Dietary Variation and Stress Among Prehistoric Jomon Foragers From Japan

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ABSTRACT  Current archaeological evidence indicates that greater dietary reliance on marine resources is recorded among the eastern Jomon, while plant dependence prevailed in western/inland Japan. The hypothesis that the dietary choices of the western/inland Jomon will be associated with greater systemic stress is tested by comparing carious tooth and enamel hypoplasia frequencies between the eastern and western/inland Jomon. Demographic collapse coincides with climate change during the Middle to Late Jomon period, suggesting dwindling resource availability. It is hypothesized that this change was associated with greater systemic stress and/or dietary change among the Middle to Late Jomon. This hypothesis is tested by comparing enamel hypoplasia and carious tooth frequencies between Middle to Late and Late to Final Jomon foragers. Enamel hypoplasia was significantly more prevalent among the western/inland Jomon. Such findings are consistent with archaeological studies that argue for greater plant consumption and stresses associated with seasonal resource depletion among the western/inland Jomon. Approximately equivalent enamel hypoplasia frequencies between Middle to Late and Late to Final Jomon foragers argue against a demographic collapse in association with diminished nutritional returns. Significant differences in carious tooth frequencies are, however, observed between Middle to Late and Late to Final Jomon foragers. These results suggest a subsistence shift during the Middle to Late Jomon period, perhaps in response to a changed climate. The overall patterns of stress documented by this study indicate wide-spread environmentally directed biological variation among the prehistoric Jomon.

KEY WORDS Jomon; enamel hypoplasia; dental caries; Japan; bioarchaeology; forager health; East Asia

This study evaluates patterns of health and subsistence behavior among the prehistoric Jomon using bioarchaeological data. Jomon populations were part of a 10,000 year foraging tradition in the Japanese islands that began between 13,000 and 10,000 years BP. Jomon foragers likely represent the descendents of Pleistocene nomads who entered Japan by crossing a land-bridge from Southeast Asia (Hanihara, 1991; Turner, 1992). These groups were relatively isolated until migrants from the Asian continent entered Japan c. 2,500 years BP. This study focuses on the Middle to Final Jomon period (5,000 through 2,500 years BP), a temporal sequence characterized by subsistence heterogeneity and population decline.

Greater focus on plant-based resources among the western/inland Jomon and marine-based foods among the eastern Jomon are evinced through tool kit and stable isotopes analyses. Discriminant function analysis of tool types from 94 Middle to Final Jomon sites separated settlement systems into three resource groups: two settlement types that best fit marine and hunting (Akazawa, 1986). The first type of settlement is characterized by stemmed scrapers, stone awls, and flake scrapers with a negative correlation with chipped stone axes (Akazawa and Maeyama, 1986). This group is concentrated above 38° north latitude in northern Japan. The second group was discriminated by grooved stone net sinkers, chipped projectile points, and polished stone axes and located in central Honshu between 137° longitude and south of 38° north latitude. This region is categorized as eastern

inland Jomon. Such findings are consistent with archaeological studies that argue for greater plant consumption and stresses associated with seasonal resource depletion among the western/inland Jomon. Approximately equivalent enamel hypoplasia frequencies between Middle to Late and Late to Final Jomon foragers argue against a demographic collapse in association with diminished nutritional returns. Significant differences in carious tooth frequencies are, however, observed between Middle to Late and Late to Final Jomon foragers. These results suggest a subsistence shift during the Middle to Late Jomon period, perhaps in response to a changed climate. The overall patterns of stress documented by this study indicate wide-spread environmentally directed biological variation among the prehistoric Jomon.

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Japan, where dietary behavior was comparable to herbivorous ungulates and Yosekura in western Japan, where dietary behavior was primarily reliant on plant resources (Akazawa, 1999). Stable isotopic evidence for plant consumption is, however, reported from coastal sites in eastern Japan, while evidence of marine consumption is recorded among some inland Jomon sites indicating some dietary variability within regions (Mina-gawa and Akazawa, 1992; Yoneda et al., 2004).

On a global scale, the level of contrast in diet between the eastern and western Jomon is more often observed during the agricultural transition, where greater frequencies of enamel hypoplasia and carious teeth are reported among many plant dependent agriculturalists (see Larsen, 1987, 1995). These declines in health and well-being are associated with a continuum of environmental changes that include increased sedentism and population density as well as the consumption of foods with poor micronutrient availability and heavy carbohydrate loads (Larsen, 1987, 1995, 2002).

Plant-based diets are associated with general growth disruption and poor nutritional status if they are not diverse and representative of the necessary micronutrients essential to growth and development (Murphy and Allen, 2003). These findings have, for example, been demonstrated in a clinical setting where animals deprived of vitamin A more frequently experienced disrupted enamel formation (May et al., 1993). Furthermore, many of the plant foods consumed by the western/inland Jomon were seasonable, and shortages may have exacerbated health during periods of resource scarcity (Akazawa, 1999). This paper, therefore, tests the hypothesis that the dietary choices of the western/inland Jomon were associated with greater levels of systemic stress and oral disease. This hypothesis will be tested by comparing frequencies of enamel hypoplasia and carious teeth between the eastern and western Jomon.

Other indications of behavioral plasticity among the prehistoric Jomon are revealed through reactions to climate change. Climatic cooling is evidenced by retreating oak forests dated to c. 5,000 years BP with intensification of this trend recorded around 4,400 years BP (Koyama, 1978; Tsukada, 1986). This environmental change is associated with depopulation in inland and eastern Japan during the Late and Final Jomon period (Koyama, 1978). One interpretation of this population decline is that food plants were unable to adapt to colder environments resulting in diminished food returns for plant dependent Jomon foragers. Diminished food returns accelerated stress among local groups causing them to seek out alternative resources from different environments. Evidence supporting this idea has, however, not been reported (Habu, 2004: 253–254). Instead, studies of Jomon dispersal patterns suggest the possibility of dietary change and migrations to less densely populated areas.

This paper, therefore, tests two additional hypotheses. First, it is hypothesized that foragers from the Middle to Late Jomon period will have greater evidence of systemic stress than Late to Final Jomon people. This hypothesis will be tested by comparing frequencies of enamel hypoplasia between Middle to Late and Late to Final Jomon foragers from western/inland Japan. Alternatively, evidence for a dietary shift associated with a behavioral response to climate change will be observed between the Middle to Late and Late to Final Jomon periods. The alternative hypothesis differs from the first by suggesting that Jomon foragers were able to respond to climate change through shifting dietary foci and mitigating stress levels. This hypothesis will be tested by comparing proportions of carious teeth between Middle to Late and Late to Final Jomon foragers.

**MATERIALS AND METHODS**

This paper uses the term eastern Japan as a geographic and subsistence designation for marine foragers from Tokai and Kanto. Western/inland Japan is a geographic and subsistence designation for Jomon gatherers from the Chubu and Chugoku regions, where dietary choices were more often based around plant gathering and cultivation. The temporal focus of this paper is the Middle to Final Jomon period (5,000–2,300 years BP).

The skeletal samples from which data were collected were recovered from the Hobi, Inariyama, Nakazuma, and Yoshigo archaeological sites in eastern Japan and the Kitamura, Ota, Tsukumo and Yosekura archaeological sites from western/inland Japan (Fig. 1). All of the sites were dated using pottery-based chronology and radiocarbon methods. The use of pottery chronology is an accurate method to estimate site occupations in prehistoric Japan because of the preponderance of systematic studies on the chronology of Jomon pottery (see reviews by Aikens, 1995; Imamura, 1996a; Habu, 2004). The approximate locations, dates, and site-specific number of dental remains from which data were collected are listed in Figure 1, and Table 1. The Middle, Late, and Final Jomon periods are dated based on radiocarbon analysis of pottery cultures.
Pottery-based chronologies date the Middle Jomon from 5,000 to 4,000 years BP, Late Jomon from 4,000 to 3,000 years BP, and the Final Jomon from 3,000 to 2,500 years BP in southern Honshu and 2,300 years BP northern Honshu (Habu, 2004). Climatic periods according to botanical and pollen analysis vary from cultural periods and include an RII period from 7,000 to 4,000 years BP (Tsukada, 1986). This period is considered a climatic optimum, where warm temperatures are found throughout the Japanese Islands and dates from the Initial to Middle Jomon periods (Tsukada, 1986). The climatic optimum is characterized by “prosperous” Jomon cultures. Such prosperity is revealed by large scale populations with complex social networks and subsistence regiments found throughout Honshu (Imamura, 1996a).

The RIIIa period (4,000–1,500 years BP) is characterized by a general cooling trend observed in central, eastern, and northern Japan and corresponds to the Late and Final Jomon periods (Tsukada, 1986). Depopulation of Chubu and Kanto as well as increased density in Tohoku and Chugoku began during the RIIIa period (Koyama, 1978).

Regional comparisons for enamel hypoplasia and carious tooth frequencies were made between sites listed as eastern and western/inland in Figure 1 and Table 1. Overall frequencies of enamel hypoplasia were limited to sites within the western/inland region of Japan because these areas had similar dietary patterns; any differences in enamel hypoplasia observed between these groups would, therefore, likely be attributable to the impact of climate change.

**Systemic stress**

Observation and recording of enamel hypoplasia and carious teeth are used by this study to understand variation in systemic stress and dietary patterns among the prehistoric Jomon. Hypoplastic defects are grooves or pits observable on tooth surfaces caused by disrupted enamel production associated with periods of systemic stress during infancy and childhood (Goodman and Rose, 1991) (Fig. 2). Hypoplastic defects were recorded as deficiencies in enamel thickness appearing as horizontal grooves or pits on tooth surfaces. Presence of enamel hypoplasia was determined by macroscopic observation aided by the use of a magnifying glass (10×), natural fluorescent lighting, and a 100 W Toshiba desk lamp. Approximately 50% or more of the crown height was present on all examined teeth. The identification of enamel hypoplasia follow Skinner et al. (1995) and Guatelli-Steinberg (2003), where adjacent perikymata were compared to possible enamel defects to prevent confusing normal variation in tooth morphology with enamel hypoplasia. Enamel hypoplasia ranged in severity from macroscopically apparent to those that could not be viewed without the assistance of a magnification device. Frequencies of enamel hypoplasia are reported according to the proportion of teeth with at least one defect divided by the total number of teeth observed.

**TABLE 1. Dates, locations, and curatorial locations for material used by this study**

<table>
<thead>
<tr>
<th>Sites</th>
<th>Region</th>
<th>Period</th>
<th>Dates</th>
<th>Curator</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inariyama</td>
<td>Eastern Japan</td>
<td>Late to Final</td>
<td>3000–2300</td>
<td>Kyoto Univ.(^a)</td>
</tr>
<tr>
<td>Hobi</td>
<td>Eastern Japan</td>
<td>Final</td>
<td>3000–2300</td>
<td>UMUT(^b)</td>
</tr>
<tr>
<td>Nakazuma</td>
<td>Eastern Japan</td>
<td>Late</td>
<td>4000–3300</td>
<td>Toride Board(^c)</td>
</tr>
<tr>
<td>Yoshigo</td>
<td>Eastern Japan</td>
<td>Late to Final</td>
<td>3400–2400</td>
<td>Kyoto Univ.</td>
</tr>
<tr>
<td>Kitamura</td>
<td>Inland Japan</td>
<td>Middle to Late</td>
<td>4000–3000</td>
<td>Ch. His. Soc.(^d)</td>
</tr>
<tr>
<td>Ota</td>
<td>Western Japan</td>
<td>Middle</td>
<td>5000–4000</td>
<td>Kyoto Univ.</td>
</tr>
<tr>
<td>Tsukumo</td>
<td>Western Japan</td>
<td>Late to Final</td>
<td>3000–2300</td>
<td>Kyoto Univ./UMUT</td>
</tr>
<tr>
<td>Yosekura</td>
<td>Western Japan</td>
<td>Late</td>
<td>4000–3000</td>
<td>UMUT</td>
</tr>
</tbody>
</table>

\(^{a}\) Laboratory of Physical Anthropology, University of Kyoto.
\(^{b}\) University Museum, University of Tokyo.
\(^{c}\) Toride Board of Cultural Assets.
\(^{d}\) Chikuma City Historical Society.

**TABLE 2. Distribution of linear enamel hypoplasias on antimeric first incisors and mandibular canines for eastern and western/inland Jomon foragers**

<table>
<thead>
<tr>
<th>Group</th>
<th>(N^{a})</th>
<th>% LEH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eastern Jomon I(^a)</td>
<td>47</td>
<td>21.2</td>
</tr>
<tr>
<td>Western Jomon I(^a)</td>
<td>28</td>
<td>60.7</td>
</tr>
<tr>
<td>Eastern Jomon C</td>
<td>23</td>
<td>56.5</td>
</tr>
<tr>
<td>Western Jomon C</td>
<td>39</td>
<td>61.5</td>
</tr>
</tbody>
</table>

\(^{a}\) Number of individuals with antimeric pairs of canines or incisors.

Fig. 2. Enamel hypoplasia on the right canine of a prehistoric Jomon male from the Yoshigo site.
Problems in the interpretation of enamel hypoplasia frequencies such as the under-estimation of lesions are reported in the absence of microscopic analysis (Berti and Mahaney, 1995; Hillson and Bond, 1997). Enamel defects identified by this study, therefore, represent a minimum estimate of teeth with evidence of stress episodes. Other difficulty in enamel hypoplasia interpretation arises because defects associated with localized trauma appear similar to those from systemic stress (Hillson, 1996). Recording defects at similar developmental locations on antimeres or other adjacent teeth helps define the etiology of an enamel hypoplasia because defects arising from localized trauma appear on one tooth. The mandibular canines and maxillary first incisors most frequently display evidence of enamel hypoplasia (Goodman and Armelagos, 1985). This study recorded frequencies of enamel hypoplasia on antimeric pairs of maxillary first incisors and mandibular canines to understand if significant differences in hypoplasia frequencies exist between the overall distribution of enamel defects and those observed on different tooth types. Antimeric enamel hypoplasia frequencies were calculated as the sum of mandibular canine and maxillary first incisor pairs with evidence of enamel hypoplasia on both teeth divided by the total number of antimeric maxillary first incisors and mandibular canines.

Enamel hypoplasia was also compared by individual to understand if interregional patterns of stress experienced at the individual level were similar to that suggested by cumulative tooth counts and antimeric tooth pairs. Individuals with at least one observable tooth were included in the analysis; those with enamel hypoplasia on at least one tooth were grouped into the enamel hypoplasia present category, while those lacking hypoplastic defects were grouped into the hypoplasia absent category. Individual comparisons of enamel hypoplasia frequency were divided into adults and subadults from eastern and western/inland Japan. Age groups were divided on the basis of third molar eruption; subadults lacked a fully erupted third molar, whereas adults had fully erupted third molars.

**Oral health**

Dental caries is a disease process associated with focal enamel demineralization by organic acids (Larsen, 1997: 65) (Fig. 3). Organic acids are produced by bacteria that consume food particles in the oral cavity. Carious lesions were recorded according to their presence on a specific tooth and identified based on enamel demineralization in stages that ranged in size from destruction of more than one half of a total tooth to pin-prick sized lesions. The frequency of carious teeth observed by this study is conservative because high powered microscopy often identifies carious lesions that are unobservable through macroscopic examination (Hillson, 2000). Carious lesions were identified under the same lighting described above with a 10× magnifying glass and dental mirror. Overall frequencies of carious teeth were calculated as the total number of teeth with observable carious lesions divided by the total number of teeth observed.

Dental caries is an age-progressive process more frequently involving individuals in older age classes (Hillson, 2001). Additionally, carious lesions involve molar teeth more often than the anterior dentition or premolars (Larsen et al., 1991). A subset of teeth was divided according to age and tooth class. Age classes were arranged according to first molar wear using the scoring procedures described by Buikstra and Ubelaker (1994). Carious tooth frequencies between regional and temporal groups were then compared for the anterior teeth (incisors and canines), premolars, and molars. Differences in carious teeth between males and females are another major component to studies of dental caries and dietary behavior (see Larsen et al., 1991). This study was not able to explore sex-based variation in carious teeth among Jomon skeletal samples because of poor cranial and pelvic preservation that limited the number of individuals who could be assigned to a sex.

**Statistical methods**

Intraobserver error in the recording of hypoplastic lesions is a potential methodological shortcoming of macroscopic studies of enamel defects. Intraobserver error was addressed using observations recorded from 72 teeth curated by the University of Kyushu. The teeth were scored for the absence of enamel hypoplasia (1), presence of one enamel hypoplasia (2), or presence of more than one enamel hypoplasia (3). The teeth were then rescored 2 weeks later using the same scoring criteria. A kappa statistic was applied to these observations to identify differences between the observed and expected levels of observer agreement (Cohen, 1960). Some researchers note problems with the kappa statistic because of variation in trait frequencies between populations that cause confusion in recognizing the same trait in different groups (Thompson and Walter, 1988). However, errors caused by confusing enamel hypoplasia with other anomalous features are not expected because the perikymata in the area of the enamel defects were observed for abnormality of size. The kappa statistic generated for the observations made by this study was 0.63 suggesting “substantial agreement” (0.61–0.80) between the actual and expected results (Landis and Koch, 1977). The use of this terminology to classify these results is decidedly arbitrary (Landis and Koch, 1977: 165); however, the purpose here is to provide a “benchmark” to identify the...
strength of agreement associated with the kappa statistic. Previously reported kappa statistics regarding intra-
observer error in enamel hypoplasia observation are closer to 0.80 (see Guatelli-Steinberg, 2003). However,
the series of teeth used to score this statistic was from the Yayoi period, where enamel hypoplasia frequency
and expression were less severe than the Jomon sample, so the degree of correspondence in the current study,
where enamel hypoplasia was generally more marked, is likely greater.

Overall frequencies of carious teeth and enamel hypo-
plasia were compared between geographic and temporal
groups using 95% confidence intervals. Here, 95% confi-
dence intervals around the overall frequencies of enamel
hypoplasia and carious teeth from different geographic
locations and temporal periods are not expected to over-
lap if these frequencies are different; similarity is
implied if overlap in 95% confidence intervals is
observed. Overall carious tooth frequencies are compared
for anterior, premolar, and molar tooth groups, while
overall frequencies of enamel hypoplasia are compared
for all teeth. Confidence intervals were calculated using
the standard equations published in Zarr (1997).

The G-statistic was applied as a measure of indepen-
dence for individual and antimeric tooth pair frequencies
of enamel hypoplasia between geographic and temporal
groups, as opposed to the \( \chi^2 \) test, because of the small
number of individuals yielding antimeric tooth pairs.
The G-statistic is more appropriately applied to data
where the observed minus expected cell frequencies are
greater than the expected cell frequencies (Sokal and
Rohlf, 1995; Gotelli and Ellison, 2004). Under these cir-
cumstances low expected values are often calculated and
these values may greatly increase the \( \chi^2 \) statistic (Sokal
and Rohlf, 1995; Gotelli and Ellison, 2004). The \( \chi^2 \) test is
sensitive to these circumstances because the expected
frequency is used as the denominator in the likelihood
ratio that generates the \( \chi^2 \) statistic.

RESULTS

Enamel hypoplasia

Frequencies of enamel hypoplasia observed on anti-
meric maxillary incisors were significantly greater
among the western/inland Jomon than those from east-
ern Japan (\( P \leq 0.001 \)) (Table 2). Statistically significant
differences of enamel hypoplasia frequencies between
eastern and western Jomon were not observed on anti-
meric mandibular canines (Table 2). The lack of statisti-
cally significant differences in enamel hypoplasia fre-
quency of antimeric mandibular canines between eastern
and western/inland Jomon groups is attributed to a sam-
ping bias associated with ritual tooth ablation. Antemor-
tem extraction of the mandibular canines and incisors is
routinely observed among the prehistoric Jomon and is
associated with achieved social identities (Temple and
Sciulli, 2005). The differences between enamel hypopla-
 sia frequencies observed on maxillary first incisors are,
therefore, more representative of trends in systemic
stress between the eastern and western Jomon.

The 95% confidence intervals for the overall frequen-
cies of enamel hypoplasia between eastern (95% CI =
0.328–0.409) and western (95% CI = 0.530–0.611) Jomon
people did not overlap (Table 3). In addition, the west-
ern/inland Jomon cumulative (\( P < 0.01 \)) and adult (\( P <
0.01 \)) groups have statistically significantly greater fre-
cuencies of individuals with at least one hypoplastic epi-
sode than those from eastern Japan (Table 4). Frequen-
cies of individuals with at least one hypoplastic episode
among subadult groups from these regions were not stat-
istically significantly different (Table 4). The lack of dif-
fERENCE in individual frequencies of enamel hypoplasia
among the subadult groups from eastern and western/
inland Japan is likely associated with a small sample
size. More data should, however, be collected for this
possibility to be further explored.

The Middle to Late Jomon had significantly less evi-
dence of enamel hypoplasia on antimeric maxillary first
incisors than those from the Late to Final Jomon period
(\( P < 0.01 \)) (Table 5). The confidence intervals for overall
enamel hypoplasia frequencies between Middle to Late
(95% CI = 0.511–0.620) and Late to Final (95% CI =
0.499–0.637) Jomon foragers overlapped.

Dental caries

Fewer carious teeth were observed among the west-
ern/inland Jomon when compared to those from eastern
Japan (Table 6), with deviations in dental caries preva-
ence observed at the Tsukumo and Yosekura sites when

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**TABLE 3. Regional enamel hypoplasia frequencies**

<table>
<thead>
<tr>
<th>Location</th>
<th>N teeth</th>
<th>N LEH</th>
<th>% LEH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western/Inland Jomon Sites</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kitamura</td>
<td>232</td>
<td>125</td>
<td>53.8</td>
</tr>
<tr>
<td>Ota</td>
<td>98</td>
<td>62</td>
<td>63.2</td>
</tr>
<tr>
<td>Tsukumo</td>
<td>136</td>
<td>84</td>
<td>61.7</td>
</tr>
<tr>
<td>Yosekura</td>
<td>29</td>
<td>10</td>
<td>34.5</td>
</tr>
<tr>
<td>Pooled Western/Inland</td>
<td>495</td>
<td>281</td>
<td>56.7</td>
</tr>
<tr>
<td>Eastern Jomon sites</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inariyama</td>
<td>51</td>
<td>33</td>
<td>64.7</td>
</tr>
<tr>
<td>Hobi</td>
<td>76</td>
<td>20</td>
<td>26.3</td>
</tr>
<tr>
<td>Nakazuma</td>
<td>135</td>
<td>20</td>
<td>14.8</td>
</tr>
<tr>
<td>Yoshigo</td>
<td>297</td>
<td>133</td>
<td>44.7</td>
</tr>
<tr>
<td>Pooled Eastern</td>
<td>559</td>
<td>206</td>
<td>36.8</td>
</tr>
</tbody>
</table>

a Number of teeth observed for enamel hypoplasia (combined right and left sides from mandible and maxilla).

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**TABLE 4. Regional frequencies of enamel hypoplasia by individual**

<table>
<thead>
<tr>
<th>Location</th>
<th>N individuals</th>
<th>% LEH</th>
<th>N subadults</th>
<th>% LEH</th>
<th>N adults</th>
<th>% LEH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eastern Jomon</td>
<td>164</td>
<td>48.2</td>
<td>34</td>
<td>52.9</td>
<td>106</td>
<td>48.1</td>
</tr>
<tr>
<td>Western/Inland Jomon</td>
<td>122</td>
<td>64.8</td>
<td>22</td>
<td>68.2</td>
<td>90</td>
<td>64.4</td>
</tr>
</tbody>
</table>

a Total number of individuals with at least one observable tooth.

b Percentage of individuals with at least one observable hypoplastic episode.

c Total number of subadults with at least one observable tooth (aged 0–15 years).

d Total number of adults with at least one observable tooth (age < 15 years).

e Not statistically significant result.
DISCUSSION
Evidence for nutritional variation

Population density increases are recorded in western Japan between the Middle and Late Jomon period (Koyama, 1978). Rises in chronic and acute infection as well as greater parasite loads are recorded in sedentary populations of increased density, where greater exposure to and transmission of pathogens is recorded. Greater pathogen exposure and transmission is related to increases in host-contagen ratios, contact with infected people, contaminated water supplies, and waste disposal issues (Armelagos, 1990; Jackson, 2000). Clinical studies report a relationship between enamel hypoplasia and infectious diseases. Experimental results, for example, found that sheep with elevated parasite loads were likely to form an enamel hypoplasia (Suckling and Thurley, 1984; Suckling et al., 1986). These findings are supported by bioarchaeological evidence for increased enamel hypoplasia frequencies among hunter-gatherers who had recently undergone population expansions (Walker and Lambert, 1989; Lambert, 1993; Stodder, 1997). A comparison of enamel hypoplasia frequencies between two western Jomon groups from time periods with different population densities (Ota and Tsukumo), however, shows no significant change in systemic stress levels. These results suggest that the gradual elevation of population density in western Japan is not characterized by variation in enamel hypoplasia frequencies.

Dietary choices were the primary environmental difference between the prehistoric Jomon from eastern Japan and those from western and inland locations. The subsistence economy of the western and inland Jomon was more focused on plant based resources, whereas the dietary choices of eastern coastal Jomon included greater marine consumption.

Dietary reliance on plant foods is associated with the substandard synthesis of proteins, minerals, and vitamins, particularly iron, vitamin A, and zinc (Murphy and Allen, 2003). Poor iron, vitamin A, and zinc intake are, for example, associated stunted growth in children with limited access to animal source foods (Rivera et al., 2003). This stunting occurs because of the importance of zinc, iron, and vitamin A in the development of insulin-like growth factor I, plasma concentration levels, and human growth hormone receptors. Additionally, poor iron mobilization and hemoglobin synthesis caused by a lack of vitamin A and riboflavin intake among plant dependent people act as contributing factors to iron deficiency anemia and scurvy (Murphy and Allen, 2003). These difficulties are demonstrated by greater enamel hypoplasia frequencies in famine period Chinese (Zhou and Corruccini, 1998) and undernourished people from Guatemala (Goodman et al., 1991; May et al., 1993). Prehistoric foragers who were reliant on terrestrial mammals also experienced an increase in enamel hypoplasia frequencies after the transition to plant-based agriculture (Cook, 1980, 1981, 1984; Lukacs, 1992; and others).

Another possible contributor to the elevated frequency of enamel hypoplasia among the western/inland Jomon compared to those from eastern Japan is seasonal resource depletion. The majority of the plant foods consumed by these groups were seasonally available (Koyama, 1978; Akazawa, 1999). It is possible that the western/inland Jomon suffered seasonal periods of stress during times when resources were unavailable and stored food became scarce. Similar findings are reported from the American Southwest where greater indicators of stress are associated with seasonal resource depletion (Stodder et al., 2002; and others). These findings do not downplay the role of infectious disease and population density on the development of enamel hypoplasia; rather, the goal here is to interpret these lesions within the context of the prehistoric Jomon environment. In this con-
text, the differences in enamel hypoplasia frequencies between the eastern and western Jomon likely reflect stress variation associated with dietary choices and food availability.

**Evidence for collapse**

Evidence for climate change and population collapse during the later part of the Middle Jomon period is not supported by episodes of systemic stress. Of particular interest is the even distribution of enamel hypoplasia frequencies overall, as well as the random distribution across samples and time periods of any observed differences in enamel hypoplasia (Tables 5 and 6). If the climate changes of the Middle to Late Jomon period resulted in significant resource depletion and subsequent collapse, it is expected that the combination of plant dependent diets and scarcity of food would be associated with significantly greater frequencies of enamel hypoplasia among the Middle to Late Jomon sample. These results suggest that the foragers from the Middle to Late Jomon period did not undergo a nutritional crisis during the climatic shift of approximately 5,000 years BP.

In contrast, elevated systemic stress is documented in the American Southwest where climate changes are associated with seasonal resource depletion (Stodder et al., 2002). Similarly, people exposed to the Chinese famine show marked increases in enamel hypoplasia frequencies (Zhou and Corruccini, 1998). Bioarchaeological studies of enamel hypoplasia, stature, pectoral hyperostosis, and population collapse in the Mayan lowlands, however, failed to provide evidence for intensive systemic stress during the Post Classic period (Wright and White, 1996). Instead, regional differences in stress patterns reflective of social and environmental variation are reported. Similar patterns are observed among the prehistoric Jomon, where variation in systemic stress indicators fail to support a demographic collapse associated with a nutritional crisis.

Other regions such as Tokai and eastern Kanto also experienced sharp population declines and climatic cooling during the Middle to Late Jomon period (Koyama, 1978). Elevated stress episodes are not recorded among these groups. Instead, depopulation in the Chubu, Kanto, and Tokai regions was associated with migrations to other areas such as Tohoku or western Japan. Gradual increases in density are recorded in both Tohoku and western Japan during the Middle to Late Jomon period (Koyama, 1978). These results are consistent with archaeological hypotheses that suggest the climate changes of the Middle to Late Jomon period were associated with adjustments in subsistence regiments and population dispersals into surrounding ecological zones (Habu, 2004: 254–255).

**Evidence for subsistence change and dietary choices**

Greater caries prevalence among the Late to Final Jomon suggests a cultural/behavioral shift following the Middle to Late Jomon period. Evidence for dietary change is illustrated following climatic oscillations in Northern China, where greater masticatory stress and sex-based differences in calculus are recorded during

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**TABLE 8. Observed frequencies of carious teeth within each age and tooth group**

<table>
<thead>
<tr>
<th>Age Group</th>
<th>Ant N&lt;sup&gt;a&lt;/sup&gt;</th>
<th>% carious</th>
<th>Pre N&lt;sup&gt;b&lt;/sup&gt;</th>
<th>% carious</th>
<th>Mol N&lt;sup&gt;c&lt;/sup&gt;</th>
<th>% carious</th>
<th>N teeth&lt;sup&gt;d&lt;/sup&gt;</th>
<th>% carious</th>
</tr>
</thead>
<tbody>
<tr>
<td>Middle to Late</td>
<td>84</td>
<td>0</td>
<td>77</td>
<td>2.6</td>
<td>118</td>
<td>5.0</td>
<td>279</td>
<td>2.9</td>
</tr>
<tr>
<td>Late to Final</td>
<td>77</td>
<td>1.3</td>
<td>134</td>
<td>5.2</td>
<td>216</td>
<td>18.8</td>
<td>427</td>
<td>8.1</td>
</tr>
<tr>
<td>Middle to Late</td>
<td>105</td>
<td>0.0</td>
<td>134</td>
<td>2.2</td>
<td>218</td>
<td>4.1</td>
<td>457</td>
<td>2.6</td>
</tr>
<tr>
<td>Late to Final</td>
<td>184</td>
<td>3.8</td>
<td>375</td>
<td>2.9</td>
<td>474</td>
<td>11.1</td>
<td>1,033</td>
<td>6.9</td>
</tr>
<tr>
<td>Middle to Late</td>
<td>105</td>
<td>1.9</td>
<td>121</td>
<td>6.0</td>
<td>212</td>
<td>6.1</td>
<td>438</td>
<td>4.1</td>
</tr>
<tr>
<td>Late to Final</td>
<td>110</td>
<td>1.8</td>
<td>183</td>
<td>4.4</td>
<td>285</td>
<td>19.3</td>
<td>578</td>
<td>11.2</td>
</tr>
</tbody>
</table>

<sup>a</sup> Number of anterior teeth.<br>
<sup>b</sup> Number of premolar teeth.<br>
<sup>c</sup> Number of molar teeth.<br>
<sup>d</sup> Total number of teeth.

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**TABLE 9. Confidence intervals for carious tooth frequencies**

<table>
<thead>
<tr>
<th>Group</th>
<th>ANT 95% CI&lt;sup&gt;a&lt;/sup&gt;</th>
<th>PRE 95% CI&lt;sup&gt;b&lt;/sup&gt;</th>
<th>MOL 95% CI&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Overall 95% CI&lt;sup&gt;d&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age Group 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle to Late Jomon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late to Final Jomon</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Age Group 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle to Late Jomon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late to Final Jomon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age Group 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle to Late Jomon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late to Final Jomon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> 95% confidence intervals for carious tooth frequencies in anterior tooth group.<br>
<sup>b</sup> 95% confidence intervals for carious tooth frequencies in premolar tooth group.<br>
<sup>c</sup> 95% confidence intervals for carious tooth frequencies in molar tooth group.<br>
<sup>d</sup> 95% confidence intervals for carious tooth frequencies in cumulative tooth groups.
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the Late Yangshao period (Pechenkina et al., 2002). In contrast to the prehistoric Jomon, however, carious tooth frequencies among the Late Yangshao and subsequent Longshan people do not evidence dietary change following the climatic shift of 5,000 years BP. An anomalous climate change in Northern California is associated with stable rates of systemic stress, but a decline in carious tooth frequencies suggesting a subsistence shift away from plant resources (Pilloud, 2005). Carious tooth frequencies are also used to detect dietary shifts away from terrestrial plants in prehistoric southern California, where a similar decline in carious teeth was observed in the Channel Islands area (Walker and Erlandson, 1986).

Additionally, many studies report greater frequencies of carious teeth during the agricultural transition associated with the consumption of starchy or sugary cultigens (Armelagos, 1969; Milner, 1984; Bennike, 1985; Larsen et al., 1991; Lukacs, 1992; Todaka et al., 2003; and others). The increase of carious teeth among Late to Final Jomon foragers is, therefore, consistent with a shift in subsistence behavior; perhaps related to resource instability following the climate change of the Middle to Late Jomon period.

Evidence for dietary change following climatic cooling is consistent with a model of human behavior and stress posited by Goodman and Armelagos (1989). This model predicts that environmental constraints are buffered by cultural decisions, although such systems are not always successful in overcoming episodes of stress, particularly in light of poor host resistance to disease. Consequences of poor host resistance include systemic disruptions and subsequent negative impacts on the community with regard to reproductive output, health, work capacity, and general social order. Late Jomon foragers appear to have responded to the constraint of climate change through a dietary shift, evidenced by an increase in carious teeth. Carious teeth are, however, created by the waste products of infectious bacteria such as Streptococcus mutans and Lactobacillus acidophilus in the oral cavity (Rowe, 1982). Complications associated with chronic dental caries include localized abscesses and systemic infections such as gangrene and septicaemia (Calcagno and Gibson, 1991). Overall, then, the change in frequency of dental caries from the Late to Final Jomon period is consistent with a culturally induced stressor precipitated by a subsistence shift in response to environmental constraints.

Similar frequencies of carious teeth between the Late to Final Jomon from western and eastern Japan suggest that these groups were consuming resources with comparable cariogenic properties. This pattern of consumption is possible given the seasonal calendar of Jomon foragers. While animal resources likely acted as a primary food to eastern Jomon foragers, much of this food was hunted in a seasonal capacity (see Koike and Ohtaishi, 1985; Koike, 1992; Komiya et al., 2003; Kobayashi, 2005). The consumption of other cariogenic plant resources among both the eastern and western Jomon during seasons where primary resources were less available is, therefore, a significant possibility.

Hypotheses regarding the process of dental caries in prehistoric Japan suggest that elevated carious tooth frequencies were the result of increased carbohydrate consumption. Previous studies reference taro or other starchy roots as possible contributors (Turner, 1979). Paleoenthobotanical excavations in Japan have not yet uncovered evidence of taro cultivation among Jomon foragers (see Crawford et al., 1976; Kotani, 1981; Crawford and Takamiya, 1990; D’Andrea et al., 1995; Crawford and Shen, 1998; and reviews by Imamura, 1996a; Tsude, 2001; Habu, 2004; Crawford, 2006). A carbonized yam stalk was described from the Early Jomon site of Mutsugasaki, while ethnographic analogies of rural Japanese highlight the consumption of starchy roots such as Pueraria lobata and Pteridium aquilinum (Habu, 2004: 70). A preponderance of tool kits associated with the exploitation of root and tuber plants are also reported from many late Middle to Final Jomon sites (Imamura, 1996).

These studies highlight the possibility that the prehistoric Jomon were consuming starch heavy plants such as roots and tubers. Root and tuber plants would have been attractive dietary sources after the climate change of the Middle Jomon period because of their ability to withstand cooler temperatures.

Tuber consumption is related to moderate carious tooth frequencies among foragers and farmers in prehistoric Thailand and Vietnam (Tayles et al., 2000; Oxenham et al., 2002; Pietrusewsky and Douglas, 2002). Roasted root and tuber consumption is also implicated in elevated caries prevalence among early prehistoric California foragers (Walker and Erlandson, 1986). These findings suggest that the frequencies of carious teeth observed among the Late to Final Jomon are associated with an increased exploitation of root and tuber based plants following the climate changes of the Middle Jomon period. It is important to note that these differences imply greater consumption of cariogenic plants among Late to Final Jomon groups, yet do not provide evidence of agricultural dependence; here, it is suggested that the prehistoric Jomon people expended on plant care did not reach levels consistent with an agricultural economy until after the introduction of wet rice agriculture during the Yayoi period (Imamura, 1996b; Tsude, 2001).

**Broader implications**

The trends documented by this study reveal significant differences in health and diet among the prehistoric Jomon. Patterns of biological variation among prehistoric foragers are rarely documented within the bioarchaeological literature because most projects focus on major cultural shifts among hunter-gatherers with fairly homogeneous economies to agriculture (for exceptions see Walker and Erlandson, 1986; Lambert, 1993; Stoddert, 1997; Pilloud, 2005). This study documents biological variation similar to that observed during the transition to agriculture in many regions (see Larsen, 1987, 1995, 1997, 2002). During this time, significant differences in stress patterns are associated with contrasting subsistence choices and living conditions. More specifically, in Japan, biological variation is generally considered in a temporal vacuum and mostly associated with migrations from the Asian continent around 2,500 years BP (e.g., Suzuki, 1969; Mizoguchi, 1986; Hirata, 1990; Suzuki, 1991; Turner, 1992; Nakahashi, 1993; Pietrusewsky, 1999; Todaka et al., 2003; and others; for exceptions, see Turner, 1979; Shigehara, 1994; Fujita, 1995; Suzuki, 1996). These migrations are important to changes in the cultural, ecological, and genetic landscape of prehistoric Japan, specifically the introduction of agricultural economies and genetic admixture between Jomon foragers and Yayoi agriculturalists. However, the results of this study suggest that the culturally and environmentally complex
networks of prehistoric Jomon had a great impact on biological variation before the arrival of the Yayoi. This conclusion is supported here by variation in systemic stress indicators observed among Jomon foragers from different environmental contexts, and by evidence of a dietary shift, possibly in response to environmental change.

Interregional environmental heterogeneity is, however, also documented among these prehistoric people. Geographic, seasonal, and temporal fluctuations in social complexity, sedentism, and population density are all characteristic of Jomon foragers (Koyama, 1978; Imamura, 1996a; Habu, 2004; Yoneda et al., 2004). These findings suggest that the degree of biological variation attributable to environmental variables and behavioral choices reported by this study is modest. Few data have been collected from human skeletal remains recovered at smaller Jomon sites from the eastern and western/inland regions of Japan. Bioarchaeological inquiries that consider samples of skeletal remains from single regions (i.e., western/inland Japan or eastern Japan) are, therefore, an integral component to further understanding the environmentally directed biological variation of the prehistoric Jomon people. It is expected that interregional variation in systemic stress patterns also played a significant role in directing the biological and cultural evolution of prehistoric Jomon people.

The findings of this paper also support a resource-stress model regarding the swift adoption of agriculture in prehistoric western Japan. Yayoi migrants entered Japan around 2,500 years BP (Imamura, 1996a). A population boom associated with these migrations is reported first in western Japan (Koyama, 1978; Hanihara, 1987). Agriculture was quickly adopted in western Japan, specifically in the regions of southwestern Honshu and northern Kyushu compared to a period of behavioral continuity among the eastern Jomon (Akazawa, 1981, 1982). One reason for this swift adoption of wet rice agriculture among the western Jomon was a hypothesized broad based plant dependent economy in western Japan which contrasted with the more marine focused economy in eastern Japan. Here, the significant population increase during the Yayoi period (see Koyama, 1978; Hanihara, 1987) is hypothesized to have resulted in reduced resource predictability within the broad based subsistence regiment of the western Jomon (Akazawa, 1981, 1982). While the results of this study do not support a resource related collapse among the Late to Final Jomon people, a greater degree of systemic stress is observed in western Japan. Under these conditions, prehistoric people are hypothesized to change their subsistence strategies in an effort to moderate environmental constraints (Goodman and Armelagos, 1989). The greater degree of systemic stress observed among the western Jomon likely reflect an environment where the swift adoption of agriculture helped combat the stresses of broad based plant dependent diets and possibly mitigated the impact of large-scale Yayoi migrations on resource predictability. These differences support archaeological studies of subsistence choices among the eastern and western/inland Jomon. Here, greater evidence of systemic stress among western/inland plant gatherers is consistent with the stresses associated with plant dependent economies and seasonally based resource depletion. However, frequencies of enamel hypoplasia fail to support wide-spread systemic stress associated with a resource crisis during the Middle to Late Jomon period. Instead, greater frequencies of carious teeth were observed among Late to Final Jomon foragers compared with those from the Middle to Late Jomon period. These changes suggest a subsistence shift after the climatic changes of the Middle to Late Jomon period. The presence of a dietary shift after a significant climate change follow the model of culturally induced stress of Goodman and Armelagos (1989), where behavioral decisions in response to environmental constraint often carry biological consequences. Here, these consequences are illustrated by a rise in carious teeth following climatically induced dietary change.

The results of this study also have important anthropological implications because they support the existence of environmentally directed biological variation among prehistoric foragers. Such variation is rarely documented in the bioarchaeological literature because the dietary choices and living conditions of most prehistoric foragers were confined to specific environments. Additionally, studies of biological variation among the prehistoric Jomon often focus on the origin of modern Japanese or the impact of Yayoi migrations on the spread of Jomon traits. Such questions are geared towards a genetic context. In contrast, this study documents an underlying theme of variation in systemic stress experiences and dietary behavior before the arrival of Yayoi migrants. Finally, the results of this study indicate that the swift adoption of wet rice agriculture by the western Jomon was likely facilitated by environmental constraints, as indicated by the greater degree of systemic stress recorded in the teeth of these foragers. The findings of this study suggest that both behavioral choices and the natural environment contributed significantly to evolutionary processes in Japan, crossing large portions of geographic and temporal space.

CONCLUSIONS

The results of this study support two hypotheses regarding environmental interactions among the prehistoric Jomon. First, differences in enamel hypoplasia frequencies suggest variation in systemic stress patterns among the prehistoric Jomon, with greater stress levels recorded among western/inland plant gatherers. These

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LITERATURE CITED


Kioke H, Ohtaishi N. 1985. Prehistoric hunting pressure estimated by the age composition of excavated sika deer (Cervus


