A Comparative Study of Stress Episode Prevalence and Duration Among Jomon Period Foragers from Hokkaido

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ABSTRACT This study reconstructs linear enamel hypoplasia (LEH) prevalence and stress episode duration among Jomon period foragers from Hokkaido, Japan (HKJ). Results are compared to Jomon period samples from coastal Honshu, Japan (HSJ) and Tigara Inupiat from Point Hope, Alaska (PHT) to provide a more comprehensive perspective on the manifestation of stress among circum-Pacific foragers. LEH were identified macro- and microscopically by enamel surface depressions and increased perikymata spacing within defects. Individuals with more than one anterior tooth affected by LEH were labeled as LEH positive. Stress episode durations were estimated by counting the number of perikymata within the occlusal wall of each LEH and multiplying that number by constants reflecting modal periodicities for modern human teeth. LEH prevalence and stress episode duration did not differ significantly between the two Jomon samples. Significantly greater frequencies of LEH were found in HKJ as compared to PHT foragers. However, HKJ foragers had significantly shorter stress episode durations as compared to PHT. This suggests that a greater proportion of HKJ individuals experienced stress episodes than did PHT individuals, but these stress events ended sooner. Similarity in stress experiences between the two Jomon samples and differences between the HKJ and PHT are found. These findings are important for two reasons. First, stress experiences of foraging populations differ markedly and cannot be generalized by subsistence strategy alone. Second, due to significant differences in episode duration, stress experiences cannot be understood using prevalence comparisons alone. Am J Phys Anthropol 152:230–238, 2013. © 2013 Wiley Periodicals, Inc.

KEY WORDS enamel hypoplasia; Jomon; systemic stress; perikymata; ontogeny

BACKGROUND Ecological and dietary context

The northern latitudinal range of Hokkaido is ~41.4° to 45.5° and is classified as a continental microthermal environment. Hokkaido Island experiences temperatures ranging from –10°C to 25°C with accumulations of sea ice during winter months (Fukui, 1977) and is covered by coniferous species (Tsukada, 1986). The average temperature of this region is below freezing from November through March (Fukui, 1977). Warmer temperatures are reported for this region during the Holocene Climatic Optimum (7000–3000 BP), with cooling reported for the duration of the Late/Final Jomon (3000 through 2300 BP) cultural occupation (Kawahata et al., 2003; Igarashi and Zharov, 2011). As a result, this landscape presented

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a unique set of environmental challenges for Jomon period foragers.

Sites that preserve Jomon dental material from Honshu are all located within the temperate zones of Japan. For this study, coastal Honshu includes the regions of Tokai and Sanyo, encompassing a latitudinal range of 33.6° through 35.0° N. These areas experience annual temperatures that range between 0 and 37°C with a mean annual temperature between 15 and 16°C; no sea-ice accumulation is reported and average monthly temperatures remain above freezing year-round (Fukui, 1977).

The latitudinal coordinate of the Point Hope, Alaska site is 68° N. The terrain of Point Hope is classified as dense tundra with 25%–100% ground cover. Mean annual temperatures have oscillated between −15 and −8°C over the past 500 years (Hinzman et al., 2005), with winter wind gusts reaching 50 km/h (Rainey, 1947). Approximately 115–153 mm of precipitation per year is documented for the Barrow Island/Point Hope region prior to recent changes in rainfall associated with human induced climate change (Curtis et al., 1998). In addition, daylight hours are severely restricted from November through February, though periods of twilight allow for limited hunting (Rainey, 1947). The climates occupied by the three groups represent a gradient, with temperate coastal woodlands in Honshu, subarctic pine forests in Hokkaido, and arctic tundra at Point Hope. Some similarity between the Hokkaido Jomon and Point Hope Tigara exists, as both groups experienced challenging winters, though clear differences in average annual temperature and sunlight hours are present between the two samples.

Environmental differences among the samples likely produced differences in resource procurement methods and resultant protein intake between groups. Similarities in lithic technologies used for resource procurement are found between the Hokkaido Jomon and Point Hope Tigara, with a particular emphasis on those associated with marine mammal hunting (Larsen and Rainey, 1948; Akazawa, 1986). The emphasis on tools used to hunt maritime mammals differentiates the Jomon of Hokkaido from those of Honshu and suggests dietary differences between the two groups (Akazawa, 1982, 1986, 1999). Stable carbon and nitrogen isotope analysis of human skeletal remains from Hokkaido suggest that maritime mammals contributed 40–70% of protein consumption and that fish accounted for an additional 20–40% of protein intake (Minagawa and Akazawa, 1992). Jomon foragers from Hokkaido also consumed plant foods, including starchy carbohydrates and domesticated cereal grasses (Imamura, 1996; Habu, 2004; Crawford, 2005).

Whale, seal, and fish were most frequently consumed by the Tigara inhabitants of Point Hope (Larsen and Rainey, 1948; Costa, 1980, 1982; El-Zaatari, 2008). The consumption of raw tubers is ethnographically documented during summer months among the Tikermiut of Point Hope, but access to these foods was restricted for most of the year (Larsen and Rainey, 1948). For the Honshu Jomon, isotopic data indicate that 30–50% of the diet was derived from fish and shellfish, and 30% from terrestrial mammals (Minagawa and Akazawa, 1992). Greater levels of plant food consumption among the Honshu Jomon (20–30% of protein intake) are indicated by elevated δ13C values and frequencies of dental caries in comparison to the Hokkaido Jomon (Minagawa and Akazawa, 1992; Oxenham and Matsumura, 2008). There is little evidence of maritime mammal consumption among the Jomon of Honshu, for these foods appear to have comprised only 3–17% of protein intake (Minagawa, 2001). Together, these findings suggest greater similarity between the Hokkaido Jomon and Point Hope Tigara in primary resource consumption (marine mammals), coupled with differences in secondary resources (plant foods including domesticated cereal grasses).

By contrast, differences between the Hokkaido and Honshu Jomon occur in the primary resources consumed (sea mammals and fish vs. fish), coupled with similarities in the consumption of secondary resources (plant foods including domesticated cereal grasses).

**Linear enamel hypoplasia**

LEH is produced when shortened enamel prisms are deposited by ameloblasts following a stress event (Hillson, 1996) when the distal, prism-forming section of the Tomes process (enamel secreting organ) temporarily or permanently recedes or is lost completely through extensive recession of the organ (Kierdorf and Kierdorf, 1997; Rissing, 1998; Kierdorf et al., 2004; Witzel et al., 2008). By and large, studies of dental samples from known environments confirm that increases in LEH prevalence are associated with elevated levels of nutritional stress (Goodman et al., 1991; May et al., 1993; Zhou and Corrigan, 1993; Lukacs, 1999; Lukacs et al., 2001; Guatelli-Steinberg and Benderlioglu, 2006), although other factors such as febrile disease and parasitic infection also produce LEH (Suckling and Thurley, 1984; Suckling et al., 1986; Goodman and Rose, 1991).

Bioarchaeological studies of hunter-gatherers compare frequencies of LEH during shifts in population density, diet, and social complexity and provide a baseline for understanding the relationship between the environment and growth disruption (Walker and Lambert, 1992; Yamamoto, 1992; Lambert, 1993; Lukacs and Pal, 1993; Koga, 2003; Temple, 2007, 2010; Oxenham and Matsumura, 2008; Sawada et al., 2008; Temple, 2010). Microstructures (perikymata) inside LEH have a known modal periodicity in modern human populations (Hillson and Bond, 1997; Fitzgerald, 1998; Reid and Dean, 2006; Reid and Ferrell, 2006; Smith et al., 2007) and LEH with as few as one and as many as 30 perikymata have been observed macroscopically by previous studies (Hillson and Bond, 1997). This suggests that considerable information regarding stress experiences are missed by studies only reporting LEH prevalence as these episodes may represent disruptions of different durations. To augment studies of LEH prevalence, the number of perikymata within LEH is often used to reconstruct stress episode duration (Hillson and Bond, 1997; King et al., 2002; Guatelli-Steinberg et al., 2004; King et al., 2005; Guatelli-Steinberg, 2008; Temple et al., 2012).

Anthropological studies of high latitude foragers have addressed questions of disease and nutritional stressors to better understand the biological impact of living in an environment with extended, freezing winters, hazardous terrain, long periods of resource scarcity, and exposure to marine-born parasites (Buikstra, 1976; So, 1980; Merbs, 1992; Oxenham and Matsumura, 2008, 2013). Comparisons of a health index derived from the Tigara and Ipiutak occupants of Point Hope, Alaska suggest...
lower levels of nutritional stress when compared to other individuals from the Western Hemisphere, but different patterns of infectious disease load and malnutrition between the two Point Hope samples (Dabbs, 2011). Purportedly low levels of nutritional stress among arctic foragers are often attributed to the caloric density and micronutrient availability in these diets (So, 1980; Cordain et al., 2000). By contrast, high latitude Kitoi foragers from Cis-Baikal, Siberia have elevated frequencies of LEH, despite reliance on maritime mammals and riverine fish (Lieverse et al., 2007; Lieverse, 2010). These findings indicate that the stress experiences of high latitude foragers varied, even when reliance on high calorie foods was common between groups.

Previous studies report contrasting results for LEH prevalence among Hokkaido Jomon, Honshu Jomon, and Point Hope. Lower frequencies of LEH were found in the sample of Jomon people from Hokkaido as compared to the sample of Jomon period foragers from Honshu (Oxenham and Matsumura, 2008). Conversely, elevated frequencies of LEH are reported among the Hokkaido Jomon, and these frequencies were similar to those found among a sample of Jomon people from Honshu (Hoover and Matsumura, 2008).

Studies of LEH prevalence are problematic because the presence of each stress event is treated as a comparable event. In addition, these studies yielded inconsistent results in reconstructing LEH prevalence among Jomon foragers from Hokkaido, with one suggesting similarity in stress experiences with Jomon foragers from Honshu, while another suggests similarity with mixed samples from Point Hope. This study builds upon these analyses by comparing LEH defect prevalence and stress episode duration among Jomon foragers from Hokkaido, with one suggesting similarity in stress experiences with Jomon foragers from Hokkaido samples from coastal Honshu and Tigara inhabitants of Point Hope, Alaska. These comparisons will help reveal whether the differences in diet and ecological landscapes between the Hokkaido and Honshu Jomon produced variation in LEH prevalence and stress episode duration or if the similarities between the Hokkaido Jomon and Point Hope Tigara in diet and ecological landscapes produced comparable LEH prevalence and episode stress duration.

Research hypotheses

Two null hypotheses are tested to investigate similarities and differences in the stress experience of the Hokkaido Jomon relative to the stresses experienced by the Honshu Jomon and Point Hope Tigara. First, no differences in the manifestation of stress will be observed between the Hokkaido Jomon and Honshu Jomon. This hypothesis is based on earlier findings that found no differences in LEH prevalence between these two samples (Hoover and Matsumura, 2008). Second, no differences in the manifestation of stress will be observed between the Hokkaido Jomon and Point Hope Tigara. This hypothesis is based on results suggesting a similar prevalence of LEH between these two samples (Oxenham and Matsumura, 2008).

MATERIALS

Jomon samples from Hokkaido used in the macroscopic evaluation of LEH were recovered from seven archeological sites dated between 4000 and 2300 BP, while those used in the microscopic analysis of LEH were recovered from four archeological sites dated to the same time period (Fig. 1a). The sample composition for Jomon people from Hokkaido is listed in Table 1. The number of individuals available for microscopic observation ($n = 5$) is less than the number of individuals with macroscopically observable LEH ($n = 23$). These samples differ in size because taphonomic processes render perikymata unobservable in some cases.

Jomon dental samples from Honshu were recovered from four archeological sites along the central and western coastline (Tokai and Sanyo). Dental samples from all four sites were included in the macroscopic analysis of LEH, but high resolution impressions were only collected from individuals from Inariyama,
Tsukumo, and Yoshigo. Similar to the Hokkaido sample, the total number of individuals available for microscopic observation ($n = 20$) was also lower than the total number of individuals with macroscopically observable LEH ($n = 69$).

The location of the Point Hope, Alaska site is depicted in Figure 1b. Sample composition for the Tigara from Point Hope is listed in Table 1. These remains were procured during two archeological field seasons conducted by the American Museum of Natural History between 1939 and 1941. The Tigara cultural occupation dates between AD 1300 and 1700 (Larsen and Rainey, 1948). Once again, a greater number of individuals were available for macroscopic ($n = 21$) than microscopic ($n = 9$) observation of LEH, owing to preservation of perikymata.

METHODS

Macroscopic methods

Macroscopically identified LEH were compared between the samples for two reasons. First, the study is interested in whether variation in LEH prevalence is possible to identify between the two Jomon samples and the Hokkaido Jomon and Point Hope Tigara samples as this issue has not been clarified by previous research. Second, the study is interested in the comparability of macroscopically estimated LEH prevalence and its association with stress episode duration. DHT recorded LEH for the Jomon dental series, while DGS recorded LEH for the Point Hope dental series. Recording methods used by DHT and DGS for the macroscopic sample were equivalent. LEH were recorded as deficiencies in enamel thickness appearing as horizontal grooves or pits on tooth surfaces on all anterior teeth for both samples. Examination of tooth surfaces was aided by the use of a magnifying glass (10x) and diffuse fluorescent lighting.

The identification of LEH follow Skinner et al. (1995) and Guatelli-Steinberg (2003), where adjacent perikymata were compared to possible LEH to identify the wider spacing associated with LEH. The manifestation of LEH ranged in severity from macroscopically apparent to those that could not be viewed without the assistance of a magnification device.

Intraobserver error was calculated using a kappa statistic (Cohen, 1960). DGS scored 81 (almost perfect) and DHT scored 63 (substantial agreement) (Guatelli-Steinberg et al., 2004; Temple, 2007). These values exceed those reported by earlier studies of intraobserver error (Goodman et al., 1987; Berti and Mahaney, 1995). Although the data were collected separately, preventing an interobserver test, minimal differences in LEH scoring are expected when observer methodologies are similar (Oxenham and Matsumura, 2008). In fact, the highest level of interobserver agreement in macroscopically assessing the presence of LEH is found in anterior teeth, especially in circumstances where minimum standards are set for the identification of LEH (Goodman et al., 1987; Berti and Mahaney, 1995). Both observers set identical minimum criteria for identifying LEH and limited observations to anterior teeth.

Under-enumeration of LEH has been reported in the absence of microscopic analysis because defects that are only observable microscopically are missed. Other difficulties in LEH interpretation arise because those associated with localized trauma appear similar to those caused by systemic stress (Hillson, 1996). However, LEH arising from trauma usually appear on a single tooth, while LEH produced by systemic stress ought to be observable on all teeth forming at the same time a stress episode was experienced (Hillson, 1996). In the absence of detailed estimations of age-at-defect formation, many macroscopic studies report LEH prevalence according to the manifestation of LEH on antimeres or more than one anterior tooth (Guatelli-Steinberg et al., 2004; Temple, 2007). In the present study, individuals with two or more anterior teeth with observable defects were labeled.
LEH positive. To calculate prevalence, this number was divided by the total number of individuals with two or more observable anterior teeth.

**Microscopic methods**

DHT collected the microscopic data for the Jomon dental samples. For the Jomon dental samples from Hokkaido and Honshu, high resolution tooth impressions were produced by applying Coltene President Plus Regular Body polyvinyl siloxanes to the labial surface of anterior teeth that preserve 90% or more of crown height. The reported resolution for these impressions is accurate within 1 μm (Beynon, 1987; Hillson, 1992). Casting methodology for replicas followed protocols established by Temple et al. (2012). All tooth replicas were studied using a measuring microscope provided by Spectra-Services (Rochester, NY). Measurements of perikymata spacing and enamel depth were collected using the Vision Gauge software program (VISIONx, Pointe Claire, PQ, Canada). For a detailed description of these measurements see Temple et al. (2012). Briefly, perikymata were identified as regularly spaced grooves running around the circumference of the tooth (Hillson and Bond, 1997). Perikymata spacing was measured along the y-axis of a tooth surface. The enamel surface profile was measured using the z-coordinate arm of the measuring microscope, which runs at a 90° angle to the y-axis. The measurement coordinate is set to zero (mm) at the most occlusal point of a tooth. 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.

LEH were identified by comparatively wider spaced perikymata and a depression in the enamel surface (Hillson and Bond, 1997; King et al., 2002). Low powered microscopic analysis ensured the presence of an LEH if the depression was not visible in the enamel surface profile. Figure 2 is a microscopic (10×) image of perikymata taken from a right second mandibular incisor of a young-adult male from the Takasago site (Specimen 194). The LEH in the image is outlined with a black square, and the exposed striae of Retzius planes in the occlusal wall of the defect are numbered. The defect manifests as a depression in the enamel surface combined with relatively widely spaced perikymata in the occlusal wall of the defect. Figure 3 shows the enamel depth and perikymata spacing for the same tooth. The LEH pictured in Figure 2 is listed in Figure 3 as E. Some accentuated perikymata in Figure 2 that were not labeled as LEH may be noted. These instances represent circumstances where the LEH was not possible to match across teeth or was not accompanied by an enamel surface depression, possibly because not all LEH defects manifest as typical furrow-form defects (Guatelli-Steinberg, 2003).

Recall that LEH produced by systemic stress should be observable on all teeth actively forming at the time a stress episode was experienced. Microscopically identified LEH in the Hokkaido Jomon were only attributed to systemic stress if the defect was chronologically matched on additional anterior teeth. Estimating similar age-at-defect formation for LEH across individual dentitions relied on the decile method of Reid and Dean (2000, 2006). In those cases where LEH defects were matched at the same developmental decile, the defects were attributed to the same stress episode. Deciles were based on crown heights that were calculated for the Jomon samples from Hokkaido and Honshu.

The total number of perikymata found within the occlusal wall of each matched LEH (stress episode) were counted and averaged. For this study, the occlusal wall of each LEH was defined by a combination of sloping enamel and accentuated perikymata. Modal periodicities for perikymata formation in modern humans from Europe or South Africa are either 8- or 9-days, depending on the sample (Reid and Dean, 2006; Reid and Ferrell, 2006). The average number of perikymata within the occlusal wall of each stress episode was multiplied by factors of 8 and 9 to estimate stress episode duration.

Methods for the microscopic analysis of the Point Hope Tigara dentitions follow Guatelli-Steinberg et al. (2004). Anterior teeth with 70% or more of crown height were used. LEH were analyzed on single canines. All defects were, however, matched on antimeric canines to ensure that the LEH was attributable to a stress episode and not resampled. Guatelli-Steinberg et al. (2004, p. 72–73) state that each defect was matched within the same developmental deciles between canine antimeres and that these teeth had equivalent wear. Impressions and replicas were produced using methods aforementioned, and each specimen was coated in gold palladium for scanning electron microscopy (SEM). Using SEM imaging, LEH were identified as depressions in the enamel surface with comparatively widely spaced perikymata. Where possible, the total number of perikymata within the occlusal wall of each defect was counted. For the SEM analysis, the occlusal wall of a defect was visually identified as the sloping wall of the occlusal portion of a groove in which perikymata are more widely spaced (as per Hillson and Bond, 1997). The division between the occlusal and cervical portion of the LEH could not be determined in two defects. Numbers of perikymata found in the occlusal and cervical walls of defects in the Point Hope sample are approximately equal, and halving the total number of perikymata within an LEH yields a value that approximates the number of perikymata in the occlusal wall (Guatelli-Steinberg, 2008). Thus, in these two instances, the total number of perikymata in each LEH were counted and halved.

To be certain, stress episode duration was estimated in the Point Hope sample using observations from canine teeth obtained from scanning electron microscopic analysis. This differs from the methods used to estimate stress episode duration among the Jomon samples, where measurements of enamel surface profiles and perikymata spacing were obtained using an engineer’s measuring microscope and related software. However, canine teeth and incisors have similar numbers of perikymata in the appositional zone of enamel (Hillson and Bond, 1997). In addition, LEH identified using measurements from an engineer’s measuring microscope are mostly or entirely visible upon inspection with scanning electron microscopy (Hillson and Bond, 1997; King et al., 2002). One difference between canines and incisors is the age at which imbricational enamel is visible, ranging between 0.1 and 0.7 years, depending on the teeth compared (Reid and Dean, 2000, 2006). This is not possible to correct, but may not represent a hindrance to this study since most defects in the Point Hope sample are found in the intermediate and cervical third of canines and incisors (Guatelli-Steinberg et al., in review).

Thus, there is no evidence for the formation of defects in the developmental regions that are missing from the

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Statistical analysis

LEH prevalence was compared using a Fisher’s exact test. Box plots were produced to depict interquartile ranges of stress episode duration using 8- and 9-day periodicities. Stress episode duration was compared between the samples using a one-way ANOVA with Tukey’s HSD test for each pair-wise comparison. Average stress episode durations were between samples assessed using all combinations of modal periodicities.

RESULTS

Macroscopically observed LEH prevalence is listed in Table 1. LEH prevalence did not differ significantly between the Hokkaido and Honshu Jomon period samples (X² = 1.113; P ≤ 0.401). By contrast, LEH frequencies were found to be significantly higher among the Hokkaido Jomon compared to Point Hope Tigara (X² = 8.0047; P ≤ 0.011).

Microscopic prevalence of LEH is also listed in Table 1. Box plots of stress episode duration are depicted in Figure 4. The boxes represent interquartile ranges of stress episode duration for the samples at both 8- and 9-day periodicities assigned to the perikymata. The whiskers indicate the 95% confidence intervals, and those stress episodes found above or below the whiskers represent stress episode durations that are outside the 95% confidence interval for each sample. When 8- or 9-day periodicities are assigned to perikymata, interquartile ranges of stress episode durations do not overlap between the Hokkaido Jomon and Point Hope Tigara in any series of comparisons. ANOVA indicates that the differences in stress duration between all groups at all perikymata periodicities is significantly different (F = 6.54; P < 0.0001). Significant differences (P < 0.05) in stress duration stemming from the Tukey’s pair-wise comparisons of the groups at different perikymata periodicities are reported in Table 2 using an asterisk. No significant differences in stress episode duration were found between the Jomon samples from Hokkaido and Honshu. Regardless of perikymata periodicity, stress episode durations are significantly shorter in the Hokkaido Jomon compared to Point Hope Tigara.

DISCUSSION AND CONCLUSIONS

LEH prevalence did not significantly differ between the Hokkaido and Honshu Jomon. Significantly greater LEH frequencies were found among Jomon people from Hokkaido compared to Point Hope Tigara. As such, these results corroborate the previous study by Hoover and Matsumura (2008) that found similarity in LEH prevalence between the Jomon of Hokkaido and of Honshu, but contrast with the previous study by Oxenham and Matsumura (2008), which found significant differences between the two Jomon samples coupled with similar frequencies between the Jomon of Hokkaido and a mixed sample of foragers from Point Hope. The study by Hoover and Matsumura (2008) used comparable methodologies to estimate LEH prevalence based on individuals with multiple teeth. By contrast, Oxenham and Matsumura (2008) evaluated the prevalence of all teeth with LEH. The method of basing frequencies on all teeth may over- or under-estimate the prevalence of LEH in a dental sample because individuals may contribute an unequal proportion of teeth to the sample (Temple, 2010).

Despite a significantly higher LEH prevalence among the Hokkaido Jomon compared to Point Hope Tigara, the Hokkaido Jomon had a significantly shorter average stress episode duration as compared to the Point Hope Tigara. These differences are found because LEH prevalence and stress episode duration measure two differing aspects of the stress experience. LEH prevalence decreased in postcontact American Indians of the Georgia Bight when compared to earlier foragers, but stress episode duration increased (Larsen and Hutchinson, 1992). Although this earlier study (Larsen and Hutchinson, 1992) relied on LEH width, the results were an important step towards recognizing that information derived from LEH prevalence and stress duration may differ. In another study, similar LEH prevalence between Point Hope Tigara and Neandertals from Krapina were found, yet comparatively greater stress episode durations in Point Hope Tigara were reported (Guatelli-Steinberg et al., 2004). In still another study, significant differences in LEH prevalence between females in two historic London cemeteries were found, but there were no significant differences in stress episode duration between these two groups (King et al., 2005). Thus, while concordance between LEH prevalence and stress episode duration is possible, it should not be expected.

Differences and similarities in stress episode prevalence and duration between the Hokkaido Jomon, Honshu Jomon, and Point Hope Tigara may be associated with dietary breadth. The dietary strategies of Jomon
people from Hokkaido focused on maritime mammals, though terrestrial mammals as well as wild and domesticated plants were exploited (Akazawa, 1986; Minagawa and Akazawa, 1992; Crawford and Bleed, 1998; Minagawa, 2001). This suggests that Hokkaido Jomon had access to foods with sufficient macro- and micronutrients, which may have helped mitigate stress episode duration during periods of resource scarcity (Akazawa, 1986). It does, however, remain possible that Hokkaido Jomon were more frequently met with resource shortages than the Point Hope Tigara. Indeed, seasonal challenges to resource acquisition are reported throughout the calendrical cycle in Hokkaido (Crawford and Bleed, 1998). These transitions may have resulted in nutritional insecurity; however brief, thereby producing a greater prevalence of stress episodes.

Archeological evidence suggests that dietary choices of the Point Hope Tigara were few and focused almost entirely on fat and protein derived from maritime mammals and fish (Rainey, 1947; Larsen and Rainey, 1948; Costa, 1982, 1986; El-Zaatari, 2008). Maritime mammals and fish provide an excellent and direct source of macro- and micronutrients, with elevated levels of vitamins A and D derived from fish oils, while consumption of raw organ meat likely met the need for vitamin C (So, 1980; Cordain et al., 2000). However, these fall/winter diets were deficient in micronutrients such as folic acid, calcium, and magnesium (Sayed et al., 1976; So, 1980; Bersamin et al., 2007). Micronutrient deficiencies, particularly calcium, produce LEH in numerous clinical and experimental settings (Mellanby, 1939; Gottlieb, 1941; Nikiforuk and Fraser, 1981; Goodman et al., 1987, 1991; May et al., 1993), and may help explain the differences in stress duration between the Hokkaido Jomon and Point Hope Tigara.

Infectious disease is another potential contributor to differences in LEH prevalence and stress episode duration between the Hokkaido Jomon and Point Hope Tigara. Nonspecific and specific skeletal indicators of infection are reported at low frequencies in these skeletal samples (Oxenham and Matsumura, 2013). However, maritime mammals and fish contain high parasite loads (Thompson et al., 2006). Higher frequencies of cribra orbitalia are found in the Hokkaido Jomon compared to Point Hope Tigara (Oxenham and Matsumura, 2008, 2013), and several species of parasites have been identified in coprolites (Kanehara and Kanehara, 1995; Matsui et al., 2003). Thus, the greater prevalence of LEH in the Hokkaido Jomon as compared to Point Hope Tigara could reflect more frequent incidents of parasite infection.

By contrast, lower average stress episode duration in the Hokkaido Jomon relative to Point Hope Tigara may also be associated with a greater capacity to stave off such infections either through behavioral or immunological interventions. Here, Jomon people from Hokkaido may have more successfully thwarted stressful events once in process through stronger immune responses or behavioral choices that served to mitigate parasite infection.

The synergistic interaction of nutritional status and immunological responses to invading pathogens is also important to consider when interpreting patterns of stress between Hokkaido Jomon and Point Hope Tigara. For example, elevated levels of micronutrient deprivation are associated with weakened immunological responses to invading pathogens (Chandra, 2002). Immunological activation in response to parasitic infection, helminthes in particular, is an important component to resisting or maintaining levels of infection that do not disrupt normal physiological functions (MacDonald et al., 2002; Gause et al., 2003). Thus, it may be that members of Jomon populations were more frequently exposed to pathogens, as demonstrated by elevated LEH prevalence, but they may have been more successful at responding physiologically to these challenges than the Point Hope Tigara, as demonstrated by elevated LEH prevalence. Here, the Jomon immune system is hypothesized to have been more responsive due to greater micronutrient intake, while the Tigara immune system may have been compromised by their deficient consumption of micronutrients.

The unfortunate reality of studying LEH is that any of the above offered interpretations or various combinations of infectious disease and dietary insufficiencies may have resulted in the patterns of stress reported by this study. One important set of conclusions regarding biocultural adaptation among these prehistoric people is, however, important to highlight. First, despite the fact that recent studies often emphasize the comparability of diet and ecological landscapes between the Hokkaido Jomon and Point Hope Tigara, differences in LEH prevalence and stress duration occur between the two samples. These findings point towards the Hokkaido Jomon as having experienced more frequent incidents of stress, but the duration of these stress events were shorter than the rarer, but longer, stress episodes suffered by the Point Hope Tigara. Second, despite the fact that archeological studies emphasize the disparate nature of the culture and environment between the Hokkaido and Honshu Jomon, similarities in LEH prevalence and stress episode duration occurred among members of these groups. Such findings indicate similarity in stress experiences between the ecologically and geographically distinct Jomon samples. This may be related to either shared biological and cultural factors that promoted resistance to stress events, or comparable incidences and durations of environmental challenges that have produced these episodes.

In addition, previous studies homogenized stress experiences among hunter-gatherer populations from arctic and subarctic contexts suggesting a generalized “healthy” lifestyle, the so-called “Inuit Paradox” (So, 1980; Cordain et al., 2000). The results of this study do, however, reveal some complexity in the manifestation of stress between the Hokkaido Jomon and Point Hope Tigara in terms of stress episode prevalence and duration. As noted above, frequent incidents of stress were found among the Hokkaido Jomon, but comparatively longer stress episode durations were found among the Point Hope Tigara. This suggests environmental challenges that disrupt physiological homeostasis occur through complex pathways and produce variations in the way populations experience stress. The adoption of categorical references to stress experiences of prehistoric foragers such as “healthy” or “less healthy” in response to the frequencies of non-specific indicators of stress glosses over this important finding.

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