Multi-proxy stable isotope analyses of dentine microsections reveal diachronic changes in life history adaptations, mobility, and tuberculosis-induced wasting in prehistoric Liguria (Finale Ligure, Italy, northwestern Mediterranean).

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Abstract

Objective: To reconstruct breastfeeding and weaning practices, metabolic stress including tuberculosis-induced wasting, and residential mobility of children in Neolithic and Metal Ages to infer their local ecologies.

Materials: Seven permanent teeth from individuals dated to the Neolithic, Copper, Bronze, and Iron Ages buried in nearby caves in western Liguria, Italy.

Methods: Carbon, nitrogen, and sulfur stable isotope analyses on dentine microsections. Tooth maturation was used to calculate age at death.

Results: Two Neolithic children present longer pattern of weaning and seem to have been weaned using animal protein in contrast to the earlier weaning of Metal Ages children, which were probably weaned with vegetable resources. Sulfur isotopes suggest local origin of Neolithic and Cooper Age children, and non-local origins for Bronze and Iron Age children. Intense catabolism in the last two years is apparent in the adolescent with tuberculosis.

Conclusions: Shortening in weaning patterns during the Metal Ages are probably driven by the intensification of agricultural practices and cultivation of new crops during Bronze and Iron Ages. Neolithic food choices and delayed weaning patterns may represent one of the strategies to maximize growth and immune potential in a local economy/ecology with high-infectious load. Tuberculosis was a chronic and long-lasting disease.

Significance: The first combined carbon, nitrogen, and sulfur analysis on prehistoric dentine microsections revealing changing human life history adaptations within the same region.

Limitations: Small sample size.

Suggestions for Further Research: Increase the sulfur isotope dataset, use new EA-IRMS equipment, and provide data on amino acid to better define weaning food composition.

Keywords: Breastfeeding; weaning; Neolithic; Metal Ages; infectious disease; incremental dentine analysis.

1. **Introduction**

The study of dietary intake and its changes during early life has important repercussions in the analysis of prehistoric health, paleodemography, and human life history strategies. In fact, infant breastfeeding and weaning practices (BWPs) – involving exclusive breast-feeding (EBF) duration, termination of breast-feeding (TBF), and weaning/child food choices – depend on the local physical and social ecology, including the diet and health conditions of the mother, and on the environmental pathogen load (Ellison, 2001; McDade, 2001; McDade and Worthmann, 1998; Sellen, 2007, 2009; Trivers, 1974). In addition, BWPs are linked to parenting reproductive strategies and resource allocation trade-offs, and are important determinants of fertility at a population level (Wood, 1994). Reconstructing the modality, timing, and variability of prehistoric BWPs is therefore an important field of research in evolutionary anthropology and bioarchaeology, given the number of information on past life experience, subsistence, and adaptative strategies that it can provide (review in Tsutaya and Yoneda, 2015).

Isotopic methods investigating these issues aim at identifying the timing of the infant's trophic level shift from a higher trophic position than the mother during EBF ($\delta^{15}N$ values are about 2 ‰ higher; Herrscher et al., 2017) towards a value compatible with the adult population's average $\delta^{15}N$ at the time of TBF (Fogel et al., 1989; Fuller et al., 2006; de Luca et al., 2012). Several studies on bioarchaeological samples used isotope ratio measurements of bone collagen $\delta^{13}C$ and $\delta^{15}N$ from infants of different ages at death, and compared them with the results obtained from females belonging to the same population (e.g., Jay et al., 2008), or used intra-long-bone analysis (Waters-Rist et al., 2011). However, the most reliable and detailed approach involves the use of incremental dentine collagen to reconstruct temporal changes in the isotope ratios, and to therefore assess changing childhood diet in individuals who survived early life (e.g. Beaumont et al., 2013, 2015, 2018; Sandberg et al., 2014). In addition, changes in $\delta^{15}N$ values can be related not only to dietary changes, but also to periods of physiological stress and catabolism generated by starvation, long-term disease, or harsh climatic conditions (Armit et al., 2015; Beaumont et al., 2015; DeWitte and Stojanowski, 2015; Henderson et al., 2014; King et al., 2018; Montgomery et al., 2013); an approach recently supported by experimental data on animals (Doi et al., 2017). As a result, the "incremental dentine" method is now commonly used in bioarchaeological studies (e.g. Greenwald et al., 2016; Scharlotta et al., 2018a, b).

The Neolithic Transition, which involved the adoption of a production economy based on the domestication of plants and animals resulted in changes in human diet and social organization, which had consequences, depending on the local ecology, on overall well-being [*sensu* Wood

(1998), a combination of life expectancy, nutritional status, and health], and demographic patterns (e.g. Bocquet-Appel, 2002, 2009, 2011a, b). It has been proposed that the overall demographic growth observed with the Neolithic transition was mainly a consequence of an increase in female fertility when compared to hunter-gatherers, fully compensating for increased infant mortality (Armelagos et al., 1991; Page et al., 2016). A combination of numerous factors may have positively influenced female fertility: food resources predictability and storage, better nutritional status, decreased foraging time and energy expenditure (also positively impacting on child care), earlier age at menarche leading to increased reproductive time span, and earlier weaning allowing for a shortening of interbirth interval (Armelagos et al., 1991; review in Bentley at al., 2001; Buikstra et al., 1986; Ellison, 2001; Page et al., 2016; Roth, 1981).

The direct reconstruction of diet and changing dietary composition during early life in Neolithic children is therefore fundamental to our understanding of the adaptive strategies developed concomitantly with the new management of food resources in various local ecologies. In fact, the advantages or disadvantages of the adoption of the Neolithic lifestyle, as well as their long-term evolution, need to be explored at a regional level, due to the mosaic patterns of expansion and crisis that characterized this process throughout the European continent (e.g. Bocquet-Appel et al., 2009; Cohen and Crane-Kramer, 2007; Porčić et al., 2016; Zvelebil, 2001). This study employs the incremental dentine method ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ isotopes) in a sample of directly dated children spanning the early Neolithic through the Metal Ages in the region of Finalese in Liguria (northwestern Italy). The purpose of this study is to reconstruct weaning patterns, episodes of stress, and residential mobility, in order to infer changing environmental conditions, reproductive strategies, and fertility, alongside important changes in subsistence and societal organization through time (Bogucki and Crabtree, 2004; Cunliffe, 1994, 2008; Guidi, 2000).

1.1 *Bioarchaeological background and expectations*

The western diffusion of the Neolithic production economy from the Near East reached the northwestern Mediterranean around 5800-5600 BCE, when people belonging to the Impresso-Cardial chrono-cultural complex (ICC) settled in the Liguro-Provençal Arc (Binder et al., 2017). The Square Mouthed Pottery culture (SMP) developed later and spread throughout Liguria and Northern Italy during the fifth millennium BCE (c. 5000-4300 BCE; Binder and Sénépart, 2010; Del Lucchese and Starnini, 2015). Later, Liguria was the access road for the spread of the Chassean in northern Italy from France (c. 4300-3700 BCE; Crepaldi, 2001; Maggi, 1997a). The Metal Ages in Liguria are subdivided into the Copper Age (c. 3700-2200 BCE), Bronze Age (Early: 2200-1600 BCE; Middle: 1600-1350 BCE; Late and Final: 1350-900 BCE), and Iron Age (c. 900 BCE to

Roman conquest in 180 BCE) (Bagolini and Biagi, 1990; de Marinis, 2013; de Marinis and Spadea, 2004, 2007; Del Lucchese and Maggi, 1998; Maggi et al., 1991-92).

Evidence of prehistoric human occupation in western Liguria comes predominantly from several caves and rock shelters opening within a radius of a few kilometers in the Finalese area, where important sites such as Arene Candide have yielded detailed stratigraphic successions spanning from the Upper Paleolithic to the Roman Age (Arobba et al., 2017; Maggi, 1997a; Tiné, 1999). Several bioarchaeological studies provide a picture of life during the Neolithic in this area. Based on archaeobotanical and zooarchaeological studies, subsistence was based on a variety of domesticated plants (Arobba et al., 2017; Nisbet, 2008), and on livestock breeding, especially sheep (Macphail et al., 1997; Rowley-Conwy, 1992, 1997). Isotopic analyses ($\delta^{13}C$/ $\delta^{15}N$ ratios) suggest a diet based on C_3 cereals, with a significant component of proteins derived from terrestrial animals (Le Bras-Goude et al., 2006; Goude et al., 2014). No significant consumption of fish protein during the SMP period was proposed in light of the collagen isotopic composition (review in Goude et al., 2014). The same pattern was confirmed by analyses performed on individuals from the earlier ICC from the same region (Mannino et al., 2018). These results contrast to a degree with archaeological (e.g. fishing hooks, shell blow horns made of *Charonia sp.*), archaeozoological (e.g. shells), and dental calculus findings, which highlight the continuous use of marine resources throughout the Neolithic (Desse-Berset and Desse, 1999).

Except for evidence of the utilization of caves for domestic activities, stabling, and funerary purposes (e.g. Arobba et al., 2017; Del Lucchese, 1997; Maggi and Nisbet, 2000; Rowley-Conwy, 1992, 1997), the impact on the people in the territory during Ligurian Neolithic was minimal. No trace of large settlements is present, and only few artifacts are attributed to open-air sites (Starnini and Vicino, 1993). Humans had little impact on forest coverage until the Late Neolithic (Nisbet, 1997), and land clearing through the extensive use of fire was introduced in Liguria only at the end of the Neolithic (Maggi, 1997b). The archaeological evidence of increasing socioeconomic complexity, population growth, and enlarged exchange networks observed in Italy and Europe during the Metal Ages (reviews in Bogucki and Crabtree, 2004; Cunliffe, 1994, 2008; Guidi, 2000) take the form of quarries and mines, and impacts forest coverage in the Copper Age (Maggi and Pearce, 2005; De Pascale et al., 2006), the diffusion of the Bell Beaker ceramics at the beginning of the Bronze Age (Chiarenza et al., 2012), and the increasingly structured fortified settlements during the Bronze and Iron Age (e.g. Giuggiola, 1959; Maggi, 1990) in Liguria. However, diet does not seem to vary significantly in western Liguria from the Neolithic throughout the Copper and Bronze Age, at least according to initial C and N isotopic analyses performed on various sites (Varalli et al., 2015). It is only in the Iron Age that a dietary shift, i.e. a significant consumption of C_4 plants, can be detected (Varalli et al., 2015); an occurrence in northeastern Italy that can be traced earlier to the transition between the Early and Middle Bronze Age (Tafuri et al., 2009; Varalli et al., 2016a).

1.2 *Expectations*

It is generally expected that agriculturalist populations will display an earlier TBF than hunter-gatherers (e.g. Bentley et al., 2001). Ethnographic accounts generally agree by showing, on average, a later TBF (between 3-5 years of age) in hunter-gatherers, than in agriculturalists (between 2-4 years), albeit with significant variation (e.g. Dettwyler, 2004; Kennedy, 2005; Marlowe, 2005; Sellen, 2001a, 2006, 2007, 2009; Sellen and Smay, 2001). Similar variation, but without consistent association with subsistence mode, is present in the introduction of supplementary foods immediately after birth to 1-1.5 years (Sellen, 2001a; Sellen and Smay, 2001). It should be noted that the optimal duration of EBF is 6 months (see nutritional recommendations in WHO, 2002; Butte, 2002), as an earlier introduction of supplementary foods exposes the infant to increased morbidity and gastrointestinal problems (Kramer and Kakuma, 2004). Conversely, after around 6 months, EBF cannot provide enough essential nutrients to sustain optimal growth, and the reserve of fat deposited in the first six months to buffer nutritional disruptions is rapidly depleted (Kuzawa, 1998). Cross-cultural surveys indicate that most non-industrial groups adopt attitudes and values about child feeding that are in broad concordance with the optimal practice (Sellen, 2007). However, suboptimal strategies are common and can be due to contingent factors (health of the mother and/or child), local ecologies and seasonality, and cultural practices (Sellen, 2001a, b, 2007).

The direct reconstruction of prehistoric BWPs through isotopic analysis reflects the variation described above and generally shows later TBF in Paleo/Mesolithic hunter-gatherers than in Neolithic agriculturalists (e.g. Howcroft, 2013; Howecroft et al., 2014; Reynard and Tuross, 2015; Tsutaya and Yoneda, 2015). Comparable variation is present through the Metal Ages and protohistory (e.g. Fernández-Crespo et al., 2018; Howcroft, 2013; Scharlotta et al., 2018), and only in post-medieval times is there evidence from incremental dentine studies of TBF before 2 years of age (King et al., 2005). Estimates of the introduction of supplementary foods based on isotopic ratios range from 0.5 to 2 years, according to bone and dentine studies (review in Howcroft, 2013). However, Millard (2000) suggests that studies using bone tissue may overestimate EBF cessation by 6-9 months.

In this study, we expect the Ligurian Neolithic to show an isotopic profile compatible with an earlier age of weaning (TBF) than hunter-gatherers. The scenario of variation in BWPs previously depicted for the Metal Ages (Howcroft, 2013) does not allow for clear expectations. However, we anticipate societal, technological, and subsistence changes to have affected diachronic dietary changes in early life. In particular, we expect a further shortening in BWPs, which would be compatible with the further demographic increase apparent during the Metal Ages, although with significant fluctuations (e.g. Bevan, 2017; Capuzzo et al., 2018; Müller, 2013). Furthermore, increased exchange networks may have favored the mobility of people and, concomitantly, materials, and this should be apparent in $\delta^{34}S$ profiles (see methods).

In addition to subsistence practices, the "local ecology" (*sensu* McDade, 2003: 111) of Neolithic people in Liguria, and the consequent BWPs, were probably affected by a high infectious load. In fact, the Neolithic skeletal series in the Finalese area are known for having yielded several cases of osteoarticular tuberculosis (TB; Canci et al., 1996; Formicola et al., 1987; Sparacello et al., 2017, 2018; see also Dori et al., 2019). Tuberculosis is a highly infectious, debilitating, and growth-impairing disease (Sparacello et al., 2016). One of the Neolithic individuals included in this study is Arene Candide V (excavations Bernabò-Brea and Cardini; Bernabò Brea, 1946), an adolescent who died with Pott's spine, a skeletal lesion that is pathognomonic of osteoarticular tuberculosis (Formicola et al., 1987). Since maternal gestation and milk supports the infant's immune system (McDade, 2003; McDade and Worthmann, 1999; Pacheco et al., 2015; Jeurink et al., 2019), it is possible that Neolithic mothers delayed BWPs, as observed today especially in marginal contexts with limited resources and high infectious risk (e.g. Cantrelle and Leridon, 1971; Lindstrom and Berhanu, 2000).

The study of Arene Candide V will also provide information on the course of TB in this individual and will contribute to the debate on TB virulence and host-pathogen co-evolution in the Neolithic (Sparacello et al., 2016). Tuberculosis causes severe metabolic disturbances (cytokine activation, abnormal protein metabolism, and hormonal unbalance) causing 'consumption' (Macallan, 1999; Schwenk and Macallan, 2000; del Rey et al., 2007). During such catabolic states, individuals use amino acids from their own body tissues to synthesize new proteins, resulting in an increase of $\delta^{15}N$ values (Beaumont et al., 2013; Beaumont and Montgomery, 2016; Katzenberg and Lovell, 1999). Tracing the onset of this "pathological trophic shift" will test the previous estimates of active TB duration in this individual, c. 2-3 years, based on skeletal gracilization and enamel hypoplasia (Formicola et al., 1987; Sparacello et al., 2016).

2. **Materials and methods**

We analyzed seven teeth from seven individuals unearthed from four nearby caves in the Finalese area (Arene Candide Cave, Arma dell'Aquila, Arma delle Anime, Arma dei Parmorari; Liguria region, northwestern Italy; Table 1 and Figure 1).

[Figure 1 about here]

We selected unworn teeth without taphonomic damage or pathological lesions (such as caries). We analyzed either the upper or lower first molar of all individuals, except for Arene Candide V, for which the only tooth suitable for sectioning was the upper canine (Table 1). However, it has been previously shown that results from canines and first molars are in broad agreement (Sandberg et al., 2014). The inability to use the same type of tooth for all the individuals is due to both the nature of the dental series (e.g. incomplete, damaged, or worn molars), and to administrative permits that rightfully limit the possibility of conducting destructive analyses of human remains from archaeological contexts. The methodology involved in this study destroys half of each selected tooth (see below), and we therefore minimized the impact on the Ligurian skeletal series by selecting isolated fragmentary maxillae/mandibles and one isolated tooth from disturbed contexts other than burials (Table 1). The partial destruction of the canine from the Arene Candide V burial was authorized given the potential information on TB in the Neolithic that it can provide. To minimize loss of future information, an impression of the crown of all teeth was completed using Coltène President's Jet Light Body Plus (polyvinylsiloxane). Specimens were scanned via micro-CT (using a General Electric vtome x s microtomograph hosted by UMS 3626 PLACAMAT and acquired by the LabEx LaScArBx and the Région Nouvelle-Aquitaine. Scanning conditions were 80kV and 150µA (with no filter), and numerous macro-photos were taken.

Direct AMS dating was performed on all remains in this study (except for Arma dell'Aquila RS3, which was dated in Mannino et al., 2018) to assess the broad chrono-cultural context of the remains (Sparacello et al., in press). The AMS dates obtained for the individuals extend through most of the Neolithic and Metal Ages noted in Liguria (Table 1). One individual is chronologically contemporaneous with the ICC Neolithic (Arma dell'Aquila RS3; Sparacello et al., 2018, 2019), two with the SMP Neolithic (Arene Candide V, and one juvenile from the scattered remains found in the zone G of Arene Candide cave), two chronologically overlap with the Copper Age at its tail end, one belongs to the Late Bronze Age, and one to the Iron Age of Liguria.

Each tooth was processed for incremental dentine analysis according Beaumont et al. protocol (Beaumont et al., 2013), and the collagen was extracted according to the laboratory standard protocols (e.g. Goude et al., 2018). A sagittal section of each tooth was performed with a IsoMet® precision saw in order to obtain two equal parts from the tip of a cusp to the tip of a root. Half of the tooth was preserved, and the other half was abraded with aluminum oxide by a sandblaster in order to remove the external surface of the enamel and the root. The clean sample was then demineralized in HCl (0.05M) at 4°C for several days and rinsed with distilled water after demineralization was completed. Transverse sections of dentine were realized with a sterilized scalpel, with a thickness of one millimeter when possible, or more when dentine was too fragile to allow for a thinner section (details are available in Supplementary Information Table S1). Each section was then cleaned in NaOH for 20°h to remove potential remaining contaminants, rinsed and solubilized in HCl (0.01M) at 100°C for 17h. Each solubilized microsection was frozen and freeze-dried for 24h. The collagen was then analyzed by EA-IRMS (Europa Scientific EA analyzer coupled to Europa Scientific 20-20 IRMS; IsoAnalytical Ltd, Crewe, UK). The quality control of each run was checked with in-house standard calibrated with IAEA standards; the measurement error of standards is 0.1‰ for CN and 0.2‰ for S. The preservation of collagen and reliability of isotopic data were controlled according to international recommendations: $C \geq 30\%$, $N \geq 10\%$ (Ambrose, 1993), C/N between 2.9 and 3.6 (DeNiro, 1985), S between 0.15 and 0.35, C/S between 300-900 and N/S between 100-300 (Nehlich and Richards, 2009).

Age at death was estimated from dental development and eruption, epiphyseal fusion, and diaphyseal length of long bones (AlQahatani et al., 2010; Boccone et al., 2010; Cardoso and Ríos, 2011; Schaefer et al., 2009). We calculated the approximate ages at which the development of dentine starts and ends in each human permanent tooth using the times of tooth formation described in the Queen Mary University of London (QMUL) London atlas (AlQahtani et al., 2010). This work allows estimates of the age of formation for different teeth even in cases where root formation is incomplete. In particular, when the tooth was still forming (e.g. Rc), the age corresponds to the point of formation reached at death; in cases where root formation was complete, the age corresponds to the age of formation of the apical end of the root (AlQahatani et al., 2010).

The method described in Beaumont and collaborators in 2013 (see also Beaumont and Montgomery, 2015) was used to determine the ages of the incremental dentine sections of each tooth. This method is based on the assumption that the dentine grows at a constant rate throughout different regions of a tooth (3-5µm per day, Dean et al., 1993; Dean and Scandrett, 1995; Hillson, 1996; Liversidge et al., 1993), although some studies showed variability in growth rate in the coronal and apical areas of the roots (Dean, 2009; Dean and Cole, 2013).

Before sectioning, we measured the dentine length of each tooth in order to scale the growth rate to its actual size. For each tooth, the dentine time development was divided by this length to obtain the growth time corresponding to 1 mm. These results were multiplied by the actual measurements of each single slice obtained from each tooth of the sample. In this way, we were able to take into account the variability in growth rate expected between individuals (Dean et al., 1993; Dean and Vesey, 2008; Liversidge et al., 1993). Further information about sections, age estimates and isotopic data of the individuals used for incremental dentine analysis are available in Supplementary Information Table S1.

In order to frame the incremental dentine results within the local population $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ baseline, we used a sample of adults from western Liguria, in part analyzed in previous studies (Le Bras-Goude et al., 2006; Goude et al., 2014; Mannino et al., 2018), and in part analyzed for this study. Details on the age, sex, absolute date, and chronocultural attribution of the adult sample are available in Supplementary Information Table S2.

2.1 Environmental correlates of bone and teeth stable isotope data

Carbon, nitrogen and sulphur isotope ratios ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) in bone and tooth collagen (organic matter) of archaeological populations are commonly applied to infer diet (relative protein intake), mobility (local vs. non-local) and more generally human behaviors through time (e.g. Drucker et al., 2018; Goude et al., 2018; Jovanovic et al., 2019). While bone biogeochemical composition provides general information covering the time of its formation and renewal (last years of life, depending on age and physiology; e.g. Szulc et al., 2000; Hedges et al., 2007), teeth, and more particularly sequential analysis of teeth, provide more detailed biogeochemical information regarding the moment of dentine formation (i.e. from prenatal to early adulthood; Alqahtani et al., 2010; Beaumont et al., 2013). Carbon and nitrogen isotope ratios differ in soil and plants according to different environmental parameters, as well as species and physiology (e.g. Farquhar e al., 1989; Amundson et al., 2003). Their specific composition is transferred through the trophic chain, with an increase of heavy isotopes leading to higher $\delta^{13}C$ and $\delta^{15}N$ ratios between consumers and their food resources (e.g. Bocherens and Drucker, 2003). This pattern is also valid between breastfed infants and mother's milk (see modern studies of de Luca et al., 2012; Herrscher et al., 2017). Carbon and nitrogen isotope ratios also discriminate between freshwater, marine, or terrestrial environments (eg. Schoeninger and DeNiro, 1984), and allow for palaeodietary and mobility reconstructions under conditions of well-established local isotopic baselines (see review for archaeological populations in Goude and Fontugne, 2016). Carbon isotope ratios also allow differentiation between consumers of C_3 (such as wheat, barley) and C_4 plants (such as millet), as C_4 plants exhibit high $\delta^{13}C$. Near the seashore, the identification of C_4 plants versus marine resource consumers can be accomplished by integrating $\delta^{15}N$ data (e.g. Varalli et al., 2015). Added to carbon and nitrogen, sulphur isotope ratios provide relevant information regarding environment, food resource consumption and provenience of individuals (Nehlich, 2015). Moreover, according to the geological terrain, this proxy can be more efficient in documenting mobility than strontium isotope ratios, for example (Goude et al., 2019). Measured in sequential tooth collagen, $\delta^{34}S$ would reflect fetal physiology, mother's milk composition (including diet; Battaglia and Regnault, 2001; Holm et al., 2017, and environment exploited by the mother) and different food consumption and/or mobility during weaning and childhood (Nehlich, 2015).

3. **Results**

Except for one section of a tooth (AQ_012; from ca. 2 to 5 years old), all dentine sections (n=85; from 3 to 18 sections per tooth) provided good collagen quality and reliable C and N stable isotope ratios. After sampling for C and N stable isotope ratios, the remaining collagen allowed for the S analysis of only 15 sections in 5 teeth (Supplementary Information Table S1).

Considering all dentine sections, the results for nitrogen isotope ratios ($\delta^{15}N$) range from 7.2 to 12.2‰ (Δ 5‰), for carbon isotope ratios ($\delta^{13}C$) range from -21.2 to -19.2‰ (Δ 2‰), and for sulphur isotope ratios ($\delta^{34}S$) range from -2.8 to 11.5‰ (Δ 8.7‰). Among sections within the same individual, the range of $\delta^{15}N$ varies from 4.6 to 1.7‰, the range of $\delta^{13}C$ varies from 0.4 to 1.1‰, and the range of $\delta^{34}S$ varies from 0.5 to 2.1‰. The isotopic variation is not correlated with the number of sections performed for each tooth (Pearson's r not significant), albeit the lowest variations recorded for the three isotopes were found in the ICC Neolithic individual Arma dell'Aquila RS3 (AQ 012; Table 1), for which only three sections could be analyzed (Supplementary Information Table S1).

Dentine profiles are displayed for the whole sample, by isotope studied, in Figures 1 ($\delta^{15}N$), 2 ($\delta^{13}C$), and 3 ($\delta^{34}S$). The profiles, by individual, of both $\delta^{15}N$ $\delta^{13}C$ are reported in Supplementary Information Figure 1.

The first microsections in our sample have an age midpoint spanning 1.2 and 2.6 years of age, depending on the individual (Figure 2, 3, 4 and Supplementary Information Figure 1). Although for some individuals the first section may have included dentine deposited during the first trimester, the earliest $\delta^{15}N$ value is probably influenced not only by breast milk, but also by food supplementation in all individuals. Nevertheless, for all individuals, the $\delta^{15}N$ of this first section is the highest ratio recorded (from 12.2 to 10.1‰), followed by a sharp decrease (except for one SMP individual, ACN 022, where the sharp decrease occurs after the second section, age midpoint 2.7 years: Figure 2, and

Supplementary Information Figure 1). The high δ^{15}N ratio of the first microsection indicates that animal protein, in this case breast milk, still had a significant contribution to infant subsistence.

From dentine of the values of exclusively breastfed individuals, it is possible to extrapolate the theoretical mothers' δ^{15}N ratio during pregnancy by using the most recent reference data of mother milk/nail from Herrscher and collaborators (Herrscher et al., 2017), which is ca. 2‰ lower compared to breastfed infant δ^{15}N. If we apply this correction to the first dentine microsection of the two SMP Neolithic individuals (δ^{15}N 11.9‰ and 11.6‰), theoretical mothers' δ^{15}N ratio should range between 9.9 and 9.6‰, i.e. above the values obtained from bone for the SMP adult females (n = 8; mean = 8.8‰; range 8.5-9.4‰; Supplementary Information Table S2), despite the fact that the first microsection probably does not reflect EBF alone. The ICC individual has a lowest δ^{15}N in the first section among Neolithic individuals, 10.4‰, but compatible with the 8.5‰ found in the only ICC adult female (Arma dell'Aquila 5; Supplementary Information Table S2).

Except for Parmorari 002 from the Late Bronze Age (with a δ^{15}N of 12.2‰), all individuals from the Metal Ages display a lower δ^{15}N in the first microsection than the SMP Neolithic individuals (between 10.8 and 10.1‰), despite having an earlier age estimate midpoint (Figure 2, and Supplementary Information Figure 1). Likewise, for all individuals except for Parmorari 002, the theoretical mothers' bone δ^{15}N obtained by subtracting 2‰ from the value of the first microsection falls within the range of adults' bone δ^{15}N (due to the commingled nature of the remains, it was not possible to select adult females alone. Copper Age δ^{15}N: n = 8; mean = 8.6‰; range = 6.8-9.7‰. Bronze Age δ^{15}N: n = 5; mean = 8.7‰; range = 7.9-9.0‰; Iron Age δ^{15}N: n = 2; mean = 7.6‰; range = 7.0-8.4‰; Supplementary Information Table S2). For Parmorari 002, a decrease of 3.2‰ would be necessary to reach the upper boundary of the bone δ^{15}N range in our Bronze Age sample.

After the first microsection, δ^{15}N profiles show a decrease, at least until the age of ca. 4 years old for all individuals, except for the ICC Neolithic individual, which shows a sharp increase in the third and last microsection. The decrease until the age of ca. 4 years old is steeper in the Metal Ages individuals when compared to the two SMP Neolithic individuals (Figure 2, and Supplementary Information Figure 1). After this age, the SMP and Metal Ages δ^{15}N profiles differ further: three individuals (ANI 002, Late Copper Age; PARM 002, Late Bronze Age; ANI 001, Iron Age) appear to reach a plateau, while one (PARM 003, Copper Age) shows an increase (Figure 2, and Supplementary Information Figure 1). On the other hand, the two SMP Neolithic individuals show an interruption in the δ^{15}N decrease until c. 5-6 years of age, followed by a further decrease until the age of ca. 6.5 years old (for ACN 022) and 9.5 years old (for Arene Candide V), when they plateau. Arene Candide V then shows a steady and accelerating increase in δ^{15}N in the last three microsections, beginning from c. 11.5 years of age until c. 14 years of age, i.e. close to the time of death estimated between 14 and 16 years of age.

[Figure 2 about here]

Carbon isotope ratio profiles intersect for most of the individuals along the dentine growth, except for the low $\delta^{13}C$ values of the Late Copper Age ANI 002, and for the final part of the section of the Iron Age ANI 001, which rises towards the high $\delta^{13}C$ values derived from bone tissue of this individual (Figure 3, and Supplementary Information Figure 1). The SMP individual Arene Candide V shows a more "sinusoidal" profile, briefly overlapping the low $\delta^{13}C$ values of ANI 002 around the age of c. 7 years old.

[Figure 3 about here]

The $\delta^{34}S$ dentine profiles delineate three groups, which appear to correspond to temporal trends (Figure 4). The highest $\delta^{34}S$ ratios are recorded for the ICC Neolithic (Arma dell'Aquila RS3) and the Copper Age (PARM 003) individuals (range from 10 to 11.5‰). The Late Copper Age sample (ANI 002) provides the lowest $\delta^{34}S$ ratios (-3.4 to -2.8‰). Finally, the Late Bronze Age (PARM 002) and Iron Age (ANI 001) samples show low ratios from 2 to 4.9‰.

[Figure 4 about here]

Discussion

Through isotopic analyses of incremental dentine, dietary changes in early childhood in a sample of prehistoric children from Liguria were identified. Results suggest divergent timing of BWPs, as well as dietary and mobility differences, between the Neolithic and the later Metal Ages individuals.

4.1 Reconstruction of weaning patterns and TB-induced wasting

Studies estimating the timing of the cessation of breast-feeding employing dentine profiles use the point at which $\delta^{15}N$ values cease to decline and reach a plateau (e.g. Eerkens et al., 2011; Beaumont et al., 2013; Sandberg et al., 2014; Scharlotta et al., 2018b). Based on this principle, most individuals in our sample, regardless of the chronology, show an interruption in the sharp decline of $\delta^{15}N$ values between the age of 3 and 4 years old (except for one ICC Neolithic individual, Arma dell'Aquila RS3, discussed below). However, between individuals from the SMP Neolithic and the Metal Ages there are differences in the nitrogen level and pattern within this age group. For the Metal Ages individuals, the inversion in $\delta^{15}N$ values is at the bottom of a "dip" below the average value appearing in adult bone, and is generally followed by a gradual increase. Sandberg et al. (2014) note this fairly consistent "dip" in $\delta^{15}N$ values during early childhood before reaching adult levels (see also Henderson et al., 2014). They suggest that a continuous decline in $\delta^{15}N$ beyond TBF may be related to relatively little fractionation of nitrogen due to dietary intake barely meeting the needs of growth (but not resulting in catabolism, see below; Fuller et al., 2005), possibly due to weaning foods of poor protein quality such as C_3-based gruels (Sandberg et al., 2014). The interaction between growth and nitrogen isotope discrimination is not completely understood, and may overestimate the timing of completion of weaning. Indeed, $\delta^{13}C$ values in early microsections, which are also associated with the weaning process (e.g. Sandberg et al., 2014), show a sharp decline between 0.5-1.2‰ between 1 and 2 years of age in two Metal ages individuals, and between 2 and 3 years of age in one. This signal may be related to protein derived from carbohydrate-rich weaning foods, such as vegetable gruels (Craig et al., 2009).

Conversely, for the two SMP Neolithic individuals, the point at which $\delta^{15}N$ ceases to decline sharply is above the mean value of adults, and is followed by a decline after a brief plateau. Elevated $\delta^{15}N$ levels followed by a gradual decrease have been attributed to ^{15}N-enriched weaning foods, such as different types of animal protein (Sandberg et al., 2014; Tsutaya and Yoneda, 2015). This appears consistent with the ^{13}C-enriched values shown in one SMP Neolithic child in the first two microsections (up to an age of almost 2 years), followed by a decline between 3 and 4 years. However, some authors suggest that elevated $\delta^{15}N$ levels could result from catabolism related to malnutrition (Sandberg et al., 2014; Beaumont and Montgomery, 2016). Thus, in the Ligurian Neolithic sample, it is possible that the weaning process corresponded to a period of intense metabolic stress. This may be related to a sudden and significant investment in immune defense by the child due to a high environmental infectious load, which is noted by the presence of several cases of osteoarticular TB (Canci et al., 1996; Formicola et al., 1987; Sparacello et al., 2017, 2018; see also Dori et al., 2019). This increased stress may have tipped the nitrogen balance towards negative values; a scenario consistent with the presence of linear enamel hypoplasia (Orellana-Gonzales et al., 2019), and faltering of postcranial development (Dori et al., 2019) after c. 2-3 years in the Ligurian Neolithic series. In addition, if animal milk was used introduced during weaning, it may have resulted in an increase in infant morbidity (gastrointestinal infections) and micronutrient deficiencies (reviews in Oliver et al., 2009; Claeys et al., 2013). One or more of these factors may have resulted in the $\delta^{15}N$ values detected.

The analysis of first molars and canines may provide information regarding the time span during which TBF might have occurred, through identification of peak dentine $\delta^{15}N$ and $\delta^{13}C$ values (which may be affected by rapid development during the first year of life; De Luca et al., 2012), but does not allow for a high-resolution investigation of the first year of life, when EBF might theoretically have ceased and weaning began (Beaumont et al., 2018). However, when considering the decrease in δ^{15}N between exclusively breast-fed infants and mother's adult tissues (around 2‰ based on a *in vivo* analysis of a mother-infant pair; Herrscher et al., 2017), we can infer that the δ^{15}N value in the first microsections in most individuals studied here were close to the peak. The two SMP Neolithic individuals would therefore show a smoother pattern with a later peak, possibly between 1.5-2 years of age, than Metal Age individuals, who mostly present a steeper δ^{15}N decline and estimated peaks between <1 and 1.5 years. This estimate is also supported by the few δ^{13}C data from early microsections.

In the scenario described above, the individual with the earliest age at death, between 4-6 years of age, Arma dell'Aquila RS3 from the ICC Neolithic, shows a different pattern. Its δ^{15}N profile between the first and second microsection resembles the ones of most Metal Ages individuals, but is then followed by a sharp increase in δ^{15}N coupled with no significant increase in δ^{13}C, suggesting intense metabolic stress (de Luca et al., 2012; Beaumont and Montgomery, 2016). We suggest that this individual experienced a different weaning process than the one apparent in SMP individuals, with an earlier cessation of EBF and TBF, perhaps using more vegetable-based weaning foods, possibly due to the unavailability of sufficient breast milk (eg. Moucheraud et al., 2015). This may have decreased the chances of surviving during later childhood, when Ligurian Neolithic children tend to show growth faltering, as recognized by patterns of postcranial development (Dori et al., 2019). A relationship between weaning age and survivorship has been noted in modern groups (e.g. Caulfield et al., 1999; Lindstrom and Bernau, 2000; Tenfelde et al., 2012) and suggested in bioarchaeological studies (e.g. King et al., 2005; Sandberg et al., 2014; Pearson et al., 2010), with extremes of premature or extended BWPs being correlated with high mortality. However, our small sample and its composition does not allow the determination of optimal weaning strategies for survivorship in the local ecology of Neolithic Liguria. The individual with the smoothest dentine profile in our sample, Arene Candide V, died at the age of c. 15 years, potentially due to osteoarticular tuberculosis, and displays evidence of growth faltering both in stature and long bone cortical development (Sparacello et al., 2016; Dori et al., 2019).

Looking closer at individual Arene Candide V, the reconstruction of the dentine profile displayed a sharp incremental change in δ^{15}N beginning around 11.5 years of age, and accelerating until the last microsection, around 14 years of age, i.e. close to the time of death. During the same period, the δ^{13}C profile displayed a net decrease (although composed by an increase followed by a drop in the last section). As mentioned above, divergent patterns in δ^{15}N and δ^{13}C profiles are interpreted as indicators of malnutrition (Sandberg et al., 2014; Beaumont and Montgomery, 2016). An isotopic signal of TB-induced ‘consumption’ was expected in this individual (Macallan, 1999; Schwenk and Macallan, 2000; del Rey et al., 2007), and its onset appears to be consistent with previous estimates of active TB duration, c. 2-3 years, based on skeletal gracilization and enamel hypoplasia (Formicola et al., 1987; Sparacello et al., 2016). This finding appears to confirm that by the SMP Neolithic period, TB had become a slow, chronic condition, characteristic of diseases with a long history of host-pathogen coevolution (Sparacello et al., 2016).

4.2 Neolithic vs Metal Ages subsistence patterns, adaptive strategies, and mobility

Despite the small sample size, this study highlighted a potential difference in weaning practices and diet during childhood between the SMP Neolithic and Metal Ages individuals, which may be important to understand evolving human adaptive strategies in later prehistory and protohistory. Obviously, grouping individuals under the label “Metal Ages” does not take into account the dramatic increase in socioeconomic complexity, urbanization, and demographic pressure that occurred from the Copper through the Iron Age (review in Bogucki and Crabtree, 2004; Cunliffe, 1994, 2008; Guidi, 2000). However, previous C and N isotopic analyses did not detect significant changes in diet until the beginning of the Iron Age in Liguria, when a significant consumption of C_4 plants were noted (Varalli et al., 2015). In the sample of adults used as a comparative baseline for child dentine profiles, the fact that all individuals were dated allowed for the detection of decreasing $\delta^{15}N$ ($r = 0.34$; $p< 0.05$), but especially $\delta^{13}C$ ($r=0.62$; $p<0.0001$ values, over time (up to the Iron Age, see below), which may be related to changing subsistence practices towards greater reliance on cultivated resources. In addition, the two Iron Age individuals display high $\delta^{13}C$ values, which are compatible with C_4 plants being a staple in the diet. This change in crop consumption parallels the introduction of new agricultural practices, which in northeastern Italy appear to arrive earlier, with the transition between the Early and Middle Bronze Age (Tafuri et al., 2009; Varalli et al., 2016a). Dentine profiles and bone isotopic composition values confirm that the Iron Age child in our sample may have consumed a significant proportion of C_4 plants from the age of c. 8 years (enriched $\delta^{13}C$ in later microsections and bone). However, they also suggest that significant dietary and life history changes had occurred already during the Copper Age, which shows a different pattern of weaning than SMP, especially at the end of the Copper Age, when the pattern of weaning appears similar to individuals from the Late Bronze and Iron Age. Intra-population variation in weaning strategies may be responsible for the differences observed (e.g. Howcroft, 2013; Howcroft et al., 2014), but the interpretation seems to be corroborated by the results obtained from the $\delta^{34}S$ dentine profiles.

Although the data on $\delta^{34}S$ dentine profiles are partial and could only be completed on a few individuals, three different temporal groups can be discerned. The ICC Neolithic and Copper Age individuals do not show substantial changes between c. 2.5-3.5 years, and show similar values that are consistent with data recorded in bone of individuals living close to the coast (Varalli et al., 2016b). The Late Copper Age individual displays values unique to the Mediterranean area, and more commonly found inland (Varalli et al., 2016b), sometimes in bone collagen of individuals consuming freshwater resources (Drucker et al., 2018). Finally, the Late Bronze Age and Iron Age children have a consistent $\delta^{34}S$ dentine profile from ca. 2 to 4 years old, indicating that they were living more inland (e.g. Drucker et al., 2018; Rey et al., in press.) than on the Ligurian coast. The Late Bronze Age individual shows an increase in $\delta^{34}S$ between ca. 1 and 2 years old, which could reflect mobility between different inland locations and/or a modification of food protein intake due to BWPs.

Results, therefore, suggest that changes in BWPs, inferred by $\delta^{15}N$ and $\delta^{13}C$ profiles, might be explained, in part, by the migration to Liguria of people from different residences, different subsistence strategies and crops, and different technologies for land exploitation. Particularly interesting is the difference between 1) the Copper Age individual, who shows a different weaning experience than SMP, but shares isotopic profiles with Neolithic individuals in later childhood, and 2) the Late Copper Age individual, who suggests a completely different diet ($\delta^{13}C$ values) and presumably provenience ($\delta^{34}S$ values). These trends may be associated with technological changes and increased migration linked to the diffusion of the Bell Beaker culture throughout Europe, which in Liguria, occurred in the second half of the third millennium BCE (Chiarenza, 2007; Chiarenza et al., 2012). A current project seeks to incorporate a larger sample size to untangle population mobility, diet and subsistence, and life history changes during the Metal Ages of Liguria (MetalLI project, JRF-Marie Curie COFUND, Durham University; PI AV).

4.3 Neolithic life history patterns, environmental correlates, limitations of the study, and conclusions

Although the precise timing of EBF and TBF is difficult to assess, this study has highlighted changes in BWPs accompanying subsistence changes between SMP Neolithic and the Metal Ages in Liguria. As expected, all the individuals analyzed here appear to have had shortened TBF when compared to the 3-5 years reported for hunter-gatherers, but SMP individuals show more gradual changes in isotopic ratios during growth. Overall, SMP BWPs appear to be at the later end of the variation displayed by early prehistoric agriculturalists (Cienkosz-Stepanczak et al., 2017; Fernández-Crespo et al., 2018; Howcroft, 2013; Howcroft et al., 2014; Pearson et al., 2010, 2015;

Scharlotta et al., 2018b) and modern non-industrial agriculturalists (Dettwyler, 2004; Kennedy, 2005; Marlowe, 2005; Sellen, 2001, 2006, 2007, 2009; Sellen and Smay, 2001). This may offer further evidence to inform the current debate on factors affecting female fertility among early agriculturalists (Bentley et al., 2001; Ellison, 2001; Page et al., 2016).

Population and individual variation in the timing of BWPs are considered to be the result of the cultural mediation of parental strategies to maximize the outcome of the “weanling dilemma”, i.e. the balancing between immunological protection and adequate nutrition (McDade and Worthman, 1998; Rowland et al., 1978; Waterlow, 1981), without affecting reproductive fitness within a specific local ecology. Delayed BWPs are more common in marginal environments, where appropriate weaning food resources are scarce, when growth is perceived as unsatisfactory, and when mothers maximize immunological protection in the presence of high pathogen loads (McDade and Worthman, 1998; Sellen, 2001b, 2007; Cantrelle and Leridon, 1971; Lindstrom and Berhanu, 2000). All motivations, especially the latter, may be appropriate for the SMP Neolithic of Liguria, which appears to have had a high frequency of tuberculosis. However, it should be noted that no individual studied here reached adulthood, and one SMP individual actually died with active osteoarticular TB, which affected growth and metabolism for at least two years, as reconstructed from $\delta^{15}N$ profiles. It is therefore possible that, instead of reconstructing living population life-history parameters and optimal BWPs in the Ligurian Neolithic local ecology, our sample depicts the pattern of stress observed when unsuccessful, suboptimal strategies were applied, leading to later susceptibility to environmental hardships and low survivorship. The negative relationship between longer weaning and EBF timing and later survivorship has been explored in medieval Nubia, where survivors were weaned earlier than non-survivors (Sandberg et al., 2014). In the Neolithic of Turkey (9th-8th millennium cal BC), mortality rates after 24 months are significantly higher at Çayönü Tepesi, where isotopic evidence suggests that EBF was discontinued at about 2 years, compared to Aşikli Höyük where food supplementation commenced at 1 year of age (Pearson et al., 2010).

The problem with inferring life history parameters and health of the living population from skeletal assemblages of non-survivors is a well-known issue in bioarchaeology (i.e. the “osteological paradox”; DeWitte and Stojanowski, 2015; Wood et al., 1992; Wright and Yoder, 2003). Unfortunately, this problem is unavoidable when using the incremental dentine methodology on teeth coming from a context with intense dental wear, such as the Neolithic. Another problem with the methodology used here is the necessity to compare bone and dentine isotopic ratios to make inferences about trophic shifts. Bone growth is less canalized than dental growth and possibly fails to record isotopic levels during periods of stress (Beaumont et al., 2018). In addition, isotopic fractionation and collagen turnover in bone are complex processes that have not been completely understood yet (e.g. Szulc et al., 2000; Sandberg et al., 2014; Herrscher et al., 2017; Matsubayashi and Tayasu, 2019). More research is necessary to understand whether these limitations may have influenced the interpretations made here. In addition, parental strategies and BWPs are heavily influenced by cultural factors (e.g. Sellen, 2001a, b), which are difficult to untangle in a bioarchaeological context. Thanks to recent development in the amelogenin test from enamel (Stewart et al., 2017), future research will explore nutritional differences and BWPs of prehistoric children based on sex (Fernandez-Crespo et al., 2018).

Finally, this paper presents, to our knowledge, the first δ^{34}S dentine profiles. Although results are currently incomplete, the data obtained integrated dietary/weaning reconstructions and highlighted possible differences in migration in the Neolithic and the Metal ages, which may be a consequence of changing landscape exploitation during prehistoric times. Future technical improvements, such as the new generation of EA-IRMS (EA IsoLink™ IRMS System ThermoFischer Scientific), will further lead to promising discoveries due to the decreased amount of collagen necessary for analysis.

Acknowledgements

The authors would like to thank the Soprintendenza Archeologia, Belle Arti e Paesaggio per la città metropolitana di Genova e le provincie di Imperia, La Spezia e Savona, for granting access to skeletal collections, especially the Superintendent Vincenzo Tiné and the Officers Marta Conventi, Stefano Costa, and Nico Radi. We are grateful to the directors, curators, and staff of the museums where the skeletal collections are preserved, for continuous assistance during the data collection: Daniele Arobba, and Andrea De Pascale (Museo Archeologico del Finale, Finale Ligure), Patrizia Garibaldi, Guido Rossi, Irene Molinari (Museo di Archeologia Ligure, Genova), and Monica Zavattaro (Museo di Storia Naturale – Sezione di Antropologia e Etnologia, Università degli Studi di Firenze). Thanks to Chiara Panelli, Stefano Rossi, Roberto Maggi, Vincenzo Formicola, Paolo Biagi, Giovanni Murialdo, Elisa Bianchi, Simona Mordeglia, Giuseppe “Cisque” Vicino, Maria Tagliafico, Elisa Bianchi, Simona Mordeglia, Walter Siciliano, Jacopo Moggi, Giovanna Stefania, Luca Bachechi, Chiara Bullo, and Brunetto Chiarelli for their invaluable help during the data collection, and for their scientific input. Thanks to the Editor of this journal and to the reviewers for the comments that improved the earlier version of this paper.

The AMS dates performed at “Centre de Datation par le RadioCarbone, UMR 5138 “Archéométrie et Archéologie", Lyon” benefitted from the support of the program “ARTEMIS”. We are grateful to

Sanne Palstra and all the staff of the Centre for Isotope Research (CIO), University of Groningen, for continuous assistance during the analysis.

The project BUR.P.P.H: Burial practices at the Pleistocene - Holocene transition: the changing role of pathology, violence, and “exceptional events” (PI: VSS) has received financial support from the French State in the framework of the “Investments for the future” Program, IdEx Bordeaux, reference ANR-10-IDEX-03-02. The project DEN.P.H.: Dental anthropology at the Pleistocene-Holocene transition – insights on lifestyle and funerary behaviour from Neolithic Liguria (Italy) (PI: ID) is funded by the European Union’s Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 752626. ES is co-funded by PRA 2018-Università di Pisa, "Paesaggi funerari tra rito e società. Nuovi approcci allo studio delle necropoli nel mondo antico".

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Figure 1 – Geographical location of the sites included in this study. Top: the Finalese area within the Liguria region in northwestern Italy. Bottom: the sites in the municipality of Finale Ligure: 1) Arene Candide Cave; 2) Arma dei Parmorari; 3) Arma delle Anime; 4) Arma dell'Aquila.

Figure 2: Nitrogen stable isotope ratio profile of dentine microsections for all individuals. Bone values for each individual are indicated when present. Adult variability is provided by period.

Figure 3: Carbon stable isotope ratio profile of dentine microsections for all individuals. Bone values for each individual are indicated when present. Adult variability is provided by period.

Figure 4: Sulfur stable isotope ratio profile of dentine microsections for all individuals. Bone values for each individual are indicated when present. Adult variability is provided by period.


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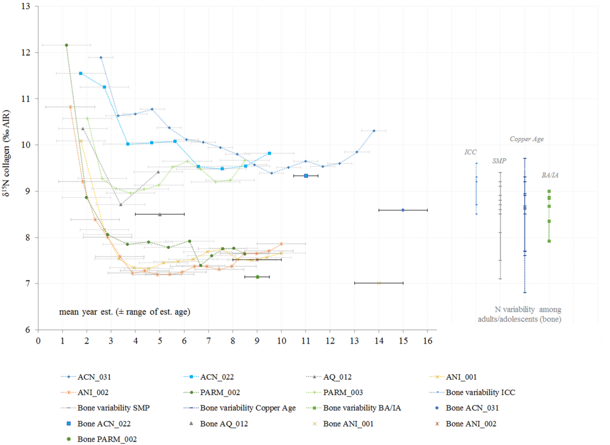
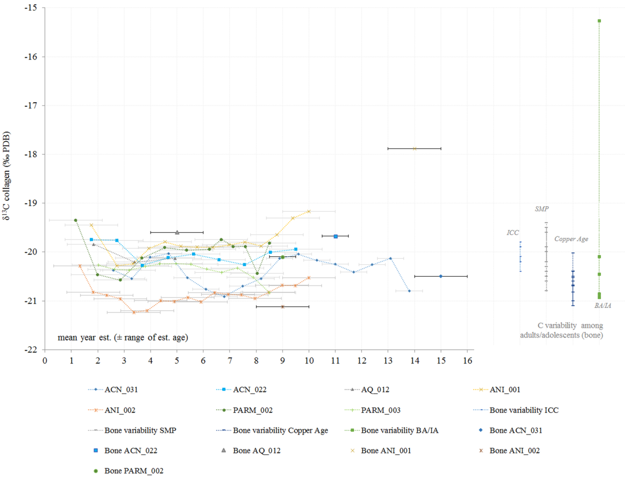
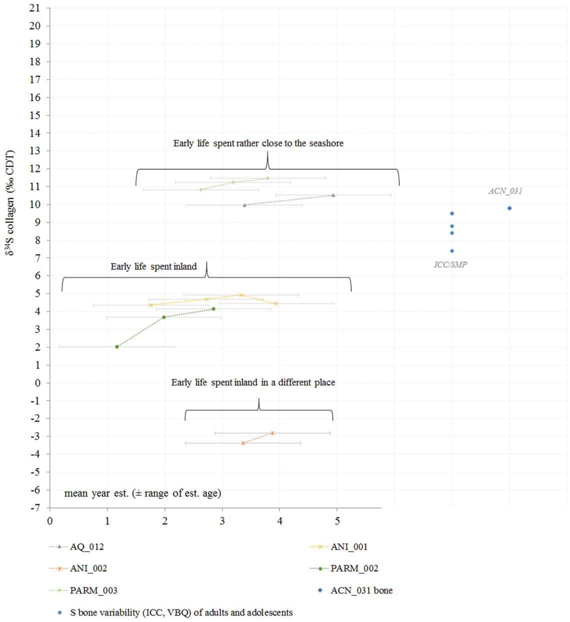
2
1
FINALE LIGURE
0 Km 1


δ15N collagen (‰ AIR)
13
12
11
10
9
8
7
6
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
mean year est. (± range of est. age)
ICC
SMP
Copper Age
BA/IA
N variability among adults/adolescents (bone)
ACN_031
ACN_022
AQ_012
ANI_001
ANI_002
PARM_002
PARM_003
Bone variability ICC
Bone variability SMP
Bone variability Copper Age
Bone variability BA/IA
Bone ACN_031
Bone ACN_022
Bone AQ_012
Bone ANI_001
Bone ANI_002
Bone PARM_002


-15
-16
-17
-18
-19
-20
-21
-22
δ13C collagen (‰ PDB)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
mean year est. (± range of est. age)
ICC
SMP
Copper Age
BA/IA
C variability among adults/adolescents (bone)
ACN_031
ACN_022
AQ_012
ANI_001
ANI_002
PARM_002
PARM_003
Bone variability ICC
Bone variability SMP
Bone variability Copper Age
Bone variability BA/IA
Bone ACN_031
Bone ACN_022
Bone AQ_012
Bone ANI_001
Bone ANI_002
Bone PARM_002


δ^{34}S collagen (‰ CDT)
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
-1
-2
-3
-4
-5
-6
-7
0
1
2
3
4
5
Early life spent rather close to the seashore
Early life spent inland
Early life spent inland in a different place
ACN_031
ICC/SMP
mean year est. (± range of est. age)
AQ_012
ANI_001
ANI_002
PARM_002
PARM_003
ACN_031 bone
S bone variability (ICC, VBQ) of adults and adolescents

BUR.DEN. ID	*Specimen identification*	*Age at death (years)*	*Sex*	*Tooth type*[1]	*Stage of tooth Development*[2]	*Cal BCE 95.4%*[3]	*Lab code*[3]	*Period*[3]
AQ 012	Arma dell'Aquila RS3 C13	*4-6*	undet.	URM1	R ¼	5644-5528	OxA-2365-50	ICC Neolithic
ACN 031	Arene Candide V BB	*14-16*	M?	ULC	complete	4720-4557	GrM-14528	SMP Neolithic
ACN 022	Arene Candide BB RS Zone G 13°T = 22	*11-12*	undet.	URM1	complete	4847-4715	Lyon-14586	SMP Neolithic
PARM 003	Parmorari RS Richard 1931-32 tooth	*8.5-9.5*	undet.	URM1	A 1/2	2620-2475	GrM-15945	Copper Age
ANI 002	Arma delle Anime RS Giuggiola C4 1657	*8.5-10.5*	undet.	LLM1	Rc	2467-2236	Lyon-14598	Copper Age
PARM 002	Parmorari RS Richard maxill. fragm.	8.5-9.5	undet.	ULM1	Rc	1397-1211	Lyon-14602	Bronze Age
ANI 001	Arma delle Anime RS Giuggiola A	*13-15*	undet.	LLM1	complete	776-488	Lyon-14597	Iron Age

Table 1 – Individuals analyzed in this study. Teeth legend: I: incisor; P: premolar; M: molar; U: upper; L: lower; R: right; L: left; [2] AlQahatani et al., 2010; [3] Individual ID, name of the specimen, ^{14}C date, and chrono-cultural attribution determined in Sparacello et al (in review).

Supplementary material related to this article can be found, in the online version, at doi: https://doi.org/10.1016/j.ijpp.2019.12.007.