

Examining Dietary Variability of the Earliest Farmers of South-Eastern Italy

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ABSTRACT Stable isotope analysis of human remains has been used to address long-standing debates regarding the speed and degree to which the introduction of farming transformed diet. In Europe, this debate has centered on northern and Atlantic regions with much less attention devoted to the arrival of farming across the Mediterranean. This study presents carbon and nitrogen stable isotope analyses of collagen from 19 human and 37 faunal remains from eight sites in the Apulia and Marche regions of south-eastern and central Italy, dating to the early phases of agricultural adoption during the first half of the 6th Millennium BC. Where collagen preservation permitted, sulfur stable isotope analysis was also performed. Overall, there was significant isotopic variation between the different geographic regions, although there was also considerable uncertainty in interpreting

these data, especially given heterogeneous isotope values for fauna from site to site. By considering isotope data from each region separately, it was noticeable that the degree of carbon isotope enrichment in humans compared to fauna was higher for individuals buried near the coast, consistent with increased marine consumption. Coastal individuals also had higher sulfur isotope values. Nitrogen isotope values were very variable between individuals and regions and, in some cases, were consistent with very high plant food consumption. Overall, early "farmers" in south-east and central Italy consumed a wide range of foods, including marine, and had much more variable stable isotope values than those observed in central and northern Europe during this period, perhaps indicating a different mode for agricultural adoption. *Am J Phys Anthropol* 149:380–390, 2012. © 2012 Wiley Periodicals, Inc.

The transition to farming at the start of the Neolithic marks a key period in European prehistory which irreversibly transformed much of the continent. It involved a shift from foraging to farming, from food collection to food production, from wild to domestic resource exploitation. From its origin in south-western Asia shortly after 10,000 BC (Harris, 1996), the dispersal of agriculture and pastoralism through Europe has been tracked through radiocarbon dating of domesticated plants and animals (e.g., Pinhasi et al., 2005). However, this evidence fails to address questions concerning the speed and completeness of the change from fishing, hunting and foraging to agriculture. Mixed subsistence patterns, as a result of hunter-gatherers "experimenting" with farming (e.g., Zvelebil and Rowley-Conwy, 1986) or of migrating "farmers" supplementing their crops and livestock with wild resources, are only rarely considered and often difficult to determine from fragmentary faunal and floral assemblages.

In an attempt to study the abruptness and completeness of the transition to agriculture, carbon and nitrogen stable isotope analyses have been widely conducted on bone collagen. This approach has the advantages of providing direct long-term dietary information relating to

specific individuals (e.g., Katzenberg, 2000; Sealy, 2001; Hedges et al., 2007). In the absence of C4 plants, the degree of enrichment of human collagen in ¹³C over ¹²C ($\delta^{13}\text{C}$) provides a direct indication of the amount of

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marine foods consumed (Richards and Hedges, 1999). Whereas the ratio of ^{15}N to ^{14}N ($\delta^{15}\text{N}$) increases with trophic level, and so can be used to identify consumers of (high trophic level) marine foods and to crudely estimate the proportion of plant and animal protein in terrestrial diets (Hedges and Reynard, 2007). This approach has been applied widely to late Mesolithic and early Neolithic human remains from northern Europe. From these data, it is argued that there was an abrupt dietary change, notably a reduction in marine resource exploitation at coastal sites, with the arrival of farming in the Neolithic (Tauber, 1981; Schulting, 1998; Schulting and Richards, 2002; Richards et al., 2003a,b). While it is debatable whether marine foods, and other wild produce, were completely abandoned at the start of the Neolithic period (see Milner et al., 2004), the carbon isotope results of a large number (ca. 90) of individuals dating to the first 500 years following the introduction of domesticated animals and plants are remarkably homogenous ($-20\text{‰} \pm 1\text{‰}$) and have been interpreted to indicate a predominantly terrestrial diet (e.g., Richards et al., 2003a). Similarly, nitrogen isotopes values are also homogenous during this period and have been interpreted to indicate diets largely based on the consumption of protein from terrestrial animals (Hedges and Reynard, 2007).

Surprisingly, there have been far fewer stable isotope studies of southern European and Mediterranean Neolithic human remains (Le Bras-Goude et al., 2006; 2010; Lightfoot et al., 2011). The expansion of farming through the western Mediterranean during the late seventh and sixth millennia is marked by the first occurrences of domesticated animals (particularly ovicaprids), domesticated wheat and barley, stylistically uniform ceramic vessels, the use of obsidian and ground stone, and small settlements (Zilhão, 2001; Guilaine, 2003). In the Adriatic, farming spread very quickly up the Dalmatian coast and across to Italy by the very start of the 6th millennium BC (Skeates, 2000; Starnini, 2002; Miracle and Forenbaher, 2005). In south-east Italy, particularly on the Murge and Tavoliere plateaus, early farming settlements are identifiable as “ditched village,” which were established in a landscape that was very sparsely inhabited in the late Mesolithic (Pessina and Tiné, 2008). Subsequent radiocarbon dates for the first appearance of these Neolithic elements across the western Mediterranean, from Italy to Portugal, are statistically indistinguishable and cluster around about 5,500 cal BC. From the radiocarbon evidence it has been suggested that the expansion of farming in this region was a punctuated event, best explained by the process of maritime pioneer colonization and the formation of enclave farming settlements (Zilhão, 2001). In this scenario, it is reasonable to expect at least a similar degree of dietary homogeneity in southern Europe compared to northern Europe during the early Neolithic, as varied forager diets were rapidly replaced by the consumption of domesticated cereals and animals brought in by migrant farmers.

The alternative hypotheses for agricultural transmission in southern Europe have emphasized a more active role of indigenous foragers (e.g., Bagolini and Broglio, 1985; Lewthwaite, 1986; Biagi, 1990; Whittle, 1996), which tempered Neolithic practices and led instead to mixed forms of subsistence. For example, in the central and northern Adriatic, the spread of farming seems to have moved at a slower pace, perhaps due to a greater density of Mesolithic hunter-gatherers (Boschian, 2000; Boschian and Riedel, 2000; Miracle and Forenbaher, 2005;



Fig. 1. Geographical location of sites.

Mlekuž, 2005). Our knowledge of late Mesolithic diet and subsistence in the Mediterranean is poor. Only very few human remains are available, but the isotopic studies that have been carried out on late Mesolithic coastal foragers show a small but significant marine component (Garcia Guixé et al., 2009; Lightfoot et al., 2010).

Focusing on south-eastern Italy, here we aimed to test whether a similar degree of marine consumption was evident in early Neolithic humans from coastal sites and also to determine the degree of dietary homogeneity across different landscapes and regions. To reach these aims, we conducted stable isotope analysis on 19 early Neolithic individual from eight sites in the Apulia and Marche provinces. As with many Neolithic funerary contexts in southern Europe, the number of burials at each site was small and the sites were distributed across different landscapes and ecological settings. Samples were obtained from sites directly on the coast as well as those inland and encompassed four different regions: the Tavoliere plain, the Murge plateau, the low-lying littoral zones of the Gulf of Taranto and the Adriatic coast in Apulia and further north near Ancona in the Marche (Fig. 1).

Therefore, to assess dietary variability in the human sample, it was necessary to control for any isotopic

variation resulting from environmental differences, rather than diet, by measuring terrestrial herbivores from each site to establish local dietary end-points. Unlike isotope studies of large assemblages of human remains, which have internal consistency permitting comparative inferences, this approach relies on assumptions regarding predictable isotopic differences between the tissues of consumers and their diet. This study therefore also aimed to explore the uncertainty associated with these assumptions and whether meaningful inference relating to Neolithic dietary variability could be drawn from such a small scattered sample.

In addition to carbon and nitrogen isotopes, we attempted to measure sulfur isotope ratios ($\delta^{34}\text{S}$) to further distinguish marine, freshwater, and terrestrial consumers (Richards et al., 2001; Privat et al., 2007; Nehlich et al., 2010), on the basis of ^{34}S variation in inorganic sulfur present in rainwater, groundwater, lakes, rivers, and oceans. In particular, the wide range of freshwater and terrestrial sulfur values (-20% to $+20\%$; Nriagu et al., 1991) contrasts with a very narrow range for marine consumers (ca. $+20\%$). One confounding factor is that consumers of terrestrial foods grown or raised in coastal zones, which are subject to "sea-spray", will also have marine $\delta^{34}\text{S}$ values. The sea-spray effect will diminish with distance inland from the coast. However, Zazzo et al. (2011) have shown that relatively high $\delta^{34}\text{S}$ values were still measured up to 100 km inland, although the precise effects will greatly depend on the local airflow. Therefore, unlike carbon and nitrogen isotope analysis, sulfur isotope analysis does not necessarily provide a direct indication of diet. Also due to the low amount of sulfur in collagen (ca. 0.2%), the method is only applicable to samples with high collagen yields (>20 mg).

MATERIALS AND METHODS

Materials

In total, 19 adult humans were obtained for stable isotope analysis. Where enough bone was available, dating based on the archeological context was confirmed by AMS of bone collagen at the CEDAD radiocarbon facility in Lecce (Table 1).

The majority of samples (15) were selected from seven sites in Apulia dating to the early phases of the Neolithic (6,100–5,400 cal BC). Four adult individuals, three males and one female, (Robb et al., 1991), were sampled from Ripa Tetta, one of the earliest Neolithic ditched villages on Tavoliere plain. The human remains were associated with Impressed ware pottery and charred cereal grains of early Neolithic date (Table 1). Human samples were also obtained from a further three inland sites (Palata, Balsignano, Masseria Maselli) on Murge plateau in central Apulia, another key area of Neolithic activity. An adult female and an adult male were recovered from Palata, a Neolithic ditched village in the Ofanto Valley. These individuals were initially attributed to the Middle Neolithic period but the site also showed evidence of earlier Neolithic activity (Radina et al., 2011). AMS dating of collagen from both specimens produced a mid-6th millennium BC date (Table 1) and these were therefore selected for isotope analysis. Two individuals, with early Neolithic AMS dates (Table 1), were selected from a further two ditched villages, Balsignano (Radina, 2002) and Masseria Maselli (Radina, 2006), situated on the Murge plateau south of Bari. A further seven individuals were

obtained from three coastal sites (i.e., <2 km from the coast) in the Salento peninsula of Apulia (Torre Castelluccia and Samari) and in central Apulia on the Adriatic coast (Grotta delle Mura). No direct dating was undertaken of these samples but in each case they were clearly associated with Impressed ware pottery and attributable to the early Neolithic period (Calattini and Greco, 2000; Orlando, 2002).

A further four human samples were selected from Fosso Fontanaccia (Portonovo) located on the coast of the Marche, where excavations revealed four circular structures containing a number of burials associated with Impressed ware pottery (Silvestrini and Pignocchi, 1998; 2000; Conati Barbaro and Silvestrini, 2005). One bone sample was AMS dated and produced a mid-6th Millennium BC date (Table 1). Even though the site is not located in Apulia, we included these samples to examine dietary variability, especially the degree of marine consumption, along the Italian Adriatic coast during the early Neolithic period.

To assist in the interpretation of the human stable isotope values, 37 faunal remains (Table 2) were obtained to check for variability in the isotope ecology across the different regions and to establish isotopic end-points. The majority were domestic caprids (*Caprinae* spp.) found in abundance at the sites investigated. At Grotta delle Mura, marine fish remains dating to Upper Palaeolithic and Mesolithic were also analyzed to provide a reference marine isotope signal. In certain cases these could be identified as mullet (*Mugilidae* spp.).

Isotope ratio mass spectrometry of bone collagen

Collagen was extracted for isotope-ratio mass spectrometry (IRMS) using a modified Longin method (Brown et al., 1988). For each human and animal sample, 0.5 g of cleaned and pulverized bone was demineralized in 0.6 M hydrochloric acid (HCl) and the resulting insoluble fractions was gelatinized in dilute HCl (pH 3). The solution was then filtered (30 kDa MWCO) and freeze-dried. To calculate carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope compositions, ~ 1 mg of the resulting 30 kDa collagen fraction was weighed in triplicate and analyzed by continuous flow isotope ratio mass spectrometry (Thermo Finnigan Delta Plus XL) in the Department of Archeological Sciences, University of Bradford. The results are reported using the delta scale in units of "per mil" (‰) relative to internationally accepted standards: V-PDB for $\delta^{13}\text{C}$ and atmospheric air for $\delta^{15}\text{N}$. The precision of analysis was ± 0.1 and $\pm 0.2\%$ for carbon and nitrogen isotope measurements, respectively.

Sulfur stable isotope investigation was performed by IRMS at Iso-Analytical (Crewe, UK) on nine samples which contained enough bone collagen to permit analysis. For each sample, about 8 mg of collagen was combusted in duplicate with vanadium oxide (V_2O_5) and the resulting gases, sulfur monoxide (SO) and sulfur dioxide (SO_2), were analyzed on a Europa Scientific 20–20 isotope ratio mass spectrometer (Crewe, UK). The results are presented in per mil notation (‰) vs. the primary $\delta^{34}\text{S}$ isotope standard V-CDT. The precision of analysis determined on repeated measurements was $\pm 0.1\%$.

Collagen extraction was carried out simultaneously from a modern bovine bone powder of known isotopic composition which was used as a reference control. To test collagen preservation and to exclude contamination

TABLE 1. Archaeological records and stable isotope results of human samples from Apulia and Marche regions

Region	Site	Sample (lab code)	Bone element	Cultural context	Age	Sex	Date (bp)	Calibrated date BC (2 σ)	%N	%C	$\delta^{15}\text{N AIR}$ (‰)	$\delta^{13}\text{C}$		$\delta^{34}\text{S}$		% collagen		
												V-PDB (‰)	C : N	V-CDT (‰)	C : S			
Marche (coastal)	Fosso Fontanaccia (Portonovo)	PN17	Long bone	Impressed ware					15.3	41.8	13.3	-20.6	3.2			3.3		
		PN3	Coastal bone	Impressed ware					13.8	38.1	12.8	-20.5	3.2			1.4		
		PN4	Long bone	Impressed ware					18.0	50.2	13.0	-20.5	3.2			2.0		
		PN6	Coastal bone	Impressed ware				LTL5191A; 6,418 \pm 50	5,480–5,310	17.0	46.8	12.6	-20.6	3.2	0.15	fail	838	261
		Cast	Coastal bone	Impressed ware						15.3	44.0	8.4	-18.8	3.4			1.8	
		Sa 20	Femur	Impressed ware	M					15.3	43.0	9.8	-19.2	3.3			1.7	
Apulia (coastal)	Torre Castelluccia Samari	Sa 21	Femur	Impressed ware	M				15.6	45.6	9.8	-19.1	3.4	0.23	18.2	528	181	
		Sa 22	Femur	Impressed ware	M				16.7	46.4	10.0	-18.7	3.2	0.20	19.4	618	223	
		Sa 23	Femur	Impressed ware	40–45	M				16.4	46.2	10.5	-19.0	3.3	0.23	20.2	536	190
		GM 10	Mandible	Impressed ware						14.4	41.7	7.8	-19.6	3.4			4.1	
		GM 11	Femur	Impressed ware						13.9	39.5	8.0	-17.7	3.3	0.15	fail	721	218
		Rp 1	Humerus	Impressed ware	30	M		6,890 \pm 60	5,860–5,600 ^a	15.5	44.5	9.3	-20.1	3.4	0.21	14.8	588	210
Tavoliere (inland)	Ripa Tetta	Rp 2	Humerus	Impressed ware	25–30	M			16.4	46.7	10.0	-19.8	3.3	0.22	12.2	576	202	
		Rp 3	Tibia	Impressed ware	25–30	M			14.2	43.4	11.3	-20.0	3.6			0.4		
		Rp 4	Femur	Impressed ware	21	F			15.5	45.5	11.7	-20.1	3.4			0.6		
		Bal III	Long bone	Impressed ware	37–46	F		6,602 \pm 30	5,570–5,480 ^{b,c}	13.6	39.9	8.1	-19.3	3.4			1.9	
Murge (inland)	Masseria Maselli Palata	Mas	Long bone	Impressed ware	18–21	F		6,542 \pm 45	16.5	48.9	8.1	-19.6	3.5			1.1		
		Pal I	Rib	Red-band painted ware ?		F	LTL5187A; 6,576 \pm 45	5,620–5,470	15.2	44.2	8.6	-19.5	3.4	0.15	fail	796	235	
		Pal II	Coastal bone	Red-band painted ware ?		M	LTL5188A; 6,561 \pm 50	5,630–5,460	15.1	43.9	9.6	-19.1	3.4			2.1		

^a Grifoni and Tozzi, 1996; AMS of a charred cereal grain found in association.

^b Radina, 2002; AMS made on the bone collagen.

^c Radina, 2006; AMS made on the bone collagen.

TABLE 2. Archaeological records and stable isotope results of faunal samples from Apulia and Marche regions

Region	Site	Sample (lab code)	Bone element	Species	Cultural context	%N	%C	$\delta^{15}\text{N}$ AIR (‰)	$\delta^{13}\text{C}$ V-PDB (‰)	C : N	%S	$\delta^{34}\text{S}$ V-CDT (‰)	C : S	N : S	% collagen			
Marche (coastal)	Fosso Fontanaccia (Portonovo)	P21	Fragment	<i>Capra hircus</i> ^a	Impressed ware	17.8	50.9	10.6	-21.0	3.3					0.9			
		P16	Fragment	<i>Cervidae</i> spp. ^a	Impressed ware	18.0	50.1	7.8	-24.1	3.3						2.0		
		P7	Fragment	<i>Ovis aries</i> ^a	Impressed ware	17.7	49.1	10.1	-22.6	3.2						5.7		
		P13	Fragment	<i>Ovis aries</i> ^a	Impressed ware	18.0	50.4	6.9	-21.2	3.3						1.9		
		P15	Fragment	<i>Ovis aries</i> ^a	Impressed ware	18.4	51.8	9.1	-22.5	3.2						3.5		
		P18	Fragment	<i>Ovis aries</i> ^a	Impressed ware	16.4	45.6	5.8	-22.5	3.2						2.0		
		P12	Fragment	<i>Sus scrofa</i> ^a	Impressed ware	18.3	51.4	9.4	-21.7	3.3						3.9		
		P19	Fragment	<i>Sus scrofa</i> ^a	Impressed ware	14.8	41.3	8.5	-21.4	3.3						5.4		
		P20	Fragment	<i>Sus scrofa</i> ^a	Impressed ware	14.9	41.3	9.0	-21.4	3.2						6.5		
		P8	Fragment	<i>Sus scrofa</i> ^a	Impressed ware	18.6	49.8	11.0	-22.1	3.3						2.5		
		P9	Fragment	<i>Sus scrofa</i> ^a	Impressed ware	16.9	47.3	9.4	-21.1	3.3						3.4		
		GM 1	Phalanx	<i>Caprinae</i> spp.	Impressed ware	16.7	48.0	6.5	-19.5	3.4						4.5		
		Apulia (coastal)	Grotta delle Mura	GM 2	Phalanx	<i>Caprinae</i> spp.	Impressed ware	15.7	44.5	5.3	-20.2	3.3					11.6	
				GM 3	Radius	<i>Caprinae</i> spp.	Impressed ware	15.3	44.7	7.1	-20.2	3.4					2.1	
				GM 4	Radius	<i>Caprinae</i> spp.	Impressed ware	13.7	39.8	6.5	-19.3	3.4					1.0	
				GM 5	Mandible	<i>Caprinae</i> spp.	Impressed ware	16.3	47.6	5.2	-20.8	3.4					3.6	
				GM 6	Mandible	<i>Caprinae</i> spp.	Impressed ware	15.9	46.9	3.8	-21.7	3.5					2.5	
				GM 7	Mandible	<i>Caprinae</i> spp.	Impressed ware	16.9	50.5	4.5	-20.8	3.5						1.9
				GM 8	Radius	<i>Caprinae</i> spp.	Impressed ware	17.6	50.7	6.5	-19.8	3.4						6.3
GM 9	Mandible			<i>Canis familiaris</i>	Impressed ware	14.8	43.5	7.8	-19.9	3.4						2.7		
GM 12	Fragment			Marine fish	Early epigravettian	16.9	47.9	9.0	-12.9	3.3						3.6		
GM 13	Fragment			Marine fish	Late epigravettian	15.3	46.3	11.7	-18.9	3.5						1.0		
GM 14	Fragment			Marine fish	Late epigravettian	17.5	50.1	14.0	-16.9	3.3						1.8		
GM 16	Fragment			Marine fish	Late epigravettian	15.7	44.8	10.0	-10.8	3.3						2.2		
GM 17	Caudal vertebra			<i>Mugilidae</i> spp.	Sauveterrian	17.2	48.3	10.6	-18.0	3.3						6.6		
GM 18	Caudal vertebra			<i>Mugilidae</i> spp.	Sauveterrian	12.3	37.2	9.2	-16.6	3.5						1.0		
Rp 5	Scapula			<i>Sus scrofa</i>	Impressed ware	15.4	44.6	8.0	-20.8	3.4						0.9		
Rp 6	Long bone			<i>Bos taurus</i>	Impressed ware	15.8	47.1	6.5	-20.2	3.5						0.9		
Rp 7	Mandible			<i>Ovis vel Capra</i>	Impressed ware	16.2	46.6	8.0	-20.7	3.3		0.20	14.0	621	216	3.0		
Rp 8	Phalanx			<i>Vulpes vulpes</i>	Impressed ware	16.2	46.6	8.0	-20.7	3.3						no coll.		
Bal III	Fragment			<i>Ovis aries</i> ^a	Impressed ware	16.2	47.2	6.2	-20.0	3.4						1.8		
Tavoliere (inland)	Ripa Tetia	fauna																
		Pal B2	Long bone	<i>Ovis vel Capra</i>	Red-band painted ware											no coll.		
		Pal C2	Vertebra	<i>Ovis vel Capra</i>	Red-band painted ware											no coll.		
		Pal B5	Long bone	<i>Bos taurus</i>	Red-band painted ware	14.7	42.2	8.1	-20.1	3.4					1.4			
		Pal C4	Metatarsus	<i>Bos taurus</i>	Red-band painted ware					>3.6						6.8		
		Pal II	Long bone	<i>Ovis vel Capra</i>	Red-band painted ware	16.5	48.4	6.7	-18.5	3.4						2.3		
		Pal US7	Long bone	<i>Ovis vel Capra</i>	Red-band painted ware	15.3	44.4	6.7	-20.4	3.4						5.1		
Murge (inland)	Balsignano	fauna																
		Pal US7	Long bone	<i>Ovis vel Capra</i>	Red-band painted ware	15.3	44.4	6.7	-20.4	3.4					5.1			

^a Species identification was performed through ZooMS.

due to exogenous carbon, nitrogen and sulfur sources, samples were assessed against the established criteria (DeNiro and Weiner, 1988; van Klinken, 1999; Fischer et al., 2007; Nehlich and Richards, 2009).

All statistical analyses were carried out using the software R version 2.12.1 or SPSS v20.

ZooMS analysis

The absence of any identifiable faunal remains at some sites (Portonovo and Balsignano) promoted the identification through protein mass spectrometry (ZooMS). This method has been shown to be particularly useful for distinguishing sheep from goat bone and is suitable for identifying very small fragments (Buckley et al., 2010). The method was applied to small fragments (<10 cm) of long bone that could only be morphologically identified as mammal. Eleven bone fragments (<20 mg) from Portonovo and one from Balsignano were prepared for matrix-assisted laser desorption/ionization time-of-flight mass spectrometry (MALDI-TOF-MS) using the ZooMS acid extraction method after Buckley et al. (2009). For each sample, ~10 mg of pulverized bone were demineralized in 0.6 M HCl. Resulting insoluble fractions were gelatinized in 50 mM ammonium bicarbonate for 3 h at 65°C. Following gelatinization, samples were centrifuged at 13,000g for 15 min and the supernatant of each sample was then digested with 2 μ l of 1 μ g μ l⁻¹ trypsin (1 μ g μ l⁻¹; 37°C; 18 h). Following digestion, each sample was centrifuged at 13,000g for 10 min and acidified with 0.1% trifluoroacetic acid (TFA). The samples were then passed through C18 ZipTip pipette tips (Agilent Technologies, Cheadle, UK) pretreated with 0.1% TFA before being eluted with 10% and 50% acetonitrile (ACN) in 0.1% aqueous TFA. About 2 μ l of each eluted sample were then spotted onto a prespotted anchorage set plate and dried. The dried plate was then analyzed using a Bruker ultraflex III MALDI TOF/TOF mass spectrometer (Bruker, Bremen, Germany) in triplicate. The resultant spectra were processed using the Bruker Flex Analysis software. Species identifications of the spectra were performed according to the criteria outlined in Buckley et al. (2009).

RESULTS AND DISCUSSION

Collagen quality assessment

From the 19 human and 37 faunal bone remains analyzed for carbon and nitrogen isotopes, collagen of satisfactory quality was obtained from 19 humans and 33 animals (Tables 1 and 2). Samples failed because their collagen yields following ultrafiltration were too low (<0.4%) or their atomic C:N ratio was outside the acceptable range (2.9–3.6). Similarly, only nine samples contained enough collagen to permit stable sulfur isotope analysis and of these only six yielded %S values within the accepted range (i.e., 0.28 ± 0.07 ; Nehlich and Richards, 2009). These were three humans from Samari and two humans and one sheep from Ripa Tetta (Tables 1 and 2).

Regional differences in marine consumption

The Italian Neolithic human data have been plotted by region (i.e., Marche, coastal Apulia, Tavoliere, Murge) in Figure 2, along with those reported from early Neolithic ($n = 5$) and late Mesolithic ($n = 5$) contexts from

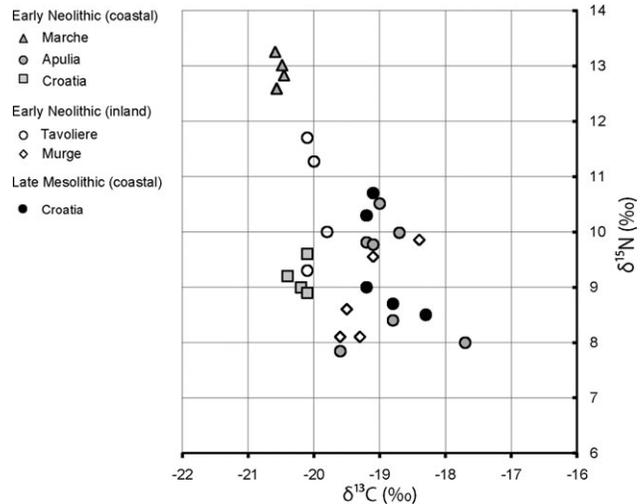


Fig. 2. Carbon and nitrogen stable isotope measurements of late Mesolithic and early Neolithic humans from south-eastern Italy (the present study) and Croatia (Lightfoot et al., 2011).

the coast of Croatia (Lightfoot et al., 2011). For the Italian samples, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values range from -20.6 to -17.7 ‰ and from 7.8 to 13.3‰, respectively and show significant differences between the regions investigated ($\delta^{13}\text{C}$ Kruskal–Wallis = 15.3, $P < 0.01$; $\delta^{15}\text{N}$ Kruskal–Wallis = 12.1, $P < 0.01$; Fig. 3). However, humans buried at coastal sites are not enriched in either isotope compared to those from inland sites, as may be expected due to increased marine consumption ($\delta^{13}\text{C}$ Kruskal–Wallis = 0.34, $P = 0.56$; $\delta^{15}\text{N}$ Kruskal–Wallis = 0.83, $P = 0.36$). To investigate this further the isotopic differences between early Neolithic terrestrial fauna ($n = 53$) and marine fauna ($n = 17$), including those reported by Lightfoot et al. (2011), were compared statistically. As expected, the distributions of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between terrestrial and marine fauna were found to be significantly different ($\delta^{13}\text{C}$ Mann–Whitney U test = 914, $P < 0.01$; $\delta^{15}\text{N}$ Mann–Whitney U test = 729, $P < 0.01$). However, the difference between the means for $\delta^{15}\text{N}$ of terrestrial and marine fauna are much smaller than anticipated (ca. <3‰; see Fig. 3b) which is attributable to high variances of both sample sets, lower values of $\delta^{15}\text{N}$ in Adriatic faunal collagen compared to Atlantic species (e.g., Richards and Hedges, 1999) and particularly high $\delta^{15}\text{N}$ values for the terrestrial fauna from Portonovo (Marche). Even considering regional values for terrestrial fauna separately, $\delta^{15}\text{N}$ values are not sufficiently variable to distinguish marine from terrestrial consumers in this case. In contrast, the differences between the mean $\delta^{13}\text{C}$ values of terrestrial and marine fauna are much greater (ca. 6‰), although the variances in terrestrial fauna are also high (see Fig. 3a), especially between regions. The regional variability in terrestrial fauna $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values was much greater than the variation observed between different species at individual sites. For example, it was not possible to distinguish sheep ($n = 4$) from pigs ($n = 5$) at Portonovo statistically ($\delta^{13}\text{C}$ Kruskal–Wallis = 2.20, $P = 0.14$; $\delta^{15}\text{N}$ Kruskal–Wallis = 0.97, $P = 0.32$), whereas substantial variation was evident even within one family of fauna (*Caprinae* spp.) between sites, which may be due to environmental differences (aridity, altitude; Sealy, 2001) and/or husbandry practices (stocking-levels, manuring, foddering;

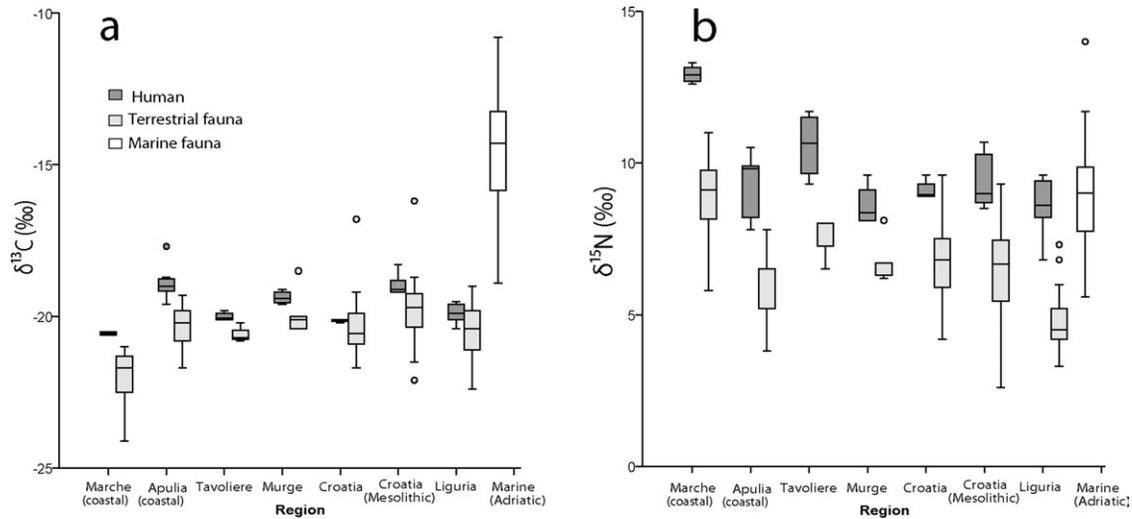


Fig. 3. Boxplot of carbon (a) and nitrogen (b) stable isotope data for humans, terrestrial and marine fauna from different regions in south-eastern Italy (the present study), Liguria (Le Bras-Goude et al., 2006) and Croatia (Lightfoot et al., 2011).

TABLE 3. Mean $\delta^{13}\text{C}$ values of humans and animals and estimated fraction of marine food in diet for a range of early Neolithic sites (unless indicated) using different assumptions (see text)

Region	Mean bone collagen $\delta^{13}\text{C}$ (‰)			Estimated fraction of marine fish in total diet by dry weight			Reference
	Fish	Terrestrial fauna	Human	Model 1	Model 2 ^a	Model 3 ^a	
Marche (coastal)	-14.5	-22.0	-20.6	6%	19%	24%	
Apulia (coastal)	-14.5	-20.2	-18.9	6%	24%	30%	
Tavoliere (inland)	-14.5	-20.6	-20.0	0%	10%	16%	
Murge (inland)	-14.5	-19.9	-19.4	0%	7%	15%	
Croatia (coastal)	-14.5	-20.3	-20.1	0%	2%	10%	Lightfoot et al., 2011
Croatia (coastal; Mesolithic)	-14.5	-19.8	-18.9	0%	16%	23%	Lightfoot et al., 2011
Liguria (coastal)	-14.5	-20.5	-19.9	0%	10%	17%	Le Bras-Goude et al., 2006

^a These models use mean dry weight % protein, carbohydrate and lipids in typical Mediterranean marine fish (85%, 0%, 15%), sheep and goat carcass and milk (81%, 0.5%, 14%) and grains, nuts and legumes (15%, 82%, 25%) which were obtained from the USDA National Nutrient Database.

Further details of the model and assumptions are provided in Supplementary Information.

Schwertl et al., 2003, 2005). This requires the isotope data from each region to be considered separately (Fig. 3).

The proportion of dietary protein derived from marine vs. terrestrial sources was crudely estimated using a simple linear mixing model (Model 1; Table 3), based on the mean human $\delta^{13}\text{C}$ values from each region and with endpoints defined by the mean $\delta^{13}\text{C}$ values of terrestrial fauna from each region and marine fauna from the Adriatic. In doing so the following assumptions are made; i) the fauna analyzed are representative of the fauna consumed with respect to their isotope values; ii) human collagen values are enriched in $\delta^{13}\text{C}$ by 1‰ compared to faunal values; iii) human collagen carbon is derived entirely from dietary protein carbon. Of these assumptions, the last one has been questioned (Hedges, 2004, 2006; Milner et al., 2004; Jim et al., 2006). Notably, if collagen carbon was also derived from dietary carbohydrates or lipids, estimated to be depleted in ^{13}C by 1 and 5‰ relative to protein respectively, the degree of marine consumption would be underestimated. This effect was crudely estimated (Model 2, Table 3) based on the model of Hedges (2004) which assumes that carbon from

ingested protein, lipid and carbohydrate contribute carbon equally to collagen. The effect would be further amplified if carbohydrates from plants are also considered to contribute to collagen, as this dietary source is further depleted in $\delta^{13}\text{C}$ compared to terrestrial animals (by ca. 1‰). This effect was modeled (Model 3, Table 3) assuming that plants and terrestrial animals contribute equally to a 100% terrestrial diet.

The overall estimations vary between the Italian sites and other early Neolithic sites along the Croatian and Ligurian coast (Table 3). From the mean human collagen $\delta^{13}\text{C}$ values, we estimate that humans buried near the coasts of Apulia and the Marche (Ancona) consumed a small but significant amount of marine fish (estimated to be ca. 5–30% by dry weight), but that the marine dietary contribution was reduced, or not evident, for those buried inland (ca. 0–15%). Within the Apulian coastal human sample, there is considerable variation around the mean $\delta^{13}\text{C}$ value. One individual from Grotta delle Mura (GM11) was likely to have consumed a much greater amount of marine food (estimated to be 25–50% by dry weight). In the absence of ^{13}C enriched C4 plants

during this period, marine consumption is the preferred interpretation. The relatively low $\delta^{15}\text{N}$ value of this individual may reflect consumption of lower trophic level marine foods, such as marine shellfish.

Demonstrating continuity in marine exploitation from the late Mesolithic is difficult in the absence of a comparative Mesolithic assemblage from Italy. However, a comparison of Neolithic individuals from the Italian coastal sites with late Mesolithic individuals from the Croatian coast (Lightfoot et al., 2011), reveals more enriched $\delta^{13}\text{C}$ values in the Neolithic sample (Table 3). These Neolithic individuals have amongst the highest $\delta^{13}\text{C}$ values reported for the Mediterranean region and are comparable to late Mesolithic individuals from El Collado, a shell midden site on the eastern coast of the Iberian Peninsula (Garcia Guixé et al., 2006). Nevertheless, the estimated dietary contribution of marine resources in the Mediterranean region in either the late Mesolithic or early Neolithic is still estimated to be modest (<30% by weight) compared to late Mesolithic humans from Atlantic Europe (Lubell et al., 1994; Schulting, 1996; Richards and Mellars, 1998), and indicates that terrestrial foods were still the major dietary component.

In contrast, isotope data from Neolithic humans from the Croatian coast (Lightfoot et al. 2011) point to a slight reduction in the degree of marine resource exploitation with the arrival of agriculture (Table 3). Similarly the early Neolithic data from the Ligurian coast also indicate at most a very small amount of marine foods in the diet (Le Bras-Goude et al., 2006; Table 3).

Sulfur stable isotope values available for Samari on the Apulian coast (Gulf of Taranto) and Ripa Tetta on the Tavoliere plain, some 50–60 km from the sea, were used to support differences in the degree of marine consumption, evident from the carbon isotope results (Table 3). Humans from Samari are 5–7‰ enriched in ^{34}S compared to humans and a domestic sheep from Ripa Tetta (Fig. 4), as expected if marine consumption were significant at this coastal site. In fact, the Samari individuals have collagen $\delta^{34}\text{S}$ values close to the marine sulfate value (+20‰) and the expected value for marine organisms (Peterson and Fry, 1987). This interpretation contrasts with the modest (5–30%) estimation of marine consumption based on $\delta^{13}\text{C}$ analysis and probably reflects a substantial contribution of marine sulfur from “sea-spray” to terrestrial foods grown or raised along coastal regions. Humans from Ripa Tetta had far less, if any, access to marine resources and are unlikely to have resided near the coast. It seems that mobility between the sea and the inland regions was restricted as envisaged by traditional models of early Neolithic sedentism.

Regional differences in the consumption of animal vs. plant protein

Cereal cultivation during the early Neolithic period, particularly on the Tavoliere and Murge, is well attested through numerous finds of grains (mainly emmer, einkorn, barley) and features interpreted to be bread ovens and storage facilities where cereals were processed and stored (Radina, 2002; Radina and Sarti, 2002; Tozzi, 2002). The extent of plant versus animal consumption is however much harder to assess from the botanical and faunal evidence. Nitrogen isotope analysis of bone collagen provides a direct way of estimating trophic level and so the relative contribution of animal versus plant protein to diet. The enrichment observed in ^{15}N between

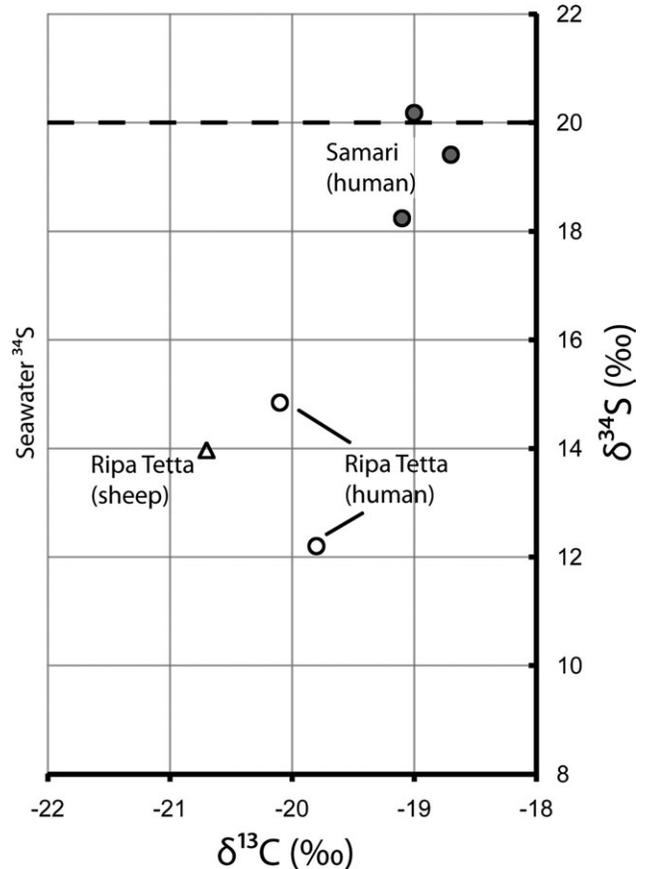


Fig. 4. Sulfur stable isotope measurements for Apulian early Neolithic humans and fauna.

humans and terrestrial fauna is shown in Table 4, calculated from the mean values for each region. From these, we can crudely estimate the amount of animal protein as fraction of total dietary protein, assuming that the fauna analyzed are representative of the fauna consumed with respect to their isotope values. Generally, a 0‰ enrichment indicates a fully herbivorous diet where +4‰ enrichment would be fully carnivorous. However, this simple interpretation (Model A, Table 4) has been critiqued by Hedges and Reynard (2007) as it fails to account for potential physiological and dietary differences between humans and herbivores. Three additional explicit models have been suggested based on different assumptions. These are [B] that cereals are enriched in $\delta^{15}\text{N}$ compared to animal forage by 1‰; [C] that humans are enriched compared to herbivores by an additional 1‰ with respect to diet; [D], in addition to [C], that enrichment in humans for an all meat diet is 1‰ less than for an all plant diet. Based on these, estimations of the % of animal protein in diet for each region are presented in Table 4.

The enrichment between early Neolithic herbivores and humans varies considerably between regions (Table 4). Notably, early Neolithic humans from the Murge show the lowest $\delta^{15}\text{N}$ and therefore are estimated to have derived a comparatively large fraction of their protein from plant foods (60–100%), an interpretation consistent with archeological finds of flint scythes, grindstones and large impressed ceramic storage jars found at these sites (Radina, 2006). These data contrast sharply

TABLE 4. Nitrogen isotope differences between humans and animals from early Neolithic sites and estimated fraction of animal protein in diet using different assumptions (see text)

Region	Mean bone collagen $\delta^{15}\text{N}$ (‰)			Estimated fraction of animal protein in total dietary protein				Reference
	Terrestrial fauna	Human	$\Delta^{15}\text{N}$ human-terrestrial	Model A	Model B	Model C	Model D	
Marche (coastal)	8.9	12.9	4.1	100%	100%	76%	68%	Lightfoot et al., 2011 Le Bras-Goude et al., 2006
Apulia (coastal)	5.9	9.2	3.3	82%	76%	57%	42%	
Tavoliere (inland)	7.5	10.6	3.1	77%	69%	52%	36%	
Murge (inland)	6.9	8.6	1.7	42%	23%	17%	0%	
Croatia (coastal)	6.8	9.1	2.3	57%	43%	32%	10%	
Liguria (coastal)	4.8	8.7	3.9	97%	95%	72%	62%	

Further details of the model and assumptions are provided in Supplementary Information.

with the majority of nitrogen stable isotope data from northern and central Europe (see Hedges and Reynard, 2007), where the differences between terrestrial animals and humans are generally 3‰ or higher from the early Neolithic to post-Roman times. This dietary difference in terms of calorific value is likely to be even more pronounced since animal products (meat and milk) have much higher protein content than plants. The data from the Adriatic do not follow an obvious geographic pattern; comparatively low plant consumption was also a feature of the Croatian early Neolithic whereas humans from coastal sites of the Apulia and the Marche, and the Tavoliere were more enriched compared to local terrestrial fauna which we suggest indicates a much greater reliance on animal products (50–100%; Table 4). Ditched enclosure settlements on the Tavoliere plain, such as Ripa Tetta, are often thought to be primarily associated with cereal cultivation (Radmilli, 1973; Tiné, 1987; Malone, 2003) so the dominance of animal protein here is interesting. At Ripa Tetta, four individuals were analyzed but their $\delta^{15}\text{N}$ values vary considerably (Table 1, Fig. 2) with two individuals ca. 4‰ enriched compared to the terrestrial herbivores, implying almost total reliance on meat or milk proteins, and two individuals with much more modest enrichment (1.8 and 2.5‰) indicating a greater consumption of plant foods.

It should be noted that these interpretations do not take into account the biases in the consumption of herbivores over omnivorous animals such as dogs and pigs which tend to have higher ^{15}N values (Table 2; Lightfoot et al., 2011). However, at Ripa Tetta, the faunal to human $\delta^{15}\text{N}$ difference is only slightly increased (0.5‰) if omnivores (a single pig) are removed. Similarly, at Portonovo (Marche) the mean $\delta^{15}\text{N}$ value for the pigs ($n = 5$) were only ca. 1‰ enriched compared to the caprids, which would increase the estimation of % animal protein in the diet by 10–15% if these were excluded. As marine fauna are only marginally enriched in ^{15}N compared to caprids and were only consumed in modest quantities, if at all (see above), it is unlikely that their inclusion would significantly affect the interpretation. Other species may have been consumed but not measured isotopically. These could include freshwater fish or wild carnivores and piscivores, such as birds and reptiles, which would be expected to be relatively enriched in ^{15}N . More significant consumption of any of these species would reduce the faunal to human $\delta^{15}\text{N}$ values and lead to an underestimation of the degree of dietary protein derived from plants. Also to note is that the consumption of leguminous vegetables, such as peas and beans, which are

depleted in ^{15}N compared to cereals (Virginia and Delwiche, 1982), would lead to an overestimation of the degree of dietary protein derived from plants. In fact, knowledge of the theoretical isotope end-point of humans eating pure plant diets is the greatest hindrance to palaeodietary reconstruction with nitrogen isotopes of bulk collagen. Using herbivorous animals as proxies has obvious limitations.

Implications for understanding the transition to agriculture

Overall, there is variability in the degree of ^{13}C and ^{15}N enrichment between early Neolithic humans across the Adriatic and contemporary herbivores obtained from the same regions. We suggest that this is related to inter-regional variation in diet, particularly as regards the degree of plant, animal and fish consumption. The first farmers of the Adriatic did not have homogenous diets as may have been expected by “pioneer colonizers” who imposed a new economic regime or stuck rigorously to cereal cultivation and stock rearing. Instead, early farming communities adapted to exploit different environments and landscapes or “foodscapes.” This is evident in the archeological record of south-east Italy as early Neolithic activity is manifest in a range of landscapes from coastal plains, valleys to high plateaus and mountains (Malone, 2003). The nature of these sites also suggests variability in food procurement strategies, from the ditched enclosures on the Tavoliere Plain in Apulia, with light soils and plentiful water supplies suited for agriculture, to coastal caves used for millennia prior to the arrival of agriculture as foci for funerary and subsistence practices (Martini, 2006).

If a large demographic change was associated with the arrival of the Neolithic in south-eastern Italy, a process akin to colonization, then it was not marked by dramatic change to a homogenous diet, as implied for northern and western Europe (e.g., Lubell et al., 1994; Richards et al., 2003a,b). One explanation may be that incoming farmers adapted their subsistence practices to accommodate the locally available resources. While agriculture and pastoralism may have been a feature of all early Neolithic communities, the overall subsistence practices were much more diverse and regionally defined by the foodscape. An alternative hypothesis is that the hunter-gatherers, while adopting elements of the Neolithic package, preserved their lifeways well into the Neolithic period. In Apulia this hypothesis would seem less likely

given the paucity of late Mesolithic activity preceding the arrival of farming (Pessina and Tiné, 2008).

Whether continued exploitation of wild foods, as suggested in this study, is applicable to the whole Mediterranean is debatable. In Liguria and eastern Provence, stable isotope studies have revealed more consistent terrestrial diets (Le Bras-Goude et al., 2006) despite the near littoral settings of sites such as Arene Candide and Abri Pendimoun. By contrast, the isotope data from early Neolithic levels at Franchthi Cave in the Peloponnese are more variable and indicate the consumption of marine fish (Papathanasiou et al., 2003). It would seem that a convenient single model cannot explain the dietary change with the arrival of agriculture across the Mediterranean, prompting study at more regional and local levels.

CONCLUSIONS

We have expanded the number of stable isotope measurements on early farmers from the Mediterranean region and shown considerable dietary variability, that includes the consumption of a small amount of marine foods. These findings contrast with data from northern Europe and point to a different and more varied uptake of agriculture in the south. However, there is still considerable uncertainty in interpreting collagen isotopic data due to inter-regional variability in the isotopic end-points for pure animal and marine diets, a total lack of knowledge of the end-points for pure plant diets, as well as uncertainties associated with fractionation of isotopes and collagen biosynthesis. Nevertheless, we show that broad but meaningful inference can be drawn from human stable isotope datasets pooled from different ecological settings, provided faunal samples from the same settings are also compared.

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