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Research article

Insights on patterns of developmental disturbances from the analysis of linear enamel hypoplasia in a Neolithic sample from Liguria (northwestern Italy)

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ABSTRACT

Objective: To assess developmental disturbances through the analysis of linear enamel hypoplasia (LEH) frequency and to infer environmental stress and life history within Neolithic communities from Liguria (Italy).
Materials: 43 unworn/minimally worn permanent anterior teeth of 13 individuals recovered from nearby caves and dated to c. 4800 – 4400 cal. BCE.
Methods: LEH defects were identified with high-resolution macrophotos of dental replicas, age at LEH was calculated via perikymata counts. LEH defects matched between two or more teeth were considered as systemic disturbances. LEH frequency by age classes was analyzed via GLZ and Friedman ANOVA.
Results: Number of matched defects per individual range between 2–12. The mean LEH per individual was highest in the 2.5–2.99 age category, with a significant increase relative to earlier growth stages, followed by a decline.
Conclusion: LEH may reflect life-history in the local ecology of Neolithic Liguria, where several individuals with osteoarticular tuberculosis have been recorded. Disease burden may have triggered developmental disturbances around the time of weaning. Age at first defect was negatively correlated with age at death and positively with the total number of defects, suggesting that early stress may have affected survivorship.
Significance: The study contributes to the reconstruction of ecological pressures among Neolithic people of Liguria, and informs on environmental challenges during the Neolithic adaptive expansion.
Limitations: The visual examination of macrophotos is prone to observer error; mid-crown tends to display more visible LEH due to tooth architecture.
Suggestions for further research: Apply different quantitative methods to examine severity and duration of disturbances.

1. Introduction

The Neolithic Transition – i.e. the adoption of a food production economy based on the domestication of plants and animals – had a major impact on human diet, health, and demographic patterns (Bocquet-Appel, 2011; Larsen, 1995; Pinhasi and Stock, 2011). Numerous studies suggest that the adoption of Neolithic way of life was accompanied by worsening health status, resulting in an increase of osteological markers of growth disturbances (Armelagos et al., 2005; Cohen and Armelagos, 1984; Cohen and Crane-Kramer, 2007; Larsen, 1995). Mortality rates increased, especially in infants (Bocquet-Appel, 2011; Page et al., 2016; Pérez-Losada and Fort, 2010), which often has been attributed to a higher infectious load among sedentary groups (Armelagos et al., 1991, 1996, 2005). Despite increased mortality rates, an increase in human population size has been suggested (Bellwood and Oxenham, 2008; Bocquet-Appel, 2011; Bocquet-Appel and Naji, 2006; Shennan et al., 2013), which offer complex scenarios that move beyond the description of a “demographic explosion” (van Andel and Runnels,

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1995; Willis and Bennett, 1994).

It has been proposed that demographic growth was mainly a consequence of an increased female fertility in sedentary populations compared to hunter-gatherers (Bocquet-Appel, 2011; Lukacs, 2008; Page et al., 2016) due to a shortening of the interval between pregnancies allowed by earlier weaning (Armelagos et al., 1991; Buikstra et al., 1986; Ellison, 2001: 293–294). The paradox between the Neolithic demographic expansion on one hand, and increased mortality and a decrease in health status on the other, could therefore be reconciled by a quality-quantity trade-off, whereby diverting energy from lactation would have enhanced future reproductive fitness, but exposed children to higher risks (Page et al., 2016). In fact, maternal milk provides passive immunity, and expediting weaning may have negative effects on health, development, and survivorship of infants (e.g. King et al., 2005; Lauer et al., 2007; Moggi-Cecchi et al., 1994; Pearson et al., 2010). The extent of these negative effects depends on the local physical and social ecology (e.g. infectious load, choice of weaning foods), which can lead to increased pathogen exposure and to investment into immune defense at the cost of growth (McDade, 2001; McDade and Worthmann, 1998; McDade et al., 2008; Sandberg et al., 2014). Reconstructing patterns of developmental disturbances in bioarchaeological samples during this critical developmental period, occurring between 1 to c. 5 years old, depending on the population (indeed, mortality between 1–5 years is a parameter to evaluate the environmental conditions of developing countries; in general, between 5–14 years of age there is a substantial drop in mortality; WHO, 2016), may therefore shed light on past environmental challenges and life-history traits.

Developmental disturbances in bioarchaeological samples can be best assessed through the analysis developing dental tissues. Although dental size seems to be strongly canalized, and therefore minimally influenced by environmental factors (Garn et al., 1965; Lewis and Garn, 1960; Tonge and McCance, 1973), these factors can result in growth disruptions, recorded as defects in the enamel of the crown (Hillson, 2014: 41). Enamel hypoplastic defects are the result of disturbances during the secretory phase of enamel formation (amelogenesis) (Goodman and Rose, 1990; Skinner and Goodman, 1992; Ten Cate, 1994). Defects can be divided into three types: furrow-form, pit-form and plane-form (Hillson, 2014: 89). Furrow-form defects, also called linear enamel hypoplasia (LEH), are horizontal bands of reduced enamel along the circumference of a tooth crown. They can be identified by an irregular spacing of perikymata, which are microscopic structures in the enamel visible at the crown surface (Hillson and Bond, 1997). Due to the incremental nature of perikymata, the chronology of enamel defects can be reconstructed with great precision (Hillson, 2014). When the time of appearance of a LEH defect is matched between two or more teeth with overlapping developmental schedules, the defect can be attributed to systemic disturbances, as opposed to local inflammation or trauma (Hillson, 1992a; King et al., 2002, 2005; Malville, 1997; Suckling, 1989).

Enamel hypoplasia represents a non-specific indicator of developmental disturbances because the causes of its occurrence may be multiple, including nutritional deficiencies and avitaminosis, congenital disorders, diseases, and metabolic disturbances (e.g. Cutress and Suckling, 1982; Goodman and Armelagos, 1985a; Suckling, 1989; Goodman and Rose, 1990, 1991; Pindborg, 1982; Sheetal et al., 2013). However, the frequency of LEH has been studied in conjunction with specific events, such as infection, parasitism, malnutrition and diet supplementation in both animals, primates, and humans (Goodman et al., 1991; Guatelli-Steinberg and Benderlioglu, 2006; May et al., 1993; Sarnat and Schour, 1941; Suckling et al., 1986; Sweeney et al., 1971). Several studies have explored the relationship between life history events, such as weaning and the development of enamel defects (e.g. Bonfiglioli et al., 2003; Corruccini et al., 1985; Goodman et al., 1984; Jacobi et al., 1992; Lanphear, 1990; Moggi-Cecchi et al., 1994; Wright, 1997), also evidenced in primates (Dirks et al., 2010) and modern children (Goodman et al., 1987, 1992; May et al., 1993; but see Blakey et al., 1994; Wood, 1996). As a result, LEH defects are considered the most reliable markers of growth disturbance in bioarchaeological research, and have been associated with the negative effects of inadequate diet, social organization, colonization, and socioeconomic inequalities (e.g. Armelagos et al., 2009; Boldsen, 2007; Cucina and Işcan, 1997; Goodman et al., 1980; review in Larsen, 2003; review in Hillson, 2014; Temple, 2014).

The purpose of this study is to investigate patterns in growth disturbances between the age of 1 and 5 years, and their possible environmental correlates, in a sample of children belonging to the Neolithic Square Mouthed Pottery Culture (SMP) of the Finalese area (western Liguria, Italy, c. 5000-4300 BCE). The spread of the Neolithic lifestyle throughout the European continent is characterized by a mosaic pattern of expansion and crisis, and therefore needs to be explored through a regional approach (Bocquet-Appel et al., 2009; Clare et al., 2008; Cohen and Crane-Kramer, 2007; Meyer et al., 2015; Pinhasi and Stock, 2011; Zvelebil, 2001). The narrow geographic and temporal foci of this study allow for a chrono-culturally and spatially homogeneous sample within a well-studied environmental and archaeological context (see below), which is fundamental to characterize past life-history, micro-evolutionary adaptations, and environmental challenges.

1.1. Archaeological background and research expectations

The western diffusion of the Neolithic food production complex from the Near East reached the northwestern Mediterranean around 5800-5600 BCE, when people belonging to the Impresso-Cardial chrono-cultural complex were settled in the Ligurian-Provençal Arc (Binder et al., 2017). The Square Mouthed Pottery culture (SMP) developed later and spread into Liguria and in Northern Italy during the fifth millennium BCE (c. 5000-4300 BCE) (Binder and Sénépart, 2010; Del Lucchese and Starnini, 2015). Evidence of SMP occupation in Liguria comes predominantly from several caves and rock shelters opening in the karstic complexes of western Liguria, especially in the Finalese area, where important sites such as Arene Candide have yielded detailed stratigraphic successions (Arobba et al., 2017; Maggi, 1997; Tinè, 1999). Many of these sites have been excavated since the mid-19th century (De Pascale, 2007, 2008; Issel, 1908; Rossi et al., 2014), and over the decades, about 200 burials and an undefined number of scattered human remains have been reported (e.g. Del Lucchese, 1997; Delfino, 1981; Issel, 1908; Panelli and Rossi, 2015, 2017; Parenti and Messeri, 1962; Richard, 1942; Sparacello et al., 2018).

Several bioarchaeological studies conducted on Ligurian cave assemblages provide a general picture of life during the Neolithic in this region. 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, 1997, 1998). Isotopic analysis ($\delta^{13}C$/ $\delta^{15}N$ ratios) supports the scenario of a diet based on cereals, with a significant component of proteins derived from terrestrial animals (Le Bras-Goude et al., 2006; Goude et al., 2014). Environmental factors possibly played a role in the emphasis on pastoral activities, inferred from the bioarchaeological data. Liguria is a highly mountainous region, and at the time was covered by a thick forest, particularly of holm oak groves (Castelletti and Castiglioni, 1999), which did not leave much space for pastures or agriculture. Indeed, it has been hypothesized that pollarding (i.e. recurrently cropping branches) of trees represented an alternative strategy to provide an additional source of animal fodder (Maggi and Nisbet, 2000). Biomechanical analyses suggest a high level of terrestrial mobility, especially in males, while females practiced stressful activities with both arms, possibly related to cereal grinding (Marchi et al., 2006, 2011; Sparacello and Marchi, 2008; Sparacello et al., 2011, 2014). This agropastoral lifestyle, in a land with low productivity, probably required a high labor input, as corroborated by the high diaphyseal mechanical robusticity observed in this group (Marchi et al., 2006, 2011; Sparacello and Marchi, 2008; see also Macintosh et al., 2017).

Ligurian Neolithic people display a reduction in stature compared to earlier hunter-gatherers settled in the same area (Formicola, 1983, 1997), have a high frequency of enamel hypoplasia (Formicola, 1986, 1987), and as seen in many early agriculturalist groups, are affected by dental caries (Formicola, 1987; Sparacello et al., 2018). Unsanitary conditions and a high pathogen load for the SMP skeletal series in the Finalese are inferred from the presence of several individuals with lesions compatible with osteoarticular tuberculosis, both adults and juveniles (Canci et al., 1996; Dori et al., 2019; Formicola et al., 1987; Sparacello et al., 2017, 2018). Tuberculosis is a highly infectious, debilitating, and growth-impairing disease (Sparacello et al., 2016), which manifests in the skeleton in a small fraction of affected individuals (estimates ranging from 1 % to 3–5 %; Turgut, 2001; Vigorita, 1999). This suggests that the prevalence of this disease among Neolithic people in Liguria may have been high.

In such contexts, exposure to pathogens would come at the cost of growth in developing individuals (McDade, 2003). Indeed, Ligurian Neolithic children appear to experience postcranial growth faltering by the age of four, while prior to the age of three they appear to grow similarly to modern, well-nourished children (Dori et al., 2019). This is possibly due to the termination of breast milk supplementation and therefore passive immunity in the third year of life, as reconstructed in two individuals through isotopic analysis (Goude et al., 2019). We expect these developmental disturbances to manifest with similar timing in developing enamel crowns, given their sensitivity to environmental factors (Hillson, 2014).

2. Materials and methods

2.1. The study sample

Table 1 provides the sample composition, which consists of 43 permanent teeth from the dentitions of 13 individuals. All individuals were buried in three caves located within a radius of 5 km from each other in the Finalese area: Arene Candide, Pollera, and Boragni/Strapatente (Fig. 1). All individuals have been directly dated via AMS to the second quarter of the fifth millennium BC (Table 1; Sparacello et al., 2019) except for Boragni/Strapatente 1 that belongs to the third quarter of the same millennium. At that time, the Neolithic Square Mouthed Pottery culture was attested in Liguria (Maggi, 1997).

We selected anterior teeth that overlap in their developmental schedules from approximately 1 year to 5 years of age: first and second incisors, and canines from upper and lower jaws. Compared to the posterior dentition, the morphology of anterior teeth allows for a better observation of the perikymata (Hillson and Bond, 1997). Since LEH observation is affected by occlusal and buccal wear (King et al., 2002), only individuals with a good state of preservation of their permanent anterior teeth, either mandibular or maxillary, were included. This means teeth without taphonomic or abrasion damage, with a maximum degree of wear of "3″ on Molnar's scale (1971), and with more than 80 % of their crown height preserved (as per Guatelli-Steinberg et al., 2018). The resulting sample is composed of subadults and one late adolescent, which is the only individual for which sex could be determined (Bruzek, 2002; Ferembach et al., 1980) (Table 1). Age at death was estimated from dental development and eruption, epiphyseal fusion, and diaphyseal length of long bones (AlQahtani et al., 2010; Boccone et al., 2010; Cardoso and Ríos, 2011; Owings-Webb and Suchey, 1985; Ríos and Cardoso, 2009). Although the sample size is small, most of the extant Neolithic skeletal collection from Liguria was surveyed, and these are the only remains that fully satisfy the conditions for the study (including direct dating).

2.2. Imaging

Impressions of anterior teeth crowns were produced by applying Coltène President's Jet Light Body Plus (polyvinylsiloxane) after cleaning the surfaces with acetone (100 %). Positive casts were made using Epotek 301, an epoxy resin mixed with the hardener in a proportion of 4:1 (e.g. Hillson, 1992b). Two drops of Epotek 11 Blue were added to the mixture so that the replica would be blue, instead of clear (e.g. Jernvall and Selänne, 1999). The resulting replicas have more opaque and less reflective surfaces compared to teeth, which allow for easier visualization of the perikymata and higher quality pictures.

Dental replicas were digitized with macrophotography using the motorized Leica™ Macroscope Z16 APO coupled with a Canon EOS 600D 18 Megapixel digital camera. The macroscope is characterized by a fully apochromatic zoom system for high contrast and high resolution, which are ideal for detailed analyses of 2D images. For the image capture, the casts were positioned with the axis of their labial surface perpendicular to the axis of the macroscope, and teeth surfaces were recorded with a Y tube of 1.25x, a 16:1 zoom, and the zoom factor set to 0.57 × . Images were optimized for exposure, contrast and brightness to better highlight perikymata, and imported and measured in ImageJ v1.52e.

For two teeth (URI1 - Arene Candide 6621.1, and ULI1 - Arene Candide 1 Tin.) presenting a degree of wear of "3″ on their occlusal edges (Molnar, 1971), the crown height was reconstructed using Adobe Photoshop™ CC 2015 following Saunders et al. (2007) and O'Hara (2016; see also Guatelli-Steinberg et al., 2018). The reconstruction involved only a small portion of the crown height (cusp tip) to the first decile; the reconstructions count as a "missing observation" for these individuals and deciles, and do not affect the sample statistics for the counts of LEH by age, except for sample size.

2.3. Identification of LEH and reconstruction of defect chronology

The identification of LEH was performed on casts and macrophotos following Skinner et al. (1995); Guatelli-Steinberg (2003) and Temple et al. (2012), where the lower limits of observable defects were lines or grooves across the circumference of the crown that appeared accentuated compared to adjacent perikymata under magnification (for example, defect A in Fig. 2). The defects may vary in width and depth, ranging from slight variation in the prominence of individual perikymata to furrows of varying depth and width that are visible without magnification (for example, defect B in Fig. 2). Multiple macrophotos taken with different light orientation (see Section 2.5) and observation on the casts themselves with the naked eye and under magnification up to 10x allowed for a better identification of LEH defects. As apparent from Fig. 2, the identified LEH would be readily visible by examining the cast under magnification; the high-resolution image provided by macrophotos is in turn fundamental to position the defect (yellow dots in Fig. 2) and counting perikymata. This study was based on visual identification of the LEH defects; perikymata depth and spacing were not quantified.

The reconstruction of LEH chronology was based on the location of the defects on the labial surface within established deciles of crown height, which are characterized by non-linear and tooth-specific development schedules (Reid and Dean, 2000). Each surface was divided into deciles (based on the crown height), and all defects were marked using consecutive letters (Fig. 2). In order to estimate an exact chronology, in days and years, the numbers of perikymata included in each decile were counted on the macrophotos. The timing of LEH defects was calculated by applying the equation published by Temple and collaborators: $D_{dt} = \{(AD_i{*}365) + (N_{pkg}{*}8)\} / 365$[1] (Temple et al., 2012, p.

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[1] *Ddt*: age at defect formation; *ADi*: age of individual (in years) before the LEH defect, calculated from the age of formation of the most recent decile above the

Table 1
The sample of individuals included in this study.

Site	Inventory number	Museum[a]	Sex	Age at death (years)	Dating Lab code	AMS 14C date (cal. BCE 2σ)[b]	Tooth type[c]	N. of teeth
Arene Candide	6621.1	MSNF Florence	n.d.	15-17	GrM-13684	4726–4557	URI1, ULI2	2
Arene Candide	6627.1	MSNF Florence	n.d.	6-8	GrM-13420	4690–4544	LLI1, LRI2, LLI2, LLC, URI1, ULI1, ULC	7
Arene Candide	1 Tin.	MAF Finale Ligure	M	18-20	Beta 109802	4704–4374	ULI1, ULC	2
Arene Candide	3 Tiné	MAF Finale Ligure	n.d.	8-9	Beta 109801	4782–4502	LLI1, LLI2, URI1, ULI2	4
Arene Candide	BB T11-S22 G1	MAF Finale Ligure	n.d.	11-12	Lyon-14587	4836–4709	URC, ULC	2
Arene Candide	V BB	MAF Finale Ligure	n.d.	c. 15	GrM-14528	4720–4557	LRC, ULI2, URI1, URC	4
Pollera	6687.1	MSNF Florence	n.d.	7-8	GrM-13501	4792–4620	LRI1, LLI2	2
Pollera	6683.1	MSNF Florence	n.d.	c. 12	GrM-13507[d]	4722–4558	LRI1, LRI2, LRC	3
Pollera	6682.1	MSNF Florence	n.d.	6-8	GrM-13506	4707–4555	LRI1, LRI2, LLC, URI1, ULI2, URC	6
Pollera	1	MAL Genova	n.d.	10-12	GrM-13669	4785–4616	LLC, ULI2, URC	3
Pollera	20	MAL Genova	n.d.	6-8	GrM-14514	4715–4556	LRI1, ULI1	2
Pollera	34	MAL Genova	n.d.	13-16	GrM-14515	4723–4558	LLC, URC	2
Boragni/Strapatente	1	MAF Finale Ligure	n.d.	6-8	Lyon-14607	4531–4369	LRI1, LRI2, ULI1, ULI2	4
							Total N. of teeth	43

[a] MSNF: Museo di Storia Naturale – Sezione di Antropologia e Etnologia, Università degli Studi di Firenze; MAF: Museo Archeologico del Finale; MAL: Museo di Archeologia Ligure.

[b] Calibrated using OxCal 4.3.

[c] I: incisor; C: canine; U: upper; L: lower.

[d] Radiocarbon date refers to Pollera n° 6684.1 of the catalogue of the MSNF, which has been attributed to the same individual as 6683.1 (Burial n° 9 excavations Rossi 1885–1892).

1636). However, we modified the constant from "8" to "9", which represents the modal values of days for perikymata formation in human populations when the anterior teeth are pooled together (see Reid and Dean, 2006). Several studies (Goodman and Song, 1999; Hillson and Bond, 1997; King et al., 2002, 2005; Reid and Dean, 2000; Ritzman et al., 2008; Temple et al., 2012) demonstrated that this approach provides more accurate results in comparison with distance-based methods (e.g. Goodman et al., 1980; Goodman and Rose, 1990, 1991; Swärstedt, 1966), which assume constant times of enamel apposition in different regions of the crown. In addition, the distance-based methods do not consider the imbrication of the enamel and the crown initiation times (Goodman and Rose, 1990; for a review see King et al., 2002, 2005; Goodman and Song, 1999; Ritzman et al., 2008; Skinner and Goodman, 1992). Only LEH defects matching in at least two teeth in the same individual were considered as systemic growth disruptions (Reid and Dean, 2000). Defects were matched among different tooth types (upper vs lower, first vs second incisor, or incisor vs canine) for all individuals except for one, which had only antimere canines available. Table 1 provides a detailed overview of which teeth were used for each individual.

2.4. Intra- and inter-observer error

The visual assessment of LEH defects, even with magnification allowing for a better evaluation of perikymata spacing, involves a certain degree of subjectivity when not using measurement-based methods (Bocaege and Hillson, 2016; Bocaege et al., 2010; Danforth et al., 1993; Hassett, 2014; McGrath et al., 2018). Additional error between observations and observers can be expected during the matching of LEH among teeth, due to the necessity of identifying and counting each perikymata. Using the same dental replicas, two observers (ID and EOG) performed the observation of LEH defects and chronological matching twice, spacing the observations by a few weeks. Following Guatelli-Steinberg (2003), Cohen's Kappa Statistics were calculated on the number of matched LEH per individual, transforming the number of matched LEH into categorical intervals. Given that the intervals can be considered as ordinal ratings, Kendall's Coefficients of Concordance (Kendall and Babington Smith, 1939) were also considered to integrate Cohen's Kappa. This coefficient evaluates whether each observer has assigned the same order to a list of objects or whether their responses may be regarded as random.

2.5. Methodological problems in perikymata count and LEH detection using external surface of teeth

A well-known methodological problem with identifying LEH and counting perykimata is the fact that the spacing among perikymata depends on the internal geometry of teeth. Close to the cusp, the angle of the striae of Retzius is shallower, resulting in perikymata that are more difficult to identify and LEH that are less apparent. Conversely, near the cementoenamel junction (CEJ), the angle of the perikymata is steep and closely packed, and thus LEH is difficult to discern (Guatelli-Steinberg et al., 2012; Hillson and Bond, 1997; McGrath et al., 2019). In order to maximize the precision of the observations in the different tooth regions, at least three photographs of each cast were taken, orienting the cast and the light sources to highlight the perikymata in the cusp area and near to the CEJ (e.g. Supporting Information Figures S1 and S2). Data from different photographs, taken on the same tooth, was overlapped by taking advantage of "landmarks" resulting from microscopic imperfections in the cast. Still, LEH identification from the first and last decile may not be as reliable as the rest of the observations, and this issue was taken into account in the data analysis.

2.6. Statistical analyses

Matched LEH defects were counted in age intervals of 0.5 years between the age of 1 and 5 years (i.e. 1–1.49, 1.5–1.99, 2–2.49 years, etc.; King et al., 2002, 2005). In order to test whether one or more age intervals presented a higher mean number of LEH defects than the others, we ran a Generalized Linear/Nonlinear Model (GLZ) (McCullagh and Nelder, 1989) using the age interval as categorical predictor and the number of LEH defects of each individual in each class of age as dependent variable. Count data imply a Poisson distribution, and a Chi-Square Goodness of Fit Test on our data was performed. To account for small mean counts, overdispersion (standard deviation higher than the mean) and zero-inflation (numerous

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(*footnote continued*)
defect; this value is multiplied by the number of days in year (365); *Npkg*: number of perikymata between the beginning of the most recent decile and the LEH defect; *8*: indicates the mean and the modal number of days for perikymata formation in humans. The division of this summation by the constant 365 provides a chronological estimate for LEH defect formation in the form of years (Temple et al., 2012).

Fig. 1. Geographical location of the three caves included in this study. Top: the region of Liguria in northern Italy; bottom: the caves in the municipality of Finale Ligure (1: Arene Candide; 2: Pollera; 3: Strapatente).

observations with zero counts), the analysis was run using a quasi-Poisson or negative binomial distribution, as recommended in O'Hara and Kotze (2010). We also ran a non-parametric Friedman ANOVA by ranks in order to take into account non-independent samples, i.e. by considering the LEH counts in the various age categories as repeated measures on the same individual. The correlations among age at first defect, the total number of matched LEH per individual, and estimated age at death were explored via Pearson's correlation. Statistical analysis was performed using STATISTICA 10© (StatSoft, Inc 1984–2011).

3. Results

3.1. Intra-observer error

The intra-observer error of number of LEH per individual, dividing the observations in four categories (number of LEH: 0–4, 5–9, 10–14, 15+) resulted, for both observers, in Cohen's Kappa of 0.87 ($p < 0.001$ for both observers), with Kendall's Coefficient of Concordance of 0.95 ($p < 0.05$). The inter-observer error resulted in a Cohen's Kappa ranging between 0.64 and 0.88 ($p < 0.01$), depending on which observations were compared, with a Kendall's Coefficient above 0.92 ($p < 0.05$). The intra- and inter-observer errors correspond to a level of agreement ranging from "moderate" to "almost perfect" (Landis and Koch, 1977), but the Kendall's Coefficient is generally very high, suggesting that while there can be some disagreement on the number of matched LEH, the general pattern is shared among observations and observers. In order for the underlying pattern to emerge, the four observations were averaged, resulting in a mean count of matched LEH per individual and mean count of matched LEH per age category in Table 2. The four observations used to create these tables are available

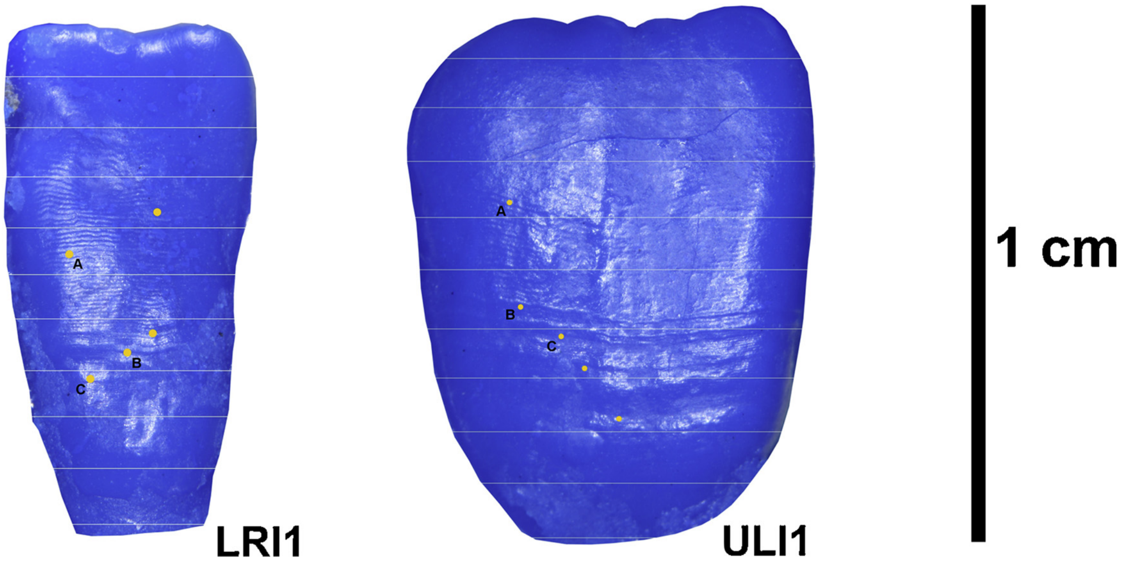

Fig. 2. LRI1 and ULI1 of Pollera 20. The dots identify observed defects. Matched defects are identified with consecutive uppercase letters.

Table 2
Numbers of matched LEH between at least two or more anterior teeth per individual, and per class of age, and age at first and last LEH defect. Mean counts and mean ages result from averaging among four observations, the table with each observation is available in Supporting Information (Table S1-4). Non-matched defects are not indicated.

Mean count of LEH per individual Individual[a]	Age classes								Mean count of total HLE for individual	Mean age at first defect (years)	Mean age at last defect (years)
	1-1.49	1.5-1.99	2–2.49	2.5–2.99	3-3.49	3.5-3.99	4-4.49	4.5–4.99			
AC 6621.1	–	–	0	1.25	1.5	1	1.25	0	5	2.8	4.4
AC 6627.1	0.75	1.5	1.5	2.5	2.75	0.75	0.75	0	10.5	1.5	4.1
AC 1 Tin.	–	0	0	0.5	0.75	1	0	0.25	2.5	2.9	4.1
AC 3 Tiné	1.5	1.5	1	1.75	1.5	0.25	0.25	0	7.75	1.3	3.6
AC BB T11-S22 G1	–	0	0	1	1	1	1	0.75	4.75	2.8	4.6
AC V BB	–	0	0	1	2	1	3	0	7	2.8	4.4
PO 6687.1	0	0.5	1.25	0.75	0.5	0.75	–	–	3.75	2.0	3.6
PO 6683.1	0	0	0.5	1.25	1.25	0.5	–	–	3.5	2.6	4.0
PO 6682.1	1	1.5	1.25	2	1.75	2	1	0.5	11	1.4	4.4
PO 1	–	0	1.75	1.5	0.5	1	1.75	0	6.5	2.3	4.3
PO 20	0	1	0	2	0	0	–	–	3	1.9	2.8
PO 34	–	0	0	0	0	1	1	0.5	2.5	3.9	5.0
STRAPA 1	0.75	1	1.5	1.5	1.75	1.25	1	0	8.75	1.7	4.3
Mean count for class of age	**4.00**	**7.00**	**8.75**	**17.00**	**15.25**	**11.50**	**11.00**	**2.00**	**76.5**		

[a] AC: Arene Candide; PO: Pollera; STRAPA: Boragni/Strapatente.

in Supporting Information (Tables S1-S6).

3.2. Defect frequency and chronology using GLZ

Table 2 shows how matched LEH were observed in all the individuals, with the total number of matched defects per individual ranging from 2 to 12 (Supporting Information Tables S1-S6). Considering only the individuals for which the first age class (1–1.49 years) could be studied ($n = 7$), the first enamel defect on average appears at 1.7 years of age ($SD = 0.5$), ranging from 1.3 to 2.6 years. In the cases where only the individuals for which the last age class (4.5–4.99 years) could be studied ($n = 10$), age at last defect is on average 4.3 years of age ($SD = 0.4$), ranging from 4.1–5 years (Table 2, and Supporting Information Tables S1-S6).

Table 2 also shows a sharp increase in the defect count between 2.5–2.99 years in comparison with the earlier age categories. In order to investigate the statistical significance of this increase, we ran a GLZ and a Friedman ANOVA. Fig. 3 shows the results of the GLZ ANOVA, taking into account the small mean counts, over-dispersion, and zero-inflation by using a quasi-Poisson or inverse binomial distribution (Table 3; Chi-Square test for the Poisson distribution: $p = 0.08$; Chi-Square test for the binomial distribution: $p = 0.93$; the distribution fitting was performed by rounding to the nearest integer). Diachronically, the mean count of LEH per individual sees a sharp rise at the age category 2.5–2.99 years. The evaluation of the predicted confidence intervals (equivalent of a post-hoc least square distance in this setting) displayed in both Fig. 3 and Table 3 suggests that the significance of the model (Wald X^2: $p < 0.01$) is mainly driven by low means between 4.5 and 5 years, but also in part by the increase at 2.5-2-99 years, which is also the age class in which the prevalence of LEH in the sample is highest (Table 3). The same statistically significant pattern (Wald X^2: $p < 0.001$) is present when considering only the individuals for which all classes of age between 1 and 4.99 years could be examined ($n = 4$; Fig. 4a), and when considering only the individuals for which all classes of age between 1 and 3.99 years could be examined (Wald X^2: $p < 0.05$; $n = 7$; Fig. 4b). This indicates that individuals with missing information for the first or last classes of age – due to the development schedules of the teeth used (Table 1), or to minimal wear (in two teeth, see above) – did not have a major impact in the general pattern of results. Finally, a similar pattern is present when considering individuals by site (Arene

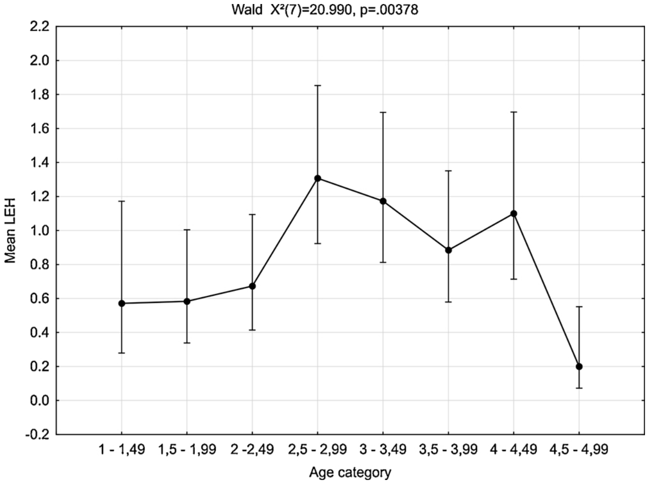

Fig. 3. Mean number of matched HLE and 95 % confidence intervals for the classes of age included in this study (see Table 2 for sample size in each class of age, ranging from 7 to 13). The confidence intervals are calculated using a quasi-Poisson distribution (see methods) to correct for small mean counts, overdispersion, and zero-inflation of the data.

Table 3
Sample statistics statistics (average among four observations, the table with each observation is available in Supplementary Information) for each age category included in this study (between 1 and 5 years of age, 0.5 years increments). The standard error (SE) and 95 % confidence intervals (CI) are calculated using a quasi-Poisson distribution (see methods) to correct for small mean counts, overdispersion, and zero-inflation of the data.

Age Category	N	Proportion of Individuals with LEH	Mean LEH per individual	SE	CI -95 %	CI + 95 %
1 - 1.49	7	0.50	0.57	0.37	0.28	1.17
1.5 - 1.99	12	0.46	0.58	0.28	0.34	1.00
2 -2.49	13	0.46	0.67	0.25	0.41	1.09
2.5 - 2.99	13	0.87	1.31	0.18	0.92	1.85
3 - 3.49	13	0.75	1.17	0.19	0.81	1.69
3.5 - 3.99	13	0.77	0.88	0.22	0.58	1.35
4 - 4.49	10	0.78	1.10	0.22	0.71	1.7
4.5 - 4.99	10	0.18	0.20	0.52	0.07	0.55

Candide and Pollera), but results are not significant at the $\alpha = 0.05$ level (Supporting Information Figure S3a, b).

3.3. Correlations

The GLZ models the confidence intervals using the appropriate distribution for count data, but considers the classes of age as independent samples. Evidence against this assumption derives from the fact that, in our sample, the age at first defect is correlated with the total number of matched defects, i.e. individuals with earlier defects tend to have more defects ($r = -0.71$; $p < 0.01$; $r = -0.78$; $p = 0.05$ when considering only individuals for which the first class of age could be analyzed). In addition, age at first defect is correlated with the age at death, i.e. individuals with earlier defects tend to die younger ($r = 0.81$; $p < 0.001$; $r = - 0.76$; $p < 0.05$ when considering only individuals for which the first class of age could be analyzed). Individuals with more LEH have a tendency towards a lower estimated age at death, but the correlation is not significant at the $\alpha = 0.05$ level ($r = -0.54$; $p = 0.06$; Supporting Information Figure S4a, b, c).

3.4. Defect prevalence and chronology using Friedman ANOVA

In order to take into account the possible dependence between observations over time, the non-parametric repeated measures Friedman ANOVA by ranks was performed. When considering the individuals for which all age categories were observable ($n = 4$), the pattern is similar to the one obtained using the GLZ, and the results are significant ($p < 0.01$; Fig. 5a). When excluding the first class of age, the sample size increases ($n = 9$), and both the increase in LEH at 2.5–2.99 years and the decrease at 4.5–4.99 years contribute to a significant ANOVA ($p < 0.01$; Fig. 5b). When maximizing the sample size, i.e. when considering the 12 individuals for which all classes of age between 1.5 and 3.99 years could be observed (Fig. 5c), results are still significant ($p < 0.05$) due to the increase in the mean LEH in the class of age 2.5–2.99 years. Indeed, a pairwise comparison between the class of age 2–2.49 years and 2.5–2.99 years results in a significant difference (Friedman ANOVA: $p < 0.05$). The same pattern is present when considering the individuals by site, although results are not statistically significant for Pollera cave (Supporting Information Figure S5a, b).

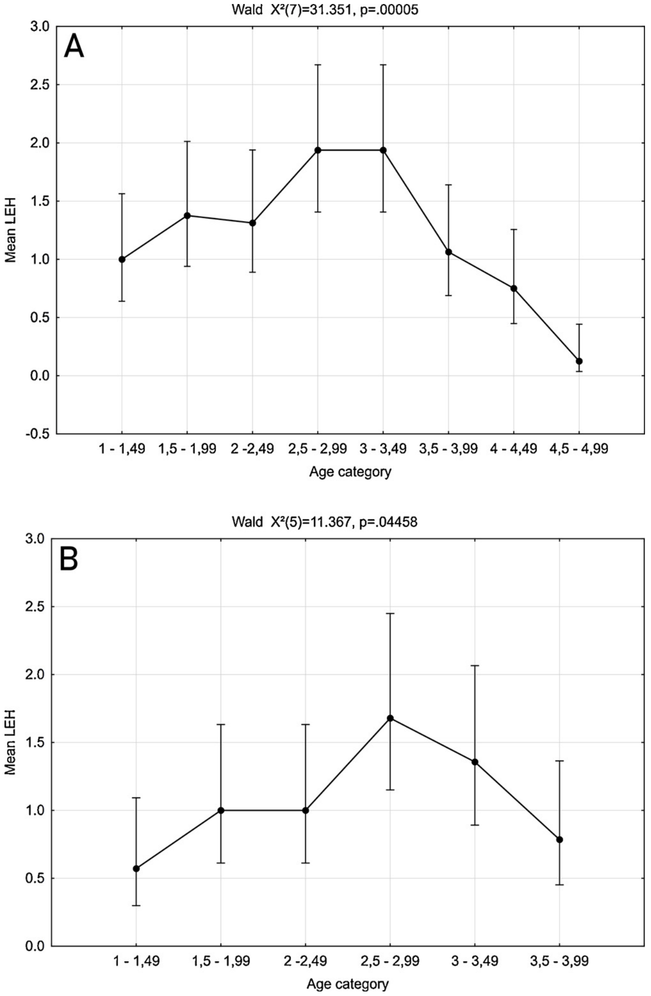

Fig. 4. Mean number of matched HLE and 95 % confidence intervals for the classes of age included in this study, when considering: A) only the individuals for which all classes of age between 1 and 5 years could be examined ($n = 4$); B) only the individuals for which all classes of age between 1 and 4 years could be examined ($n = 7$). The confidence intervals are calculated using a quasi-Poisson distribution (see methods) to correct for small mean counts, overdispersion, and zero-inflation of the data.

3.5. Defect prevalence and chronology when excluding the first and last decile

In order to take into account the fact that internal tooth geometry may render observations close to the cusp and the CEJ less reliable, we

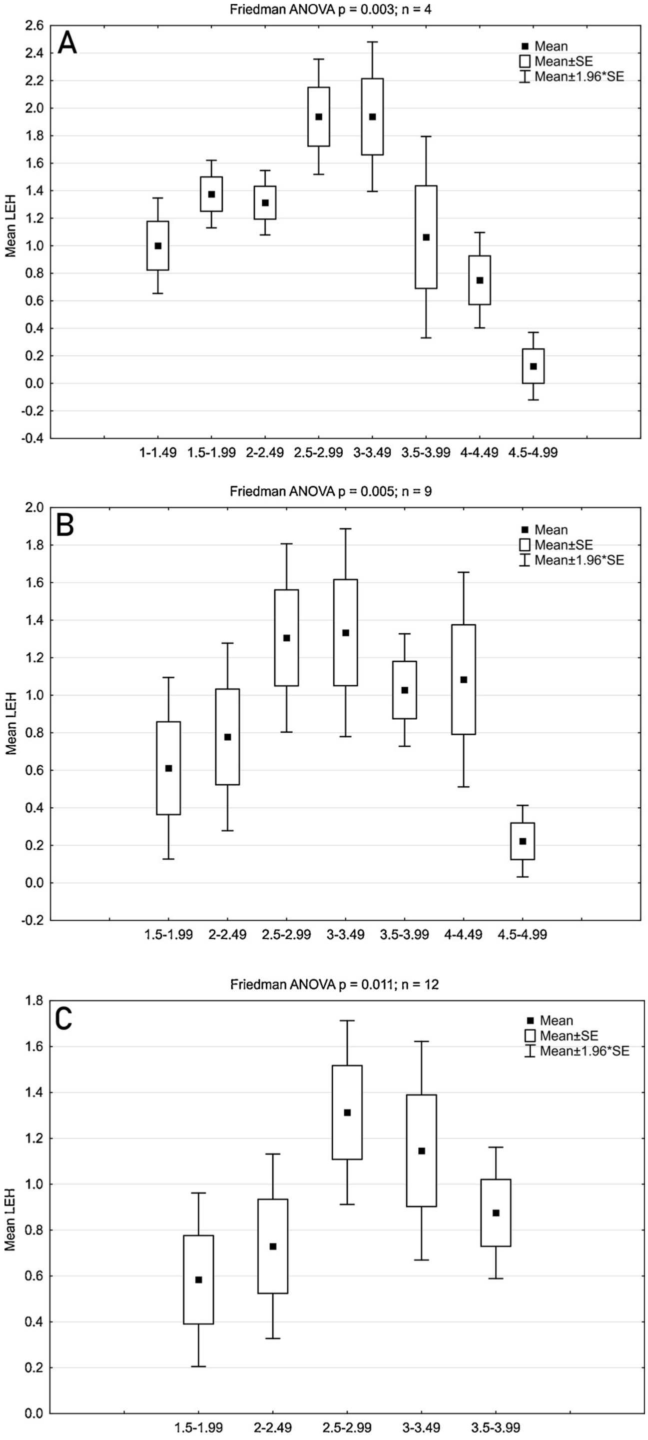

Fig. 5. Boxplots from the Friedman ANOVA: A) Including only the individuals for which all classes of age between 1 and 5 years could be examined (n = 4); B) Including only the individuals for which all classes of age between 1.5 and 5 could be examined (n = 9); C) Including only the individuals for which all classes of age between 1.5 and 4 could be examined (n = 12).

ran the analysis by excluding every observation that relied on the comparison of data from the first and last decile (a table detailing those comparisons is present in Supporting Information Table S7). This led to minor changes regarding the exclusion of certain classes of age for some individuals (see Table Supplementary Information S6). Also in this setting, the pattern is the same as described above: the mean number of LEH per individual shows a sharp rise at the age category 2.5–2.99 years, with a significant pairwise comparison with the previous class of age 2–2.49 years (Wald X^2: $p < 0.05$; Friedman ANOVA: $p < 0.05$; Supporting Information S8).

4. Discussion

Through the analysis of linear enamel hypoplasia (LEH) matched in at least two anterior teeth, this study aimed to analyze patterns of systemic developmental disturbances in a sample of Square Mouthed Pottery Neolithic children from the Finalese area (northwestern Italy). Compared to many bioarchaeological studies attempting to investigate Neolithic human biocultural adaptations, this study has the advantage of having a very narrow temporal and geographical focus (Arene Candide, Grotta Pollera, and Boragni/Strapatente are within a 5 km radius). Given the chronological and archaeological context of the burials, there is little doubt that they belong to the SMP Culture, with presumably a well-defined set of biocultural adaptations to a specific local ecology.

4.1. LEH prevalence and environmental stress

The percentage of individuals affected by enamel defects in a bioarchaeological sample is often considered an indicator of overall environmental stress in the population. For example, among ancestral Puebloan populations of Colorado, Malville (1997) found a correspondence between an increase in matched LEH frequency and archaeological indicators of nutritional stress (increased exploitation of marrow from small game). Populations with over 40 % of the individuals displaying LEH are considered affected by chronic nutritional and disease stress (Goodman and Rose, 1991; Hillson, 1979). The frequency of matched LEH in Ligurian children is 100 %: all individuals had between 2 and 12 defects. This value is similar to the 82 % reported by Formicola (1986, 1987; based on visual assessment of macroscopic defects in available dentitions) in a subsample of adults and adolescents from the same sites studied here, and is in agreement with the expectation of widespread growth disturbances in Ligurian children, based on postcranial faltering (Dori et al., 2019).

Direct comparisons of these results with other bioarchaeological studies – which could add to the characterization of environmental factors in Liguria – are often rendered problematic by the different methods used, i.e. reports of LEH prevalence by tooth type, or by including in the count individuals with at least one defect (e.g. Berbesque and Hoover, 2018; Boz, 2005; Lanphear, 1990; Wood, 1996). Malville (1997) considered only surface defects visible without magnification and associated with depressions in the enamel surface. Compared to studies considering matched defects by individual, results for Ligurian children appear similar to those reported for postmedieval London (100 % frequency, and between 2 and 19 defects; King et al., 2005), where poor nutrition and harsh living conditions were often coupled with poor infant feeding practices. However, SEM and magnification of 50x were used in that study (see also King et al., 2002). Particularly relevant would be a comparison with other Neolithic sites, e.g. the large skeletal series from Çatalhöyük (Turkey; Boz, 2005), which is comparable to the Ligurian series in terms of chronology, diet, and subsistence (e.g. Pearson et al., 2015; Richards et al., 2003). The Çatalhöyük population appears to have had relatively good health (Hillson et al., 2013; Larsen et al., 2019), does not show growth faltering displayed by Ligurian children (cf. Dori et al., 2019; Ruff et al., 2013), and has no evidence of tuberculosis (Larsen et al., 2019). Macroscopic LEH prevalence at Çatalhöyük is reported for permanent canines as 27.1 % (16/59; pooled sample of adults and children), although it is mentioned that frequency in children between 1.5 and 5 years is higher (Boz, 2005:590). In the sample of children analyzed here, 100 % of canines (8/8) have LEH defects. In order to compare Ligurian data with Boz (2005), a preliminary visual macroscopic analysis limited to canines was performed. Results show that in the entire Ligurian Neolithic skeletal series, 76.3 % of lower permanent canines (29/38; pooled sample of adults and children) have at least one LEH defect. Although this comparison is not ideal due to the inclusion of unmatched defects, which can have a different etiology than matched defects, this suggests that SMP Neolithic people experienced a higher level of environmental stress compared to Neolithic Çatalhöyük.

4.2. Age at peak stress, local ecology, and life history traits

The age interval during which LEH defects are more numerous and found more frequently in our Ligurian Neolithic sample, often referred to as "age at peak stress" (e.g. Lanphear, 1990), is 2.5–3.5 years old. During this age range, the frequency of LEH by individual nearly doubles, as well as the mean LEH per individual. This is not uncommon among early agriculturalists: a similar peak was observed using 10x magnification in the Corded-Ware Neolithic (Tomczyk et al., 2012), and among prehistoric Native American agriculturalists (Goodman et al., 1984, using matched defects and binocular microscopy; Hodges, 1986, matched defects and naked eye observation; Malville, 1997). Using a quantitative assessment of perikymata spacing in a microscopic setting (Alicona InfiniteFocus), a peak in proportion of individuals with LEH at that age interval was observed at Neolithic Çatalhöyük (Bocaege, 2015). It has been proposed that modern industrial and agricultural samples appear to show peak prevalence of LEH earlier, within the first three years of life (Goodman et al., 1987; Lanphear, 1990; Sarnat and Schour, 1941), but none of these studies use matched defects. In addition, significant variation within modern and postmedieval groups has been observed (Goodman et al., 1987; Lanphear, 1990), due perhaps to differences in socioeconomic status, such as those found in the early introduction of food supplementation in wealthy families in postmedieval London (King et al., 2005). Methodological differences can also explain variability in the results. However, in a study comparing prehistoric agriculturalists using a consistent methodology (matched defects, 4x magnification), Cucina (2002) observed a shift in peak mean LEH per individual from later age at death groups (between 3 and 4 years of age) towards earlier age at death groups (1 and 2.5 years of age) in concomitance with a shift from mixed hunting/farming Neolithic subsistence towards more intensive agriculture in the Copper and then Bronze Ages (Trentino, northeastern Italy). It therefore appears that variation in subsistence practices and environmental conditions may be factors influencing the age at which LEH frequency and mean number per individual peak.

Whether variation in the mean onset and peak of LEH frequency is more specifically related to life history events, especially weaning, is debated. Still, variability in infant feeding practices is consistently discussed when analyzing temporal patterns of LEH frequency (King et al., 2005). The transition from exclusive breast feeding to the introduction of supplementary foods, and finally weaning, can expose the weanling to nutritional stress and infectious disease, and ultimately developmental disturbances, especially in environments with scarce resources and high pathogen load (McDade, 2003; McDade and Worthmann, 1998). However, only some studies have found a correlation between documented weaning practices and LEH patterns (Corruccini et al., 1985; King et al., 2005; Moggi-Cecchi et al., 1994), while others have not, suggesting that LEH peaks postdates reported weaning times (Blakey et al., 1994; Saunders and Keenleyside, 1999; Wood, 1996). Therefore, caution should be exercised when linking LEH profiles to weaning, and the discussion should be integrated by the direct assessment of dietary changes in children using stable isotope analyses on dentine (e.g. Beaumont and Montgomery, 2015; Beaumont et al., 2013, 2015, 2018; Sandberg et al., 2014). Recently, a joint analysis of LEH timing (using the same decile method applied to our sample; Reid and Dean, 2006) and intra-tooth isotopic analysis of dentine in five Medieval Nubian children found that hypoplastic stress events occurred during rather than after or before the weaning process, which was reconstructed via δ^{15}N diachronic profiles (Sandberg et al., 2014). Interestingly, the age of mean frequency of LEH defects in the same group was around 4 years of age using the distance-based method (van Gerven et al., 1990), i.e. LEH peaked after weaning was completed in most children (Sandberg et al., 2014), suggesting that the non-correspondence between LEH and breastfeeding practices may be influenced by the methods used to create LEH frequency profiles.

The isotopic analysis of dentine microsections in two teeth from the Ligurian SMP Neolithic suggests that they may have terminated breast feeding around 3 years, i.e. towards the later end of the spectrum for prehistoric agriculturalists (Goude et al., 2019). Although the sample size is small, this would correspond with the observed increase in LEH at 2.5–3.5 years of age. In addition, the estimated timing of weaning, and the pattern of peak LEH, seem to correspond with the pattern of postcranial growth shown by same children (Dori et al., 2019). In our sample, mean LEH per individual remains rather low until 2.5 years of age, followed by a sharp increase. Similarly, postcranial development appears to be comparable to a sample of modern well-nourished children (the Denver Growth Study) up to the third year of life (Dori et al., 2019). After this age, all children aged 4–9 years at death have attained a lower percentage of the adult size than the modern sample, and many are significantly stunted. Strikingly, the two individuals with the greatest growth stunting also display the greatest number of LEH in this study (AC 6627.1 and PO 6682.1, Table 1; Dori et al., 2019), which suggests a relationship between an individual's LEH count and the degree of developmental disturbance.

Postcranial growth faltering suggests that rather than be due directly to weaning, the timing of the sharp increase in LEH may be related to the local ecology of Neolithic Liguria and to the biocultural strategies put in place by SMP people to cope with it. Environmental factors impacting developmental patterns may include dietary deprivation, high labor input (Johnston et al., 1976; Martorell, 1985), and infectious diseases and parasites (Solomons et al., 1993; Stephensons, 1987). Within agriculturalists, the overreliance on staple foods with poor nutritional properties (e.g. maize), seem to coincide with poor growth (Cook, 1984; Goodman et al., 1984). Archaeological evidence suggests that the subsistence of Ligurian Neolithic people included a strong pastoral component (Macphail et al., 1997; Rowley-Conwy, 1992, 1997, 1998), which is confirmed by isotopic studies showing a significant consumption of animal protein beginning in early life (Le Bras-Goude et al., 2006; Goude et al., 2014, and 2019). In this context, the effect of disease may have been relatively more important. Indeed, pathogen load may have high in the Neolithic of Liguria, given that several individuals display skeletal evidence of osteoarticular tuberculosis (Canci et al., 1996; Dori et al., 2019; Formicola, 1986; Sparacello et al., 2018). Evidence of tuberculosis is rare in the bioarchaeological record (Roberts and Buikstra, 2003), and skeletal lesions manifest only in a small percentage of the affected individuals (estimates ranging from 1 % to 3–5 %; Turgut, 2001; Vigorita, 1999). These factors suggest a high prevalence of this highly infectious disease in the Ligurian Neolithic population. Active tuberculosis is a debilitating disease that impairs skeletal development (Mansukoski and Sparacello, 2018; Sparacello et al., 2016), but also the more common latent and subclinical states require a constant investment in immune defenses (Ulrichs et al., 2005; Lin and Flynn, 2010), possibly diverting energy from growth (Ganmaa et al., 2012; see also McDade et al., 2008). Prolonging breast feeding, and therefore passive immunity, into the third year (Goude et al., 2019) may have contributed to optimal growth (Dori et al., 2019) and low LEH presence and frequency until 2.5–3 years of age. After this age, increased pathogen load and the sudden investment in immune function by developing children may explain the timing of the significant increase in LEH observed here.

4.3. Limitations of the study: osteological paradox, methodological limitations and results comparability

In bioarchaeology, one of the main interpretative limitations is the fact that samples of dead individuals may not be representative of the living population, biasing attempts to reconstruct past lifestyle and health, known as the "osteological paradox" (DeWitte and Stojanowski, 2015; Wood et al., 1992; Wright and Yoder, 2003). Studying LEH partially addresses this problem since tooth enamel does not undergo remodeling during life (e.g. Gage et al., 1989; Hillson, 2005) and may therefore be more representative of conditions experienced during the life of the individual. Assessing the presence of LEH has the advantage of recording early metabolic insults, after which the individual survived (see Gage et al., 1989; Hillson, 2005). However, a negative correlation between survivorship and hypoplasia defects has also been noted in archaeological populations (Armelagos et al., 2009; Goodman and Armelagos, 1988, 1989; Holland, 2013; King et al., 2005; Lorentz et al., 2019; Temple, 2014), which could impact inferences regarding lifestyle and environmental conditions of a once-living population. For instance, the methods used in this study, which include only non-worn (or minimally-worn) anterior teeth, limits the investigation to individuals who died in childhood or as late adolescent/young adults. As seen in other bioarchaeological studies (King et al., 2005; Lorentz et al., 2019; Temple, 2014), we found a significant correlation between the age of appearance of the first defect and the total number of defects (individuals with earlier defects will tend to have more), as well as between the age of appearance of the first defect and age at death (individuals with earlier defects will die younger). These results may suggest that early developmental disturbances will have repercussions along the entire lifespan, and will affect survivorship (Armelagos et al., 2009; Berbesque and Doran, 2008; Gowland, 2015). However, it is also possible that instead of reconstructing the living population's patterns of stress during development, or even life-history and optimal reproductive/weaning strategies, our sample reflects the pattern of stress of frail individuals, or *unsuccessful* strategies, leading to later susceptibility to environmental hardships and low survivorship.

Another potential problem with our inferences involves methodological limitations inherent in visual scoring of LEH. It has been demonstrated that hypoplasia in permanent teeth tend to occur more frequently and are more apparent in the crown midsection (Goodman et al., 1980; Goodman and Armelagos, 1985a, b; Goodman and Rose, 1990) due to the internal structure of teeth (more obtuse striae of Retzius angles; Guatelli-Steinberg et al., 2012, 2014; McGrath et al., 2018). In addition to leading to different timing of susceptibility to LEH between tooth types, this may partially explain why most studies on anterior dentition consistently find high defect frequencies between 2–4 years of age (Blakey et al., 1994; Goodman and Rose, 1990). If tooth architecture is the key factor in determining LEH visibility, we would expect LEH frequency to be normally distributed across age categories (Blakey et al., 1994; Corruccini et al., 1985) and similar LEH frequencies regardless of the population under study. In contrast, even when using similar data collection methods, there appears to be significant variation in LEH onset and peak LEH frequency within different populations (e.g. Cucina, 2002; Malville, 1997). This variation suggests that methodological factors do not entirely account for varying LEH occurrence. However, the fact that observations near the cusp and the CEJ appear less reliable remains a methodological problem that we attempted to minimize during data collection (taking several photographs with different orientation, see Supplementary Information Figures S1 and S2) and analysis (verifying results involving the first and last deciles).

Another problem is the comparability of our results with those derived from bioarchaeological and modern samples, especially when diachronic patterns of LEH appearance and frequency are compared. Observation techniques differ and range from naked-eye observation (Ash et al., 2016; Cucina and Işcan, 1997; Goodman and Rose, 1990; Jarošová and Dočkalová, 2008; Wood, 1996), varying levels of magnification (e.g. Blakey et al., 1994; Moggi-Cecchi et al., 1994), macrophotography (Berbesque and Doran, 2008; Berbesque and Hoover, 2018), and microscopy (Bocaege, 2015; Guatelli-Steinberg et al., 2014; King et al., 2002, 2005; Temple et al., 2012). Using magnification and high-resolution macrophotos of dental replicas allows detection of LEH defects that are less apparent to the unaided eye (Hassett, 2014). However, results based on this method cannot be compared to results obtained through microscopic measurement of perikymata spacing, where the minimum threshold of defect identification is much lower (Bocaege and Hillson, 2016; Hassett, 2014). In addition, the 'severity' of defects was not evaluated in our study, as it has been in others (e.g. Berti and Mahaney, 1995; Blakey et al., 1994; Corruccini et al., 1985) by using defect duration (Bocaege, 2015; Hassett, 2014; King et al., 2002, 2005) or depth (McGrath et al., 2018). In the future, taking into account defect parameters beyond mean count per individual might elucidate the intensity of stress, allowing for a comparison of "peak stress" among populations beyond its timing.

The limited ability to compare the Ligurian sample with other bioarcheaological and modern groups curtails assessment of environmental correlates of developmental disturbance. In fact, since different teeth are more sensitive to developmental disturbances (Goodman and Armelagos, 1985b; Goodman et al., 1980; Guatelli-Steinberg et al., 2012, 2014; Hillson and Bond, 1997), chronological peaks of LEH frequency might be based on tooth type rather than environmental conditions (e.g. Lanphear, 1990; Moggi-Cecchi et al., 1994; Wood, 1996). Recent research has explored variation in developmental speed between regions within teeth, and by tooth type (Liversidge et al., 1993; Guatelli-Steinberg, 2003; Reid and Dean, 2000, 2006; Ritzman et al., 2008; Skinner and Goodman, 1992), allowing matching defects between different teeth. In our study, matching LEH from different teeth provides a chronological profile of LEH occurrence, which reflects the early history of developmental disturbances in the individual. In the future, through the use of standardized macro and micro methods, a larger comparative dataset will be created that allows evaluation of defect characteristics, timing, and frequency across space and time.

5. Conclusions and future directions

This study provides a dental assessment of developmental disturbances in the Squared Mouth Pottery Neolithic of Liguria through the analysis of linear enamel hypoplasia. The narrow chronological and geographic setting is ideal for the reconstruction of Neolithic local ecologies and life history parameters, because all individuals belonged to the same population with a presumably well-defined set of biocultural adaptations to specific environmental challenges.

Results indicated that a sharp increase in mean LEH is present at 2.5–3.5 years of age, followed by a decline in the number of defects at older ages. Although small sample size and limitations inherent in the methods suggest caution in the interpretation of the results, the peak in LEH frequency parallels the termination of milk supplementation into the third year of life, estimated by isotopic analysis of dentine microsections. Moreover, it appears that around the same ages, Ligurian Neolithic children begin showing significant postcranial growth faltering. Given the evidence of infectious disease (tuberculosis) in this skeletal series, the LEH pattern signal the end of passive immunity in an environment with high pathogen load, where disease burden and investment into the immune system impacted growth. However, results also indicate that the age at first defect was negatively correlated with age at death and positively correlated with the total number of defects, suggesting that the pattern may not represent experiences of the once-living population.

Further studies are necessary, and will be conducted, in order to characterize the link between early environmental conditions and dental development in the SMP Neolithic of Liguria. Methods involving the identification and measurement of perikymata and defect depth using the confocal microscope are being conducted. Likewise, microscopic analysis via histology, SEM, and synchrotron Micro-CT will be employed to reveal more precisely the occurrence of enamel defects, to quantify the duration and intensity of the stress event. Finally, the comparison of dental metric traits (attained size and fluctuating asymmetry) in adults and children will further explore issues of frailty and survivorship.

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ID and the authors would like to dedicate this work to the memory of Zia Lella.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ijpp.2019.12.005.

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