pérez-Jordá et al. 2017). Domesticates were introduced to the south-western Atlantic coast in the second half of the 6th millennium cal BC (Zilhão 2001; Davis and Simões 2015; López-Dóriga and Simões 2015), while in the north Atlantic coast of Iberia, such as the Cantabrian region, the earliest domesticated plants and animals were adopted much later, in the 5th millennium cal BC (Cubas et al. 2016).

Moreover, there has been a long, contentious debate about the impact of the expansion of farming upon local forager diets, where the application of stable isotope analysis has been particularly fruitful. Consumer diets can be determined by measuring the stable isotopes of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) in consumer tissues, such as bone collagen, and comparing these with isotopic baselines for potential food sources (van Klinken et al. 1994; Tykot 2002; Fischer et al. 2007). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of human bone collagen have been successfully used to estimate the relative contribution of marine versus C_3 -based terrestrial resources in coastal populations due to distinctive isotopic signatures in these ecosystems, allowing generic discriminations (Jennings et al. 1997; Richards and Hedges 1999). Isotopic analyses across Atlantic coastal areas of Europe have shown a marked dietary difference between Mesolithic foragers, with substantial consumption of marine foodstuffs, and Neolithic farmers, whose diets were essentially based on terrestrial resources (Lubell et al. 1994; Richards and Hedges 1999; Richards et al. 2003; Bonsall et al. 2009; Schulting 2011). Similar results have been reported for the Iberian Peninsula, although considerable variability has been observed at the regional scale (Fontanals-Coll et al. 2014; Guiry et al. 2015; Peyroteo-Stjerna 2016; Salazar-García et al. 2018). Indeed, since the early 2000s, there has been an extraordinary increase in palaeodietary studies based on stable isotope analysis of carbon and nitrogen in human bone collagen from Mesolithic and Neolithic populations in this region (e.g. Cunha and Umbelino 2001; Arias 2006; García-Guixé et al. 2006; Roksandic 2006; Umbelino 2006; Umbelino et al. 2007; Arias and Schulting 2010; Lillios et al. 2010; McClure et al. 2010; Carvalho and Petchey 2013; Fernández-López de Pablo et al. 2013; Jackes et al. 2014; Fontanals-Coll et al. 2014, 2015, 2017; Salazar-García et al. 2014; Gibaja et al. 2015; Gibaja et al. 2016; Guiry et al. 2015, 2016; Umbelino et al. 2015; Alt et al. 2016; Jackes and Lubell 2016; Peyroteo-Stjerna 2016; Remolins et al. 2016; Waterman et al. 2016; Fernández-Crespo and Schulting 2017; Salazar-García et al. 2017; Sarasketa-Gartzia et al. 2018).

This paper reviews the isotope literature reporting $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of human individuals from archaeological sites dated to the Mesolithic, Early Neolithic, Middle Neolithic and Late Neolithic–Chalcolithic in the Iberian Peninsula. A Bayesian mixing model (FRUITS; Fernandes 2015) was used to estimate the average relative contribution of terrestrial and marine resources to dietary calories for each time period. The aims of this

paper are twofold: (i) provide a regional and long-term synthesis of dietary changes associated with the introduction, expansion and establishment of farming economy in this region from ca. 8000 to 3000 cal BC; and (ii) offer a comprehensive isotopic database for addressing the dietary implications of early food production in the Iberian Peninsula.

Materials and methods

We analysed the bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values currently available for human individuals from archaeological sites dated between ca. 8000 and 3000 cal BC in the Iberian Peninsula (SI 1). Archaeological sites were grouped in two main regions (Atlantic, Mediterranean) and in generic chrono-cultural periods: Mesolithic (ca. 8000–5500 cal BC), Early Neolithic (ca. 5500–4500 cal BC), Middle Neolithic (ca. 4500–3500 cal BC) and Late Neolithic–Chalcolithic (ca. 3500–3000 cal BC) (Fig. 1). Samples considered in this study are accompanied by their contextual and geographical information, cultural attribution and sample identification (sample code and type, age and sex) (SI 1). Our analysis did not distinguish between coastal and inland sites since in some areas, such as the Atlantic coast of Iberia, the existence of estuarine ecosystems allows marine resources to be exploited at considerable distances from the coast (e.g. Van Der Schriek et al. 2007; Vis et al. 2008). The quality of the published material is extremely variable and data criteria are rarely presented with sufficient detail to allow a critical evaluation of analytical procedures (Roberts et al. 2018). Samples were therefore screened according to established quality criteria for collagen preservation. Samples with C:N ratios outside the 2.9–3.6 range (van Klinken 1999; DeNiro 1985) were discounted as well as samples published without reporting these parameters. For this reason, some geographic areas, such as the Cantabrian region (Arias 2006, 2012), are not well represented in our database.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of faunal remains from prehistoric and historic archaeological sites in the Atlantic and Mediterranean regions were compiled to establish regional stable isotope baselines (SI 2). Fauna $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were grouped according to their habitat: marine (fish and mammals) and terrestrial (ungulates). Because of the paucity of marine isotope values for the Iberian Peninsula, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fish and marine mammals from Mesolithic and Early Neolithic contexts from the central Mediterranean (Mannino et al. 2012, 2015), Bronze Age in the Balearic Islands (García-Guixé et al. 2010) and Late Medieval data from the Atlantic (López-Costas and Müldner 2016) have been also included.

Statistical analyses were performed using R package v3.4 (R Development Core Team 2013). Different statistical tests were performed to test the normality of the distributions:

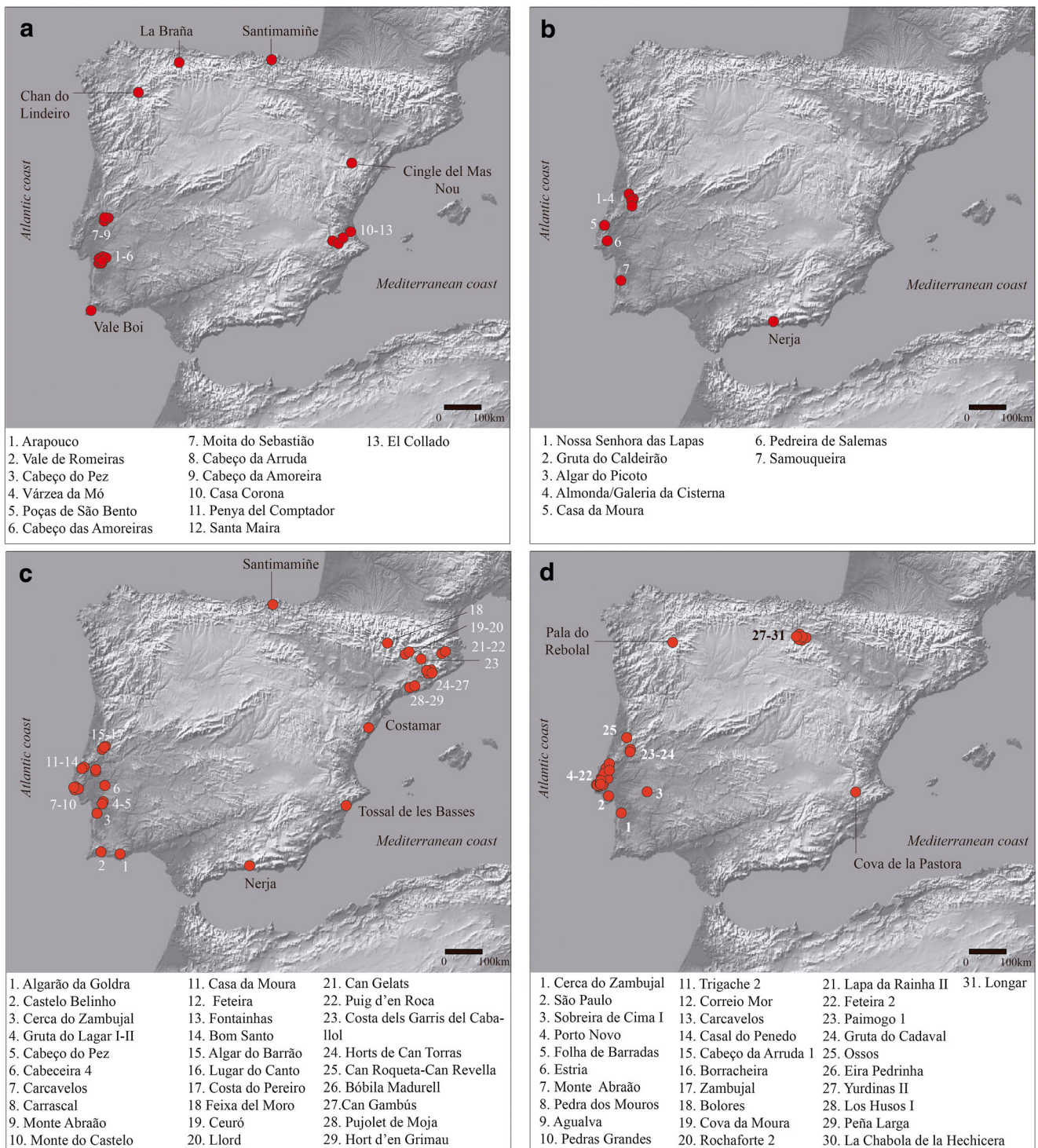


Fig. 1 Iberian Peninsula and the location of archaeological sites with stable isotope measurements of human bone considered in this study. **a** Mesolithic; **b** Early Neolithic; **c** Middle Neolithic; **d** Late Neolithic–Chalcolithic

Shapiro–Wilk (S-W, for statistical populations with less than 50 cases) and Lilliefors corrected Kolmogórov–Smirnov (K-S, for populations with more than 50 individuals). The results show that the isotope data were not normally distributed in all cases (SI 3 and 4). Non-parametric tests were then applied to compare two samples (Wilcoxon-Mann-Whitney, W) or more

than two samples (Kruskal-Wallis, K-W). A *p* value of 0.05 (H_1 acceptance with $p \leq 0.05$) was used as the significance threshold.

For each time period (Mesolithic, Early Neolithic, Middle Neolithic and Late Neolithic-Chalcolithic) and region (Atlantic, Mediterranean), the average percentage of

dietary carbon (equivalent to caloric contribution or dry weight contribution) derived from marine and terrestrial resources was estimated using a Bayesian Mixing Model in FRUITS 3.0 (Fernandes et al. 2014). While $\delta^{15}\text{N}$ values in bone collagen only reflect the sources of dietary proteins and the position of the consumer in the food chain due to relatively predictable dietary isotope fractionations (+3–6‰; Jim et al. 2006; O'Connell et al. 2012), the $\delta^{13}\text{C}$ values may reflect the contribution of different dietary macronutrients, such as proteins, carbohydrates and lipids, to individual diets (Jim et al. 2006; Webb et al. 2017). A routed, concentration-dependent weighted model was used taking into account two dietary proxies ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and two food groups (marine, terrestrial). Isotopic baselines (Mediterranean and Atlantic) were derived from published isotope data from animal bones and are reported in Table 2. Although terrestrial plants were undoubtedly an important portion of the diet of Mesolithic and Neolithic populations (e.g. Umbelino 2006; López-Dóriga et al. 2016; Peña-Chocarro et al. 2018), the absence of isotopic values for both wild and domestic plants in the region prevents their quantification.

The model was developed using the assumptions and uncertainties exactly as described by Fernandes (2015) as this considers the dietary contributions of protein and energy macronutrients. Rather than modelling individuals separately based on their collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, we aimed for broad comparisons by using the population means for each region and each period, and by taking the standard deviations of the means as the uncertainties (Fernandes et al. 2015).

Results

Fauna bone collagen

Faunal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are represented by 283 specimens from the Atlantic ($n = 42$) and Mediterranean ($n = 241$) regions (Table 1), with a disproportionate amount of terrestrial mammals (ungulates, 83%) compared to marine animals (fish

and mammals, 17%) (García-Guixé et al. 2006; Salazar-García 2009, 2012; Salazar-García et al. 2014, 2017; Fontanals-Coll et al. 2015; Fernández-Crespo and Schulting 2017; Navarrete et al. 2017).

Terrestrial faunal remains from the Mediterranean region have significantly higher $\delta^{13}\text{C}$ ($W = 2006$; p value = 5.614×10^{-5}) and $\delta^{15}\text{N}$ ($W = 1862$; p value = 1.012×10^{-5}) values compared to animals from the Atlantic region (Table 1). While no significant differences were observed for the $\delta^{13}\text{C}$ values of the marine animals between these regions ($W = 94$; p value = 0.1737), the fish and sea mammals from the Atlantic region have $\delta^{15}\text{N}$ values significantly higher than those of specimens from the Mediterranean ($W = 244$; p value = 0.002). This presumably reflects fundamental differences in food webs between the Mediterranean Sea compared to the Atlantic Ocean (Stambler 2014).

The significant variability observed in the isotope values of faunal remains from the Mediterranean and the Atlantic regions emphasises the importance of building local to regional baselines to estimate the contribution of each food source. The average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of terrestrial and marine resources for each region were used to establish the isotopic composition of macronutrients of each food group and the parameters required for modelling (Table 2).

Human bone collagen

A total of 763 individuals were analysed from sites in the Atlantic ($n = 481$) and Mediterranean regions ($n = 282$) (Fig. 1 and Table 3). Most individuals were dated to the Middle Neolithic ($n = 315$), followed by the Late Neolithic–Chalcolithic ($n = 276$), Mesolithic ($n = 150$) and Early Neolithic ($n = 22$). Information about age and sex were not always available, preventing further analysis across populations.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values show significant variability over time within and between regions (Fig. 2a, b). The largest range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values is observed among Mesolithic individuals of the Atlantic region. Although the paucity of isotope values from the Early Neolithic prevents robust comparisons

Table 1 Faunal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values grouped into two categories: terrestrial (ungulates), marine (fish and mammals)

		$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)				<i>N</i>
		Mean	SD	Max	Min	Mean	SD	Max	Min	
Atlantic	Terrestrial	−20.8	1	−18.9	−22.1	4.3	1.6	9.6	2.1	35
	Marine	−12	0.6	−11.5	−13	12.5	2.03	15.1	9.2	7
Mediterranean	Terrestrial	−20	1.1	−11.4	−21.9	5.3	1.4	9	2.6	200
	Marine	−11.6	1.6	−8.9	−15.2	9.2	2.1	12.1	3.6	41

Table 2 Average and standard deviations of terrestrial and marine faunal collagen isotope values. The estimated protein and lipid isotope values and the macronutrient composition (%dry weight carbon content) were calculated according to Fernandes (2015)

	$\delta^{13}\text{C}$ dietary protein (‰)	$\delta^{15}\text{N}$ dietary protein (‰)	$\delta^{13}\text{C}$ dietary lipids (‰)	Protein (%C)	Lipids (%C)
Atlantic					
Terrestrial	-22.8 ± 1	6.2 ± 1	-28.8 ± 1	30 ± 2.5	70 ± 2.5
Marine	-13 ± 1	14.5 ± 1	-19 ± 1	65 ± 5	35 ± 5
Mediterranean					
Terrestrial fauna	-22 ± 1	7.3 ± 1	-28 ± 1	30 ± 2.5	70 ± 2.5
Marine fauna	-12.6 ± 1	11.2 ± 1	-18.6 ± 1	65 ± 5	35 ± 5

across regions for this time period (e.g. Mediterranean), there is a decrease in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variability in the Atlantic region. The narrow isotopic variability continued through the Middle to Late Neolithic–Chalcolithic, and these differences were statistically significant for both $\delta^{13}\text{C}$ (K-W = 172.81, $df=3$, p value < 2.2e-16) and $\delta^{15}\text{N}$ values (K-W = 130.53, $df=3$, p value < 2.2e-16). In the Mediterranean region, Mesolithic and Middle Neolithic populations had the most variable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, while considerably narrower isotopic distributions were recorded during the Late Neolithic–Chalcolithic. These differences were also statistically significant for both $\delta^{13}\text{C}$ (K-W = 120.25, $df=3$, p value < 2.2e-16) and $\delta^{15}\text{N}$ values (K-W = 7.9449, $df=3$, p value = 0.04716). Worth noting is the lower variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Mesolithic populations in the Mediterranean region compared to the Atlantic. These differences could be a consequence of sample size, but most likely reflect differences in the isotope ecology and diet of populations between these regions, with considerable consumption of marine resources by some Atlantic foragers, as also estimated by Bayesian calculations.

Mesolithic (ca. 8000–5500 cal BC)

Stable isotope values of Mesolithic populations indicate diets based mainly on C_3 -terrestrial foods in both regions of the peninsula (Fig. 2a, b; Fig. 3a; Table 4). For the

Atlantic region, Bayesian modelling estimates that terrestrial and marine resources provided average contributions to dietary calories of $91.8 \pm 6.2\%$ and $8.2 \pm 6.2\%$, respectively. However, marine resources may have contributed as much as ca. 23% of dietary calories in some areas. Indeed, considerable intake of marine resources has been reported for individuals from sites such as Cabeço do Pez, Cabeço da Amoreira, Cabeço da Arruda and Moita do Sebastião in Portugal (e.g. Lubell et al. 1994; Fontanals-Coll et al. 2014; Guiry et al. 2015; Peyroteo-Stjerna 2016). The wide range of $\delta^{13}\text{C}$ values in the Atlantic region also suggests that distinct terrestrial ecological niches were exploited (e.g. Waterman 2012; Fontanals-Coll et al. 2014). For the Mediterranean region, the Bayesian model estimates average contributions of terrestrial and marine resources of $95.5 \pm 3.7\%$ and $4.5 \pm 3.7\%$, respectively, to dietary calories. The maximum estimated contribution of marine resources to diet was ca. 14% (Table 4). A higher consumption of marine resources in this region was found at the sites of El Collado, Santa Maira and some individuals from Cingle del Mas Nou (García-Guixé et al. 2006; Salazar-García et al. 2014).

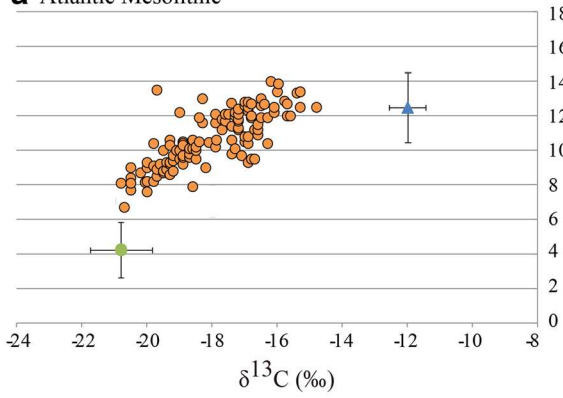
Early Neolithic (ca. 5500–4500 cal BC)

Isotopic values from the Atlantic and Mediterranean regions are consistent with diets based on C_3 -terrestrial

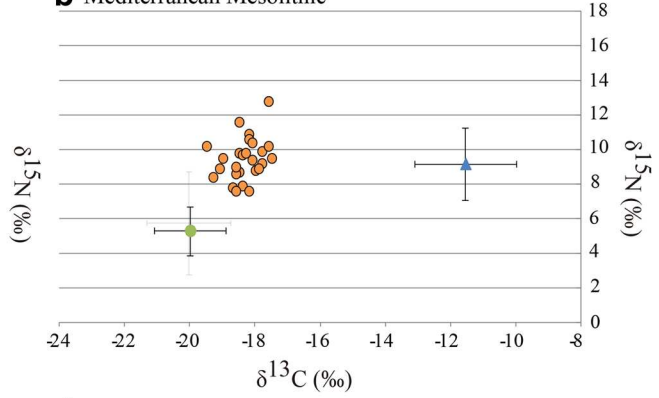
Table 3 Human $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values grouped by period

	Period	$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)			
		Mean	SD	Max	Min	Mean	SD	Max	Min
Atlantic	Mesolithic ($n=124$)	-18	1.4	-14.8	-20.8	10.7	1.6	14	6.7
	Early Neolithic ($n=20$)	-19.6	1	-15.3	-20.2	8.9	1.8	16.5	7.9
	Middle Neolithic ($n=174$)	-19.4	0.8	-14.8	-21.3	9.1	1.2	13.4	6.7
	Late Neolithic–Chalcolithic ($n=163$)	-19.9	0.5	-18	-21.3	8.6	0.8	11.7	6.9
Mediterranean	Mesolithic ($n=26$)	-18.4	0.5	-17.5	-19.5	9.5	1.2	12.8	7.6
	Early Neolithic ($n=2$)	-19	0.6	-18.5	-19.4	9.3	1.5	10.3	8.2
	Middle Neolithic ($n=141$)	-19.5	0.7	-16.8	-21	9.2	1	13.1	6.1
	Late Neolithic–Chalcolithic ($n=113$)	-20.1	0.3	-19	-20.8	9.3	0.5	10.6	8.1

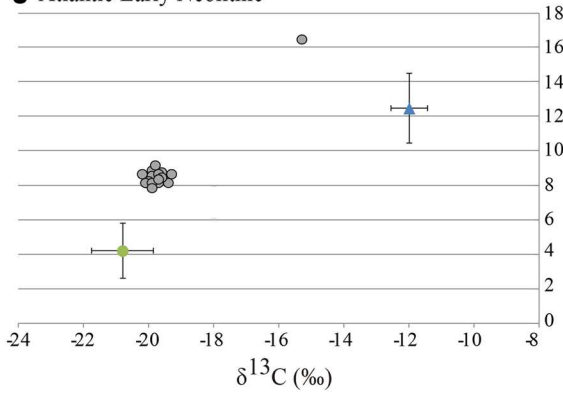
a Atlantic Mesolithic



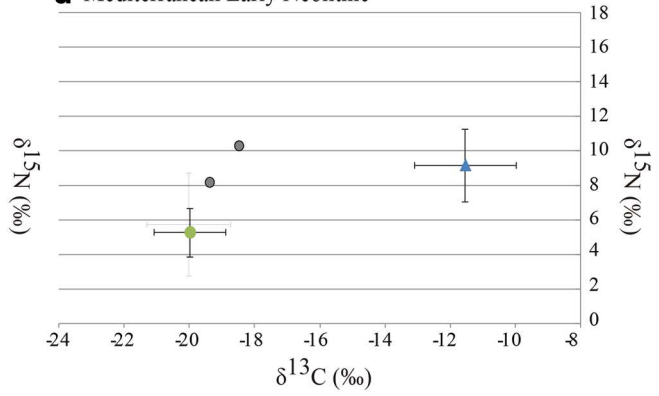
b Mediterranean Mesolithic



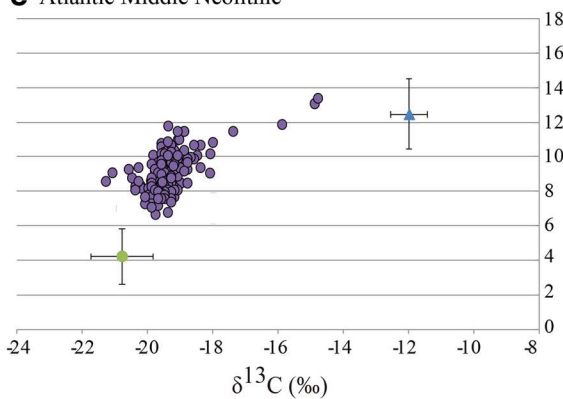
c Atlantic Early Neolithic



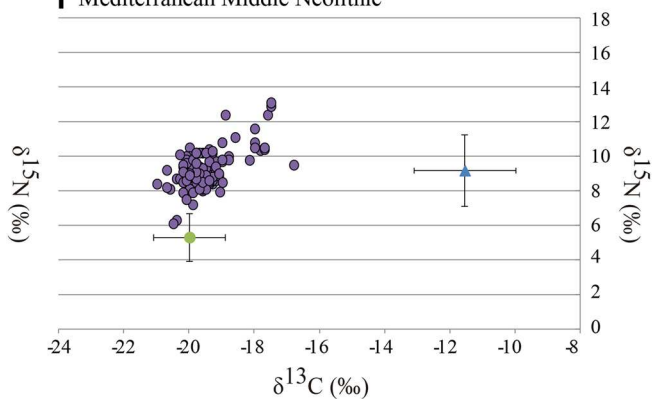
d Mediterranean Early Neolithic



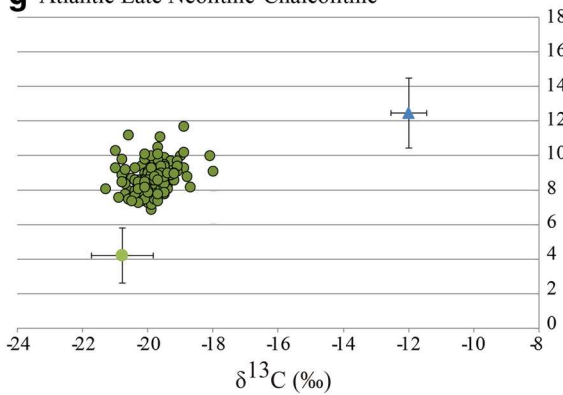
e Atlantic Middle Neolithic



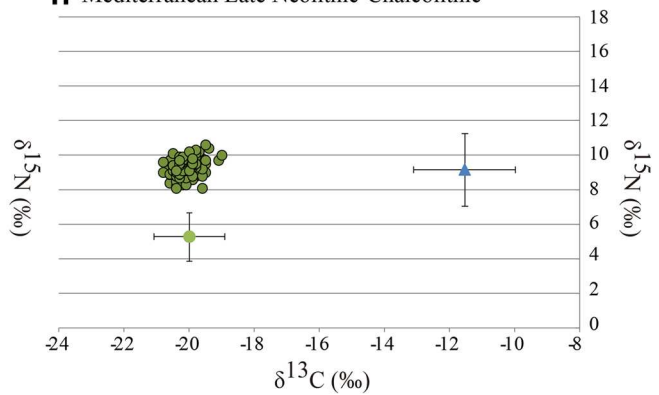
f Mediterranean Middle Neolithic



g Atlantic Late Neolithic-Chalcolithic



h Mediterranean Late Neolithic-Chalcolithic



▲ Marine ● Terrestrial

Fig. 2 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variation in human bone collagen and faunal remains in the Atlantic and Mediterranean regions of the Iberian Peninsula from the Mesolithic to the Late Neolithic

resources, with an overall decline in marine intake (Fig. 2c, d; Fig. 3a, b). For the Atlantic region, Bayesian estimations indicate that terrestrial and marine resources provided average contributions of $95.7 \pm 3.7\%$ and $4.3 \pm 3.7\%$ of dietary calories respectively (Table 4). The model estimates that the maximum amount of carbon from marine resources was *ca.* 14% (Table 4). One individual has considerably higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig. 2c; Samouqueira 1 in Portugal; Lubell et al. 1994), but its cultural attribution is controversial (Zilhão 2000). Similar results were obtained for Early Neolithic individuals from the Mediterranean sites, where Bayesian model estimates that terrestrial and marine resources accounted for averages of $96.1 \pm 3.3\%$ and $3.9 \pm 3.3\%$ of dietary calories, respectively, while the maximum contribution of marine resources was *ca.* 13% (Tab. 4).

Middle Neolithic (*ca.* 4500–3500 cal BC)

Again, most of the samples have isotopic compositions consistent with C_3 -terrestrial resources. This is supported by Bayesian estimations of the terrestrial mammal contribution to dietary calories with average values of $96.8 \pm 2.7\%$ for the Atlantic and $97.4 \pm 2.4\%$ for the Mediterranean (Table 4). Although the Middle Neolithic shows a clear shift toward a terrestrial-based diet, marine resources were consumed at a detectable level in several areas of the Peninsula (Fig. 2e, f). The average contribution of marine resources to dietary calories was $3.2 \pm 2.7\%$ and $2.6 \pm 2.4\%$ in the Atlantic and Mediterranean regions respectively, but intakes of marine products up to 9–10% of the diet may have occurred in both regions (Table 4, Fig. 3a, b). These values

are represented by individuals from Cerca do Zambujal and Lagar I (Guiry et al. 2016; Jackes and Lubell 2016) in the Atlantic region, and two individuals from Tossal de les Basses (Salazar-García et al. 2016) and one individual from Can Gambús (Fontanals-Coll et al. 2015) in the Mediterranean area (SI 1).

Late Neolithic–Chalcolithic (*ca.* 3500–3000 cal BC)

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the Atlantic and Mediterranean regions are narrowly distributed and fall at the end-point of C_3 -terrestrial resources (Fig. 2g, h). The Bayesian model estimates average contributions of terrestrial resources to dietary calories of $98.1 \pm 1.08\%$ for the Atlantic and $98.4 \pm 1.5\%$ for the Mediterranean. Marine resources contributed less than 6–7% in both regions (Table 4, Fig. 3a, b).

Discussion

The results show significant differences in human diets over time, from the Mesolithic to the Late Neolithic–Chalcolithic, while they also varied geographically across the Atlantic and Mediterranean regions of the Iberian Peninsula. The distribution of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and Bayesian estimations for Mesolithic populations reveal diets largely dominated by C_3 -terrestrial resources, here represented by ungulates. Terrestrial resources including both animals and plants were the most significant component of the diet, in agreement with other lines of evidence (Umbelino et al. 2007; Marín 2013; López-Dóriga et al. 2016). The noticeable isotopic variability also indicates highly diversified diets, with groups exploiting a variety of ecological patches and environments (Arias 2006; Fontanals-Coll et al. 2014; Salazar-García et al. 2014; Peyroteo-Stjerna 2016). Marine

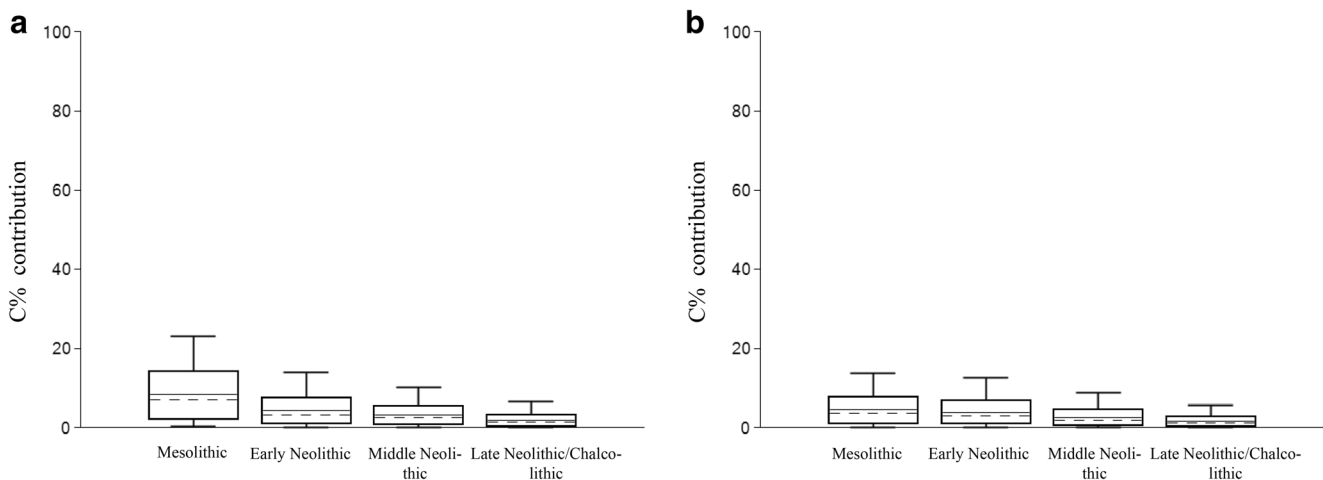


Fig. 3 Estimated marine calorie intake for the Atlantic (a) and Mediterranean (b) populations in each chronological period. Boxes represent a 68% credible interval while the whiskers represent a 95%

credible interval. The horizontal continuous line represents the estimated mean and the horizontal discontinuous line represents the estimated median

Table 4 Carbon contribution (%) of terrestrial and marine resources to the diet for each population

			Terrestrial vs. marine total carbon contribution to diet (%)						
			Mean	SD	2.5pc	Median	97.5pc	16pc	84pc
Atlantic	Terrestrial	Mesolithic (<i>n</i> = 124)	91.8	6.2	76.8	93.1	99.7	85.6	97.9
		Early Neolithic (<i>n</i> = 20)	95.7	3.7	86.2	96.7	99.9	92.4	99.1
		Middle Neolithic (<i>n</i> = 174)	96.8	2.7	90	97.5	99.9	94.3	99.3
		Late Neolithic–Chalcolithic (<i>n</i> = 163)	98.1	1.8	93.4	98.6	100	96.6	99.6
	Marine	Mesolithic (<i>n</i> = 124)	8.2	6.2	0.3	6.9	23.2	2.2	14.4
		Early Neolithic (<i>n</i> = 20)	4.3	3.7	0.1	3.3	13.8	0.9	7.6
		Middle Neolithic (<i>n</i> = 174)	3.2	2.7	0.1	2.5	10	0.7	5.7
		Late Neolithic–Chalcolithic (<i>n</i> = 163)	1.9	1.8	0.1	1.4	6.6	0.4	3.4
Mediterranean	Terrestrial	Mesolithic (<i>n</i> = 26)	95.5	3.7	86.3	96.4	99.8	92.1	99
		Early Neolithic (<i>n</i> = 2)	96.1	3.3	87.5	96.9	99.9	93.1	99.1
		Middle Neolithic (<i>n</i> = 141)	97.4	2.4	91.3	98.1	99.9	95.3	99.5
		Late Neolithic–Chalcolithic (<i>n</i> = 113)	98.4	1.5	94.4	98.8	100	97	99.7
	Marine	Mesolithic (<i>n</i> = 26)	4.5	3.7	0.2	3.6	13.8	1	7.9
		Early Neolithic (<i>n</i> = 2)	3.9	3.3	0.1	3.1	12.5	0.9	7
		Middle Neolithic (<i>n</i> = 141)	2.6	2.4	0.1	1.9	8.7	0.5	4.7
		Late Neolithic–Chalcolithic (<i>n</i> = 113)	1.6	1.5	0	1.2	5.6	0.3	3

resources contributed up to 23% of dietary calories, particularly along the Atlantic coast. Consumption of marine resources by Mesolithic populations in the Atlantic region was possibly facilitated by the higher marine productivity and the larger tidal zones for shellfish gathering compared to the Mediterranean (Fa 2008).

A decline in the consumption of marine foods took place with the introduction of farming in the Early Neolithic, which is particularly noticeable in the Atlantic region, although it is important to highlight the low number of human remains dated in the Early Neolithic in the Iberian Peninsula in comparison to those dated to the Mesolithic and later periods (Fig. 1b). The paucity of data from Mediterranean regions prevents a meaningful comparison with the Atlantic, but we can expect a similar pattern (Salazar-García et al. 2018), even though archaeozoological records show that marine resources were still exploited as food in some areas (e.g. Benito 2015). Middle Neolithic individuals show the consumption of marine resources within economic contexts dominated by C₃-based terrestrial diets. Higher human $\delta^{15}\text{N}$ values during the Middle Neolithic in both Atlantic and Mediterranean Iberia have also been attributed to the consumption of freshwater resources (Carvalho et al. 2016; Fontanals-Coll et al. 2017), but these might alternatively indicate protein intake from livestock raised intensively on food leftovers (such as pigs) and/or manured plants (Albarella et al. 2007; Bogaard et al. 2007, 2013; Navarrete et al. 2017).

A definitive rupture with foraging subsistence strategies appears to have occurred during the Late Neolithic–Chalcolithic. The narrow isotopic distribution of individual diets, in particular in the Mediterranean region, suggests an intensification of farming practices in an

increasingly anthropogenic landscape where productive cycles (crops and livestock) were fully integrated. While this meta-analysis does not provide qualitative information on which resources were consumed, the interpretations are generally supported by archaeozoological records showing an increasing frequency of domesticated animals from the Early to the Late Neolithic–Chalcolithic in the Iberian Peninsula (e.g. Altuna and Mariezkurrena 2009; Valente and Carvalho 2014). The isotopic distribution of the Late Neolithic–Chalcolithic therefore probably reflects the establishment and intensification of food production systems as indirectly evidenced by structural changes in settlement patterns, intensification of regional exchange networks and enhanced technological capacity (Bernabeu et al. 2013).

Conclusions

Built on a large dataset of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of human and faunal remains in the available literature, this study offers a long-term, regional synthesis of the transition from foraging to farming in the Iberian Peninsula. From the Mesolithic to the Late Neolithic–Chalcolithic, humans have largely relied on C₃-based terrestrial resources for food complemented, in some coastal areas, with marine organisms. Considerable isotopic variability among Mesolithic individuals could be associated with versatile and diversified subsistence strategies, adapted to the mosaic of environmental conditions in the Iberian Peninsula. The onset of farming triggered the

replacement of heterogeneous diets based on a broad spectrum of resources—including terrestrial animals from different ecological niches, marine resources and wild plants—to fully terrestrial diets dominated by farming products (crops and livestock) under increasing human control of their production cycles.

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