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Chronology and periodicity of linear enamel hypoplasia among Late/Final Jomon period foragers: Evidence from incremental microstructures of enamel

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ABSTRACT

This study estimates age-at-defect formation and periodicity of linear enamel hypoplasia (LEH) using incremental microstructures of enamel. Results are compared to previous studies and between sites from different regions of Japan (Costal Honshu, Inland Honshu, and Hokkaido). High resolution impressions were collected from the dental remains of 32 individuals from nine archaeological sites. Casts were produced from these impressions and studied under an engineer's measuring microscope. LEH were identified based on enamel surface depressions and accentuated perikymata. Age-at-defect formation was estimated using histological methods. LEH periodicity was estimated using counts of perikymata between defects. Age-at-defect formation ranged between 1.1 and 5.8 years, while interquartile ranges were between 2.9 and 4.1 years. LEH periodicity ranged between 0.1 and 1.7 years, with an average of 0.2 years. There were no significant differences in average age-at-defect formation between regions. Significantly higher LEH periodicities were observed among Jomon foragers from Hokkaido and Inland Honshu compared to Coastal Honshu. Earlier ages-at-defect formation and lower stress periodicities were found by this study compared to earlier research. These differences are attributed to the inclusion of individuals with intact tooth crowns and use of objective, microscopic methods to identify LEH. The interquartile ranges for ages-at-defect formation are consistent with isotopically estimated ages for reductions in breast milk consumption. The lack of differences in average age-at-defect formation between geographic groups may reflect similar environmental stress burdens associated with this process. Comparatively shorter intervals between defects among Late/Final Jomon foragers from Coastal Honshu suggest elevated ecological stress burdens among this sample.

1. Introduction

Linear enamel hypoplasia (LEH) is a condition associated with grooves or furrows observed on tooth crowns, where insufficient enamel is deposited during the secretory phase of amelogenesis (Goodman and Rose, 1990, 1991). Enamel production is stopped earlier than normal resulting in a depression in the enamel surface and accentuated striae of Retzius (Hillson, 1996). The process is mostly transitory as the gradual return to prismatic shape of enamel rods is reported in the cervical walls of defects (Boyd, 1970; Hillson and Bond, 1997). LEH most often form in response to increased energetic burdens associated with nutritional deprivation and infectious disease, though congenital anomalies and traumatic injuries are also causative agents (Suckling and Thurley, 1984; Suckling et al., 1986; Goodman et al., 1991; May et al., 1993; Hillson, 1996; Zhou and Corruccini, 1998). Because teeth do not remodel and enamel is laid down in a chronological fashion, LEH provide an indelible marker of growth disruptions experienced at specific ages during the course of ontogeny—the defects remain permanently observable in teeth, and it is possible to estimate the age at which these disruptions occurred (Hillson, 1996).

Studies of LEH chronology estimate the ages-at-defect formation in a wide variety of contexts. Estimating age-at-defect formation in dental samples provides evidence of adaptive challenges that humans encountered and that biological and cultural buffering systems were often swamped, resulting in physiological perturbation to the individual (Goodman et al., 1988). By and large, bioarchaeological studies report increased LEH prevalence between 2.0 and 4.0 years of age (reviewed by: Larsen, 1997; Hillson, 2014),

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though there is some variability in this range (Goodman and Song, 1999). For example, ages-at-defect formation in samples of enslaved Africans from Barbados are consistent with age-at-breast-feeding cessation and suggest that stressors associated with this process may have produced LEH in these samples (Corruccini et al., 1985). By contrast, age-at-defect formation in a sample of enslaved African Americans from 18th and 19th century plantations in Maryland and Virginia are distributed at ages after the initiation of the weaning process suggesting other environmental factors such as infectious disease and malnutrition were associated with these defects, though the possibility for overlap between weaning and LEH at earlier ages is still considered a plausible interpretation (Blakey et al., 1994). Importantly, however, a number of studies argue that these distributions are potentially biased by tooth crown geometry: striae of Retzius outcrop onto the enamel surface at less acute angles in the occlusal compared to cervical sections of a tooth, causing LEH to be poorly defined, and quite possibly, inflating peak ages for growth disruption in archaeological samples (Goodman and Armelagos, 1985; Blakey et al., 1994; Hillson and Bond, 1997; Guatelli-Steinberg et al., 2012).

LEH periodicity addresses the amount of time between successive defects. Macroscopic studies infer seasonal stress patterns based on LEH periodicity in Pliocene hominines, fossil primate, modern human, and Great Ape dental samples (Macho et al., 1996, 2003; Nelson, 1999; Skinner and Hopwood, 2004). Among modern humans, microscopic approaches have also yielded evidence for greater stress burdens in the Medieval compared to historic inhabitants of London based on differences in LEH periodicities between the two samples (King et al., 2005). Couched within the findings of these studies is evidence that microscopic methods yield considerably lower periodicities than macroscopic approaches. This difference may reflect the ability of microscopic methods to identify more LEH or to count perikymata between defects rather than measuring the distance between LEH. Overall, these studies suggest that LEH periodicity is an important component to the evaluation of stress in past populations, and that microscopic approaches may yield more precise evidence for the periodicity of these growth disruptions.

Jomon foragers are the descendants of a Paleolithic population that migrated into Japan around 25,000 BP (Imamura, 1996; Kobayashi, 2005). One set of hypotheses suggests that the ancestors of these Paleolithic migrants were from Southeast Asia (Hanihara, 1991), while another argues that the ancestors of Jomon people originated in Northeast Asia (Omoto and Saitou, 1997; Pietrusewsky, 1999; Hammer et al., 2006; Hanihara and Ishida, 2009; Adachi et al., 2009, 2011). Recent samples of ancient-DNA dated to the Initial phase of the Jomon period reveal that these populations were genetically heterogeneous and that conclusions regarding the early affinity of these groups should be cautiously interpreted (Adachi et al., 2013).

The prevalence of individuals with LEH was explored among prehistoric Jomon people from different regions of Japan, and differences in these frequencies were associated with variation in resource availability, dietary quality, and infectious disease (Shigehara, 1994; Koga, 2003; Temple, 2007, 2010; Oxenham and Matsumura, 2008). Elevated frequencies of individuals with LEH are, however, a hallmark of many Jomon dental samples (Yamamoto, 1992; Shigehara, 1994; Koga, 2003; Temple, 2007, 2010; Hoover and Matsumura, 2008; Sawada et al., 2008; Temple et al., 2013). Thus, regional variation in LEH prevalence among Late/Final Jomon period people remains an open question.

One study explored LEH chronology and periodicity among Late/Final Jomon period people, and suggested that LEH are distributed between 2.5 and 5.5 years of age and have periodicities between 0.4 and 0.9 years (Yamamoto, 1992). Unfortunately, this study did not use microscopic methods to identify LEH, so many defects may not have been observed (Hillson and Bond, 1997; King et al., 2002; Temple et al., 2012). In addition, the chronologies of LEH reported by Yamamoto (1992) were estimated using models that assume a linear rate of tooth growth. These methods are no longer accepted standards as histological studies have demonstrated a non-linear rate of crown growth (Reid and Dean, 2000, 2006) and methods to estimate age-at-defect formation based on histological estimations of tooth crown growth are decidedly more accurate (Ritzman et al., 2008).

Using previous research on LEH among Late/Final Jomon period people as a framework, this study has several goals regarding the estimation of age-at-defect formation and LEH periodicity among these samples. First, ages-at-defect formation and LEH periodicities will be compared to the results of previous studies (i.e., Yamamoto, 1992). In addition, the distribution of age-at-defect formation among Late/Final Jomon period people will be used to best infer the environmental hazards associated with LEH formation. Finally, average age-at-defect formation and LEH periodicity will be compared between georgraphic groups (Coastal Honshu, Inland Honshu, and Hokkaido) to evaluate the possibility of variation in stress burdens between Late/Final Jomon period foragers from different ecological zones.

2. Materials and methods

2.1. Materials

All archaeological sites yielding dental remains utilized by this study are mapped in Fig. 1. Table 1 lists the number of individuals ($n = 32$) with dental remains that had observable perikymata, teeth, and matched-LEH by region. The number of individuals with observable perikymata is significantly lower than the number of individuals with macroscopically observable LEH reported by earlier studies (Temple, 2007, 2010). The number of individuals with observable perikymata is small because of taphonomic factors influencing preservation of enamel microstructures, the inclusion of individuals with 90 percent or more of observable crown height (see below), and the need to match LEH on more than one tooth.

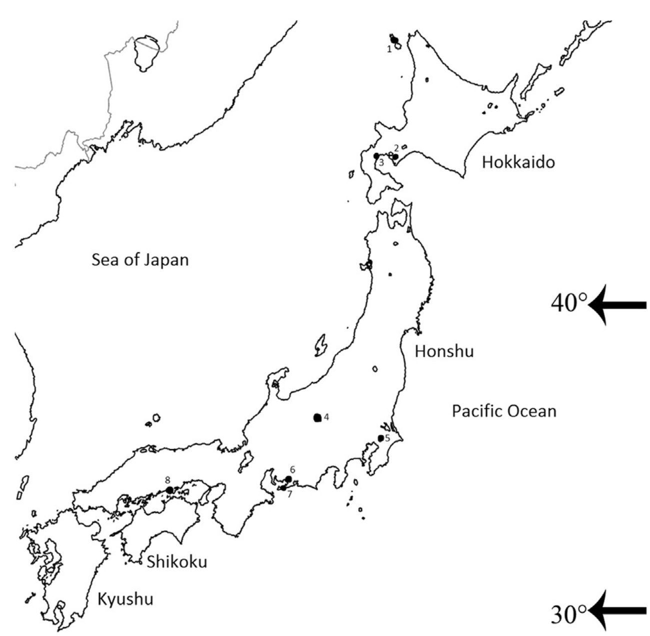

Fig. 1. Archaeological sites that yielded dental remains used in this study: 1, Funadomari; 2, 2, Takasago; 3, Koten-Onsen; 4, Kitamura; 5, Nakazuma; 6, Inariayama; 7, Yoshigo; 8, Tsukumo.

Table 1
Sample composition, including total number of individual with observable perikymata, total number of teeth with observable perikymata, and total number of matched LEH by region.

	N Individuals	N Teeth	N LEH
Hokkaido	5	21	30
Coastal Honshu	20	71	256
Inland Honshu	7	19	76

Dental remains from Late/Final Jomon period archaeological sites from Hokkaido, Coastal Honshu, and Inland Honshu were targeted in this study. These regions are referred to as "geographic groups" in the statistical analyses of data. Coastal Honshu sites include dental remains recovered from Inariyama, Tsukumo, Nakazuma, and Yoshigo. Including Tsukumo with the Coastal Honshu group may seem problematic as comparatively elevated LEH frequencies were observed among Jomon people from western Japan (Koga, 2003; Temple, 2007, 2010). Originally, these differences were attributed to dietary distinctions between the two groups: LEH prevalence may have been present in western and inland people because of a greater reliance on plant foods (Temple, 2007, 2010). Recent studies of stable carbon and nitrogen isotopes suggest, however, that dietary differences between these groups were minimal (Kusaka et al., 2010), and the samples were all derived from the same biotic region of Japan (Tsukada, 1986). Therefore, pooling these samples is appropriate. Dental remains were also recovered from four archaeological sites on Hokkaido (Hiroo, Kotan Onsen, Takasago, and Fundadomori) and one site from Inland Honshu (Kitamura). Dates for all of the sites used in this study were obtained from radiocarbon methods (Kusaka et al., 2009) or pottery chronology. Pottery chronology is an appropriate method to date Jomon period sites due to the large number of descriptive studies that are consistent with radiocarbon dates (Imamura, 1996; Habu, 2004).

2.2. Data collection

High resolution impressions were collected from the labial surfaces of intact anterior teeth using Coltene President light/regular body polyvinyl siloxane. This material has a documented resolution of 1 μm (Beynon, 1987). All teeth utilized by this study retained 90 percent or more of crown height. Relative completeness was assessed based on average crown heights for Jomon maxillary and mandibular central incisors that were established by previous studies (Kaifu, 2000). Methods described by Guatelli-Steinberg and Reid (2008) were applied to all other anterior teeth with evidence of slight attrition. In these circumstances, crown height was reconstructed by following the contour of each cuspal side and projecting it until both sides met.

Replicas were produced from the surface impressions using EpoFix resin (Streuers Inc., Cleveland, Ohio, United States). Perikymata spacing and enamel surface profiles were measured from replicas using a measuring microscope (Spectra Services, Rochester, New York, United States) and Vision Gauge Software (Vision X, Inc., Point Claire, Quebec, Canada). Detailed descriptions of the methods employed to produce replicas and measure perikymata spacing and enamel surface profiles are provided in Temple et al. (2012).

LEH were identified as accentuated perikymata spacing combined with depressions in the enamel surface (Hillson, 1992; King et al., 2002). Fig. 2 demonstrates a typical perikymata spacing and enamel surface profile. The black bars represent the distance between exposed striae of Retzius planes (perikymata spacing) measured along the y-axis of the tooth, from the cuspal tip to the cementoenamel junction. The grey bars are measurements of the

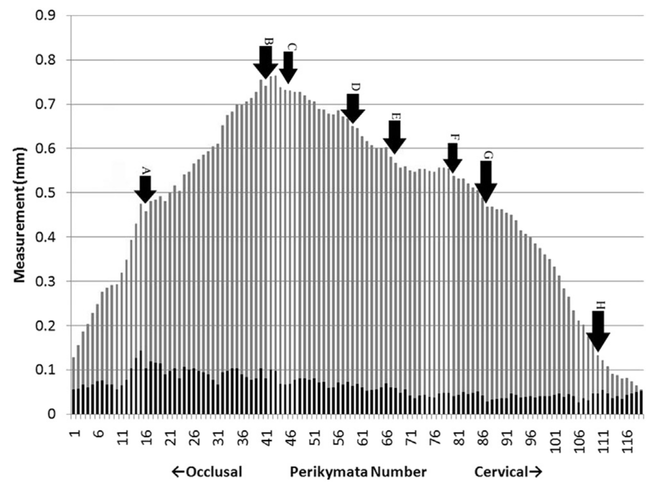

Fig. 2. Enamel surface and perikymata spacing profile of a right mandibular second incisor for individual 194 from the Takasago site. Black bars indicate measurements of perikymata spacing, while grey bars indicate the distance between the optical lens and the focal point (enamel depth). Matched LEH defects are identified by letters and arrows. LEH defect E is pictured in Fig. 3A.

enamel surface profile, which were taken at 90° angles to the y-axis of the tooth at each exposed striae of Retzius plane. Measurements increase in millimeters as the tooth surface is moved closer to the optical lens and decrease as the tooth is moved further from the optical lens. Matched LEH (see below) are indicated with arrows and letters. Fig. 3 is a microscopic image of LEH in three different individuals. In Fig. 3, black outlines are traced around LEH and numbers are placed on the exposed striae of Retzius planes between perikymata grooves in the occlusal wall of each defect. A minimum of six exposed striae of Retzius planes were identified in the occlusal wall of the defect in Fig. 3. The LEH in Fig. 3 is listed in Fig. 2 as Defect E.

The estimation of age-at-defect formation should follow methods that divide teeth into deciles associated with tooth development and include appositional enamel and crown initiation times as constants in this procedure (Reid and Dean, 2000, 2006). The modal periodicity for perikymata formation in Northeast Asian foragers from the *Cis*-Baikal region of Siberia was 8-days (Antanova, 2011). Age-at-defect formation for each LEH was then calculated by multiplying the total number of perikymata found between the cuspal tip to the first perikyma of an LEH defect by 8.0 and adding this value to the total number of days associated with crown initiation and cuspal enamel formation for the tooth in question. This total was divided by 365, and the resultant value was taken as the age-at-defect formation for the LEH in question.

Traumatic injuries may produce LEH, and these defects are not possible to differentiate from those associated with systemic stress based on appearance (Hillson, 1996, 2014). As a result, it is necessary to chronologically match LEH, as growth disruptions associated with systemic stress will affect all teeth that were actively forming (Hillson, 1996, 2014). This study matches LEH across individual dentitions based on similarity in age-at-formation. LEH on different teeth of the same individual were matched within 0.1 of a year on two (minimum number of teeth with LEH) or more teeth. This final value (called stress episode) was taken as the age-at-defect formation and is used as the unit of analysis for age-at-defect formation in this study.

Periodicities were calculated by subtracting the age-at-defect formation for each successive stress episode from the age-at-defect formation of the previous LEH. Thus, an individual with stress episodes estimated at 1.4, 2.2, 2.8, and 3.2 years would have

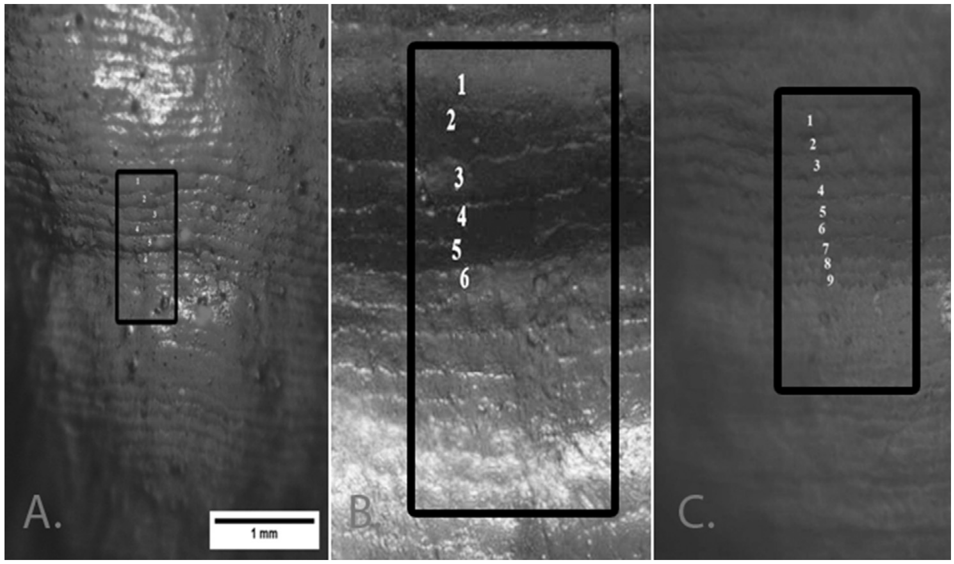

Fig. 3. Microscopic image of LEH in three individuals from the Takasago (A), Tsukumo (B), and Yoshigo (C) sites. LEH is outlined in black in each image. Numbers are placed on the exposed striae of Retzius planes between perikymata grooves. A minimum of six exposed striae of Retzius planes were identified in the occlusal wall of Fig. 3A. This defect is depicted as LEH defect E in Fig. 2.

stress episode periodicities of 0.8 (2.2–1.4), 0.6 (2.8–2.2), and 0.4 (3.2–2.8) years.

2.3. Statistical evaluation of data

Interquartile ranges and 90 percent confidence intervals were calculated for age-at-defect formation and LEH periodicity. Box plots of age-at-defect formation and LEH periodicity were also calculated to provide a visual display of the data for each geographic group and the pooled sample. All data were tested for normality via measurements of skewness, where *t*-tests were used to evaluate the significance of this value. Where skewness does not statistically significantly deviate from zero or the data are skewed in a similar direction, average age-at-defect formation and LEH periodicity were compared between geographic groups using a one-way ANOVA with a Games-Howell post-hoc test.

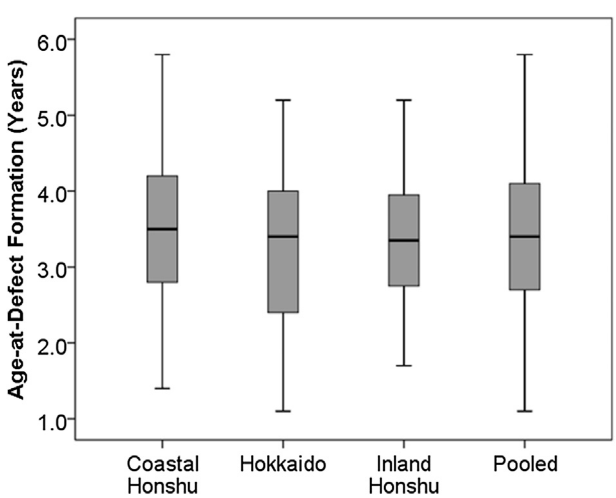

Fig. 4. Box plots of age-at-defect formation for each geographic group and the pooled sample. Boxes represent interquartile ranges, whiskers represent the 90 percent confidence intervals.

3. Results

The total numbers of matched defects are listed by geographic region in Table 1. Table 2 shows the summary statistics of age-at-defect formation by geographic region and for the pooled sample. Box plots for age-at-defect formation are shown in Fig. 4 for each geographic region and the pooled sample. Boxes depict the interquartile ranges, while whiskers are the 90 percent confidence intervals. The interquartile range for age-at-defect formation in the pooled sample is between 2.9 and 4.1 years, while the 90 percent confidence intervals are between 2.1 and 4.8 years. The range of age-at-defect formation is between 1.1 and 6.2 years. Skewness is not statistically significant for any sample, suggesting that age-at-defect formation follows a normal distribution and mean age-at-defect formation can be compared between geographic groups. No significant differences in average age-at-defect formation were found between geographic groups ($F = 0.77$; DF = 2; $P < 0.464$).

Table 2
Summary statistics for age-at-defect formation for the pooled samples and by geographic region.

Sample	Mean	Mode	Minimum	Maximum	Skewness
Pooled	3.4	3.5	1.1	5.8	0.03
Coastal Honshu	3.5	3.6	1.4	5.8	−0.009
Inland Honshu	3.4	3.9	1.7	5.2	0.3
Hokkaido	3.4	3.5	1.1	5.2	−0.008

Table 3 shows the summary statistics for LEH periodicity by geographic region and for the pooled sample. Box plots of LEH periodicity by geographic region and for the pooled sample are shown in Fig. 5. Skewness was positive and significant in each geographic region, but the data skewed in a similar direction for each region suggesting that comparing their mean periodicities is appropriate. Significant differences in average LEH periodicity were found between geographic regions ($F = 14.45$; DF = 2; $P < 0.0001$). Samples from Hokkaido and Inland Honshu have significantly higher LEH periodicities than those from Coastal Honshu in the Games-Howell post-hoc test. There was no difference in LEH periodicity between the Hokkaido and Inland Honshu samples in the Games-Howell post-hoc test.

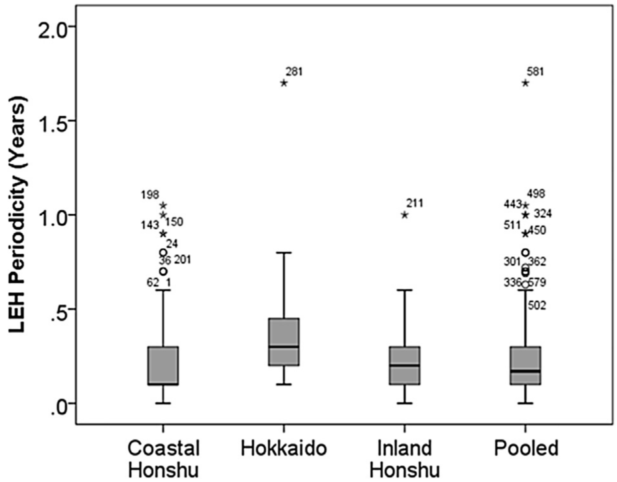

Fig. 5. Box plots of LEH periodicity for each geographic group and the pooled sample. Boxes represent interquartile ranges, whiskers represent the 90 percent confidence intervals, while symbols beyond the whiskers are either above or below the 90 percent confidence intervals.

Table 3
Summary statistics for LEH periodicity for the pooled sample and geographic regions.

Sample	Mean	Mode	Minimum	Maximum	Skewness
Pooled	0.2	0.1	0.1	1.7	2.7
Coastal Honshu	0.1	0.1	0.1	1.1	2.2
Inland Honshu	0.2	0.1	0.1	1.0	1.9
Hokkaido	0.3	0.2	0.1	1.7	2.8

4. Discussion

4.1. Linear enamel hypoplasia prevalence and chronology

A minimum of two matched LEH were identified in each individual and each tooth had at least two LEH. Macroscopic studies of LEH among Late/Final Jomon period foragers found lower LEH prevalence in these samples and differences in prevalence between geographic groups (Yamamoto, 1992; Shigehara, 1994; Temple, 2007, 2010; Oxenham and Matsumura, 2008). The results of this study suggest that LEH was more widespread among Jomon samples than previously reported and no differences in the frequency of individuals with LEH are observed as each individual was effected. Microscopic studies often find that the vast majority of individuals in skeletal samples have LEH, and identify many more LEH than macroscopic observation (King et al., 2002, 2005; Guatelli-Steinberg et al., 2004; Guatelli-Steinberg, 2008; Temple et al., 2013; Hassett, 2014). Microscopic studies may identify more defects than those using macroscopic methods due to the manner in which LEH is defined (Hassett, 2014). LEH are associated with depressions in the enamel surface and accentuated perikymata spacing in microscopic studies. Defects that are shallow and poorly defined, yet express accentuated perikymata spacing may not be readily observed by macroscopic approaches. These findings suggest that the Late/Final Jomon period foragers had high frequencies of individuals with LEH (near 100%) and few differences in LEH prevalence between geographic groups.

Age-at-defect formation was distributed between 1.1 and 5.8 years in the pooled sample, with 90 percent of LEH concentrated between 2.1 and 4.8 years. The 90 percent confidence intervals are broadly similar to the results of previous studies, which identified LEH between 2.5 and 5.5 years (Yamamoto, 1992). However, there were differences in the earliest forming defects identified by this study (1.1 years) compared to the earliest forming defects reported by Yamamoto (1992) (2.5 years). One important difference between this study and previous efforts (Yamamoto, 1992) is the criterion for inclusion based on tooth wear. This study only included teeth that preserved 90% or more of crown height. By contrast, Yamamoto (1992) included teeth without respect to tooth wear. By including teeth that were worn, previous studies may have missed LEH forming in the occlusal region of canines in individuals with elevated tooth wear, while LEH in the intermediate and cervical region of these tooth crowns was more readily recorded.

In addition, the earlier work (Yamamoto, 1992) relied only on macroscopic observation to identify LEH and may not have successfully identified defects in the occlusal third of each tooth even when tooth wear was minimal. Striae of Retzius angles are less acute in the occlusal third of anterior teeth, and this causes LEH to be comparatively shallow and less well defined in this region (Hillson and Bond, 1997; Guatelli-Steinberg, 2003; Guatelli-Steinberg et al., 2012). It is possible that previous studies failed to identify LEH at earlier ages because the expression of defects was muted by the orientation of the striae of Retzius in the occlusal third of anterior teeth. These findings suggest that previous characterizations of the range of age-at-defect formation among Late/Final Jomon period people may be associated with the limited ability of macroscopic methods to identify LEH in the occlusal third of tooth crowns, and that microscopic methods provide a more detailed picture of enamel growth disruption experienced at earlier ages.

The interquartile range for age-at-defect formation is between 2.9 and 4.1 years, while the modal age-at-defect formation was 3.4 years and median age-at-defect formation was 3.5 years. LEH found between these ages are often associated with the weaning process. Weaning is a process that begins with the introduction of complementary foods around 6-months of age and ends with the cessation of breast-feeding (Sellen, 2007). Weaning is, however, difficult to associate with age-at-defect formation for several reasons. First, the increase in LEH during these ages may be associated with striae of Retzius geometry, where defects in the intermediate and occlusal third of a tooth are easier to identify (Hillson and Bond, 1997; Humphrey, 2008; Guatelli-Steinberg et al., 2012, in press). Thus, more LEH is found at these ages due to tooth crown geometry, rather than increased stress burdens. Second, the weaning process must be isotopically estimated within a skeletal sample as there is significant variation in the ages at which this process occurs, and it cannot be estimated based on increases in the number of LEH (Humphrey, 2008).

Because LEH were identified using accentuated perikymata, striae of Retzius orientation is not considered a significant contributor to the chronological distribution of defects in this sample. In addition, weaning age has been evaluated among limited Jomon samples. For example, a considerable reduction in breast milk consumption is isotopically visible around 3.5 years in a sample of immature skeletal remains from the Yoshigo site on Honshu (Shimomi, 2008), while the Epi-Jomon site of Usu Moshiri finds a similar reduction in breast milk consumption around 4.0 years of age (Tsutaya et al., 2013). Using these estimates as a guide, it would appear that the vast majority (75%) of LEH in these samples occurs in the period leading up to the cessation of breast-feeding.

Shifts in the social identity of infants and children are also documented in the Late/Final Jomon period and should be mentioned as part of the broader pattern of social emergence associated with this process. Mortuary studies document changes in burial treatments between infancy and childhood at approximately 2.0 years of age (Yamada, 1997). Infants, aged 0.1–1.9 years, are decorated with red ochre and buried with females. Individuals between 2.0 and 5.0 years are not decorated with ochre and are buried with males. This transformation in burial practices may correspond with a broader social emergence in the Jomon identity that occurs prior to the cessation of breast-feeding and may indicate greater independence in the growing individual.

Stressors associated with the cessation of breast-feeding reflect the significant cultural, environmental, and nutritional transitions during this period. First, passive reception of immunological enzymes from breast milk significantly declines (McDade, 2003). Second, infants/children are forced to rely on foods that may be more difficult to digest and/or process in an immature oral cavity (Humphrey, 2008). Third, infants/children are susceptible to food shortages and intentional withholding of food (Rousham and Humphrey, 2002). In particular, despite the cessation of breast-feeding, children still rely on adults for the majority of food they consume (Blurton-Jones, 2007), and are therefore, highly susceptible to resource shortages. In addition, quality of weaning food plays an important role in mitigating or exacerbating stress levels based on nutritional quality (Katzenberg et al., 1996). Finally, children attain independence from adults during this time period and are subjected to a variety of external stressors from exploring local environments including physical trauma and exposure to infectious pathogens (Hill and Hurtado, 1996).

Studies that histologically evaluate the chronological distribution of LEH combined with isotopic evidence for weaning report increased LEH in the period immediately prior to (rather than following) the cessation of breast-feeding (Sandberg et al., 2014), similar to the values reported by this study. These findings suggest that social and ecological processes of maturation from infancy to childhood are costly in terms of human growth. The process of weaning itself cannot, however, be associated with the increased stress patterns observed among Late/Final Jomon period people between 3.0 and 4.0 years of age. Instead, the broader changes in the social and ecological interactions of the individual that accompanies this transition have important cumulative impacts on life histories and act to disrupt growth during this important time.

No significant differences in average age-at-defect formation were found between geographic groups. The lack of differences in average-age-at-defect formation between geographic regions may reflect the fact that stressors associated with weaning were elevated at similar ages between these locales. Future work on larger samples and studies of stable nitrogen isotopes to reconstruct the process of weaning will further clarify these patterns. However, the general findings of this study suggest that the interquartile ranges for age-at-defect formation in the Jomon samples may be associated with the social and ecological transformations that occur during the weaning process, while the lack of differences in the chronology of these defects between geographic groups may reflect similarity in the ages that these individuals were exposed to this process.

4.2. Linear enamel hypoplasia periodicity

Median LEH periodicity in these samples was approximately 0.2 years, with a range between 0.1 and 1.7 years. A previous study reported LEH periodicities between 0.4 and 0.9 years in a sample of Late/Final Jomon period foragers (Yamamoto, 1992). However, the present study identified LEH using microscopic methods, while Yamamoto (1992) relied on macroscopic observation. As noted above, LEH may be poorly defined and accentuated perikymata spacing may only be possible to identify using microscopic methods.

In addition, previous studies estimated LEH periodicity using measurements between defects (Yamamoto, 1992). However, perikymata spacing varies in different regions of tooth crowns, and the number of perikymata per millimeter increases towards the cervical region of a tooth (Reid and Dean, 2000, 2006; Guatelli-Steinberg, 2008). As a result, LEH periodicity may have been overestimated by previous studies.

Significantly greater LEH periodicity is found among Jomon people from Hokkaido and Inland Honshu compared to Coastal Honshu. This suggests that Jomon foragers from Coastal Honshu experienced repetitive stress episodes over shorter durations of time. An evaluation of LEH per individual suggests a greater number of LEH occurrences in the Coastal Honshu compared to Inland Honshu and Hokkaido samples (Table 1). Shorter LEH periodicity and more numerous episodes are associated with reduced stature and greater stress burdens among indigenous people from Australia (Littleton, 2005; Floyd and Littleton, 2006). Recent studies of body mass argue that Jomon people from Hokkaido were significantly larger than those from Coastal Honshu (Temple and Matsumura, 2011; Fukase et al., 2012). Differences in relative body size may be associated with Bergmann's rule (greater relative body mass among a northerly population due to thermoregulatory adaptation) or differences in ecological stress. Shorter stress periodicities, more numerous LEH, and smaller body mass in the Coastal Honshu compared to Hokkaido and Inland Honshu samples suggests that these trends may reflect differences in stress burdens. Jomon foragers from Coastal Honshu may have experienced a greater ecological stress burden than their counterparts from Hokkaido and Inland Honshu. Additional comparative studies that evaluate stature and growth in body size will help further support or refute this interpretation.

5. Conclusions

Age-at-defect formation and LEH periodicity were estimated in a sample of Late/Final Jomon period foragers. All individuals had a minimum of two matched-LEH. This differs from previous studies that report variation in the frequency of LEH between regions. However, shallow, poorly defined LEH may not have been observable by earlier studies that relied upon macroscopic methods. By contrast, this study was able to identify more LEH, in part, because accentuated perikymata spacing was possible to observe using a microscopic approach.

The earliest forming defects identified by this study were found at considerably earlier ages than those reported by earlier research (1.1 versus 2.5 years). Two reasons for this discrepancy are possible. First, this study only included individuals that preserved 90% or more of crown height, while earlier work did not control for tooth crown wear. Second, LEH are difficult to identify in the occlusal third of teeth because striae of Retzius angles are less acute in that region of the tooth. Microscopic methods help alleviate this problem by defining LEH based on perikymata spacing as well as depressed enamel.

The interquartile ranges of LEH in the pooled Jomon sample was between 2.8 and 4.1 years. Mortuary practices suggest identities that may reflect emerging independence after 2.0 years. Isotopic studies of Late/Final Jomon period samples estimate that the cessation of breast-feeding occurs during this time period, and the elevated frequency of LEH during this developmental window may be associated with this process. The lack of differences in average age-at-defect formation suggests that this process of social and ecological independence occurred at similar ages between geographic groups.

Average LEH periodicity was approximately 0.2 years in the pooled sample. This is considerably shorter than the range reported by earlier work (0.4–0.9 years). The shorter periodicity found by this study may be associated with the ability of microscopic methods to identify a greater number of LEH. In addition, previous studies relied on measurements of distance between LEH to estimate LEH periodicity. This may have caused an overestimation of LEH periodicity as perikymata spacing varies in different regions of teeth. Jomon foragers from Coastal Honshu had significantly shorter stress periodicities and more LEH per individual than samples from Hokkaido and Inland Honshu. Interestingly, samples from Honshu also have smaller body mass than those from Hokkaido (Fukase et al., 2012). This suggests a comparatively greater stress burden among Jomon people from Coastal Honshu. However, further comparisons of body size and growth should be evaluated between these samples to support this finding.

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