Variation in regional diet and mandibular morphology in prehistoric Japanese hunter-gatherer-fishers

Kara Hoover¹, Frank L'Engle Williams^{2}*

¹Department of Anthropology, University of Alaska, Fairbanks, AK 99775-7720, USA, kchoover@alaska.edu

²Department of Anthropology, Georgia State University, Atlanta, GA 30302-3998, USA, frankwilliams@gsu.edu

*Corresponding author

Abstract

Previous research has identified a relationship between mandibular morphology and diet (e.g., coarse or tough diets result in more robust mandibles). Prehistoric Japan is an excellent place to explore the significance of this relationship in shaping mandibular morphology due to the pronounced regional dietary variation. South/West Honshu Jōmon engaged in broad spectrum foraging, Northeastern Honshu Jōmon were fisher-gatherers, Hokkaido Jōmon were maritime (sea mammal) foragers. We test the hypothesis that diet variation across temporal and spatial zones will be reflected in mandibular morphological traits. Metric measurements were utilized to test for regional differences with both archaeological time period and biological sex as covariants. ANOVA results for region with time period as a covariate indicates all variables except corpus height and breadth are significantly different among regions but for the time period covariate, significance is only present for corpus breadth and the dimensions of the ascending ramus. ANOVA for region with biological sex as a covariate indicates all variables except corpus height are significantly different. Biological sex as a covariate demonstrates significant p-values for chin height, bicondylar breadth and minimum ascending ramus breadth. Generally, North Hokkaido, followed by Southwest Hokkaido, exhibits the largest mandibular ascending rami and tallest anterior mandibles, whereas Northeast and South/West Honshu have the smallest mandibles. Multivariate analysis indicates a separation between North and Southwest Hokkaido and South/West Honshu, whereas Northeast Honshu partially overlaps

these dietary zones. Differences in mandibular morphology are better explained by regional diets than by temporal trends and biological sex.

Key words: Prehistoric Japan; Jōmon; foragers; biomechanics; mandible

1. Introduction

One of the most influential factors shaping mandibular morphology is diet. When under strain from mastication (the mechanical processing of solid foods), muscles transmit biomechanical signals to the bones into which they are inserted. The evolution of mammalian teeth shows a marked trend towards increased tooth surface area to aid mechanical processing of food, maximize nutrient extraction, and reduce stress in mastication (Lucas, 2004). Within humans, biomechanical signals more so than natural selection and population history influence morphological variation in the mandible. Evidence from a large-scale global study of human populations with differing subsistence practices parsed the effects of neutral population history from subsistence strategy and found that changes to mandibular morphology due to dietary practices erased the genetic signals of population history; further, masticatory pressure acts preferentially on the mandible rather than the maxillary region, which is secondarily influenced by changes in the mandible (von Cramon-Taubadel, 2011).

Plasticity during maturation alters the robusticity and size of the mandible, providing direct evidence of masticatory strain after consideration of other differentiating factors like biological sex, gender division of labor, and cultural practices such as using teeth as tools (Fig. 1). One well-documented phenomenon following the adoption of agriculture is an overall craniofacial reduction resulting from a diet of softer, processed foods that required little masticatory strain. Prior to the advent of agriculture and specialized tools for food processing, humans ate varied, regional, and seasonal diets that often included tougher/coarser foods requiring processing into smaller, easily digested particles via mastication. Generally, diets comprised of hard-object exploitation or foods difficult to masticate (e.g., tough meats, roughly ground grains and/or underground storage organs) result in larger, robust lower jaws compared to diets comprised of softer foods (e.g., fruits, processed or cooked foods) which result in smaller, more gracile mandibles (von Cramon-Taubadel, 2011). A functional stimulation of mandibular growth and development suggests diets with increased masticatory strain produce longer dental arches that accommodate teeth more rapidly (Enlow and Hans, 1996). Western ‘soft’ diets tend

to result in shorter dental arches due to the lack of biomechanical signaling to the mandible (Corruccini, 1991). In addition, the joint connecting the mandible to the face via the temporal bone (the temporal-mandibular joint) has undergone a reduction in size and form in the transition from hunting-gathering to agriculture due to reduced masticatory muscle robusticity and associated changes in craniofacial form (Hinton and Carlson, 1979).

Several craniofacial muscles are recruited during mastication as well as in work tasks, such as using the teeth as a gripping organ in hide and tool production. Consistent chronic increases in mechanical stress expand muscle attachment sites and increase the maximum and minimum breadths of the ascending ramus (Bastir et al., 2004) and the robusticity of the mandibular corpus (Kanazawa and Kasai, 1998; Holmes and Ruff, 2011). Of the large number of muscles involved in oral function, the majority of those recruited in food processing attach to the mandible: food fracturing muscles (masseter, temporalis, medial pterygoid); jaw-closing muscles that aid bite force (adductors); jaw-opening muscles (abductors); other muscles that aid in rotation of the mandible (lateral and anterior-posterior); and a few involved in lip movement (Lucas, 2004). These muscle groups create mechanical strain on the mandibular bone throughout life resulting in a dynamic remodeling of bone relative to changes in muscle use (Lucas, 2004). In addition to muscle strain, other biomechanical signals for mandibular bone growth (and loss) are influenced with respect to the energy absorbed per unit of the volume of tissue, and the rhythm of loading patterns (Lucas, 2004).

Prehistoric Japan is an excellent place to examine the relationship between mandibular robusticity and diet because there are clear regional, temporal, and cultural differences in diet. During the Jōmon period (c. 15,000-2,500 cal BP), populations were mostly sedentary hunter-gatherer-fishers that were well adapted to the postglacial environmental fluctuation characteristic of Japan during the Neolithic (Habu, 2004). The Jōmon subsistence system can be described as broad spectrum foraging with no specific staple resources, regionally variable, and adapted to the seasonality of available food resources which ultimately allowed for the adoption of sedentary life (Takahashi et al., 1998). The focus of this research is the subsistence and diet changes occurring from the Middle through Later Jōmon periods on Honshu and the Middle Jōmon through the Epi-Jōmon periods on Hokkaido. We are particularly interested in whether the mandible will capture dietary variation across space and time via measurements of robusticity and size.

Is regional dietary variation a main factor shaping mandibular morphology in prehistoric hunter-gather-fishers in Japan? To address this question, we analyzed the validity of regional groupings on the basis of diet (from archaeological data) using a suite of metric traits that assess mandibular robusticity. Regions include South/West Honshu, Northeastern Honshu, North Hokkaido, and Southwestern Hokkaido. We consider two covariates. First, Jōmon diet is variable across space and time so we use archaeological periods as a covariate: Middle Jōmon (including one Early Jōmon site), Later Jōmon (pooled Late and Final Jōmon) and Epi-Jōmon (on Hokkaido). Second, we use sex as a covariate because sex can be a proxy for a gender-based division of labor and previous research (Hinton and Carlson, 1979) indicates sexual dimorphism in hunter-gatherer mandibular metrics. With the transition to agriculture, differences decreased due to a marked reduction in male morphology.

We expect the main effect of regional diet to be significant in defining groups; populations engaging in diets with foods requiring extra masticatory strain (e.g., nuts, tubers, tough meats) will have more robust mandibles. Specifically, we expect increased robusticity in regions with the broadest forager subsistence strategy such as those in South/West Honshu. Eastern Honshu Jōmon had a greater reliance on fresh fish which may have resulted in a less robust mandible. Even if diet changes slightly in response to environmental perturbations, we expect archaeological time period as a covariate to have minimal impact due to some continuity between periods (South/West Honshu continuation of broad spectrum foraging and Hokkaido continuation of maritime-based subsistence economies). Sex may have an impact in certain regions where there is a clear difference in male and female diets.

2. Regional Setting

Shell mounds are a dominant type of archaeological site in Jōmon Japan with approximately 3,000 recorded; shallow inlets on the Pacific coast are common sites whereas the Japan Sea coast has few due to the lack of tidelands (Takahashi et al., 1998). Tidewater bivalve shellfish were available year-round and provided a stable food resource in an environment largely characterized by seasonal dietary shifts; changes in resource base over time may explain the large number of shell mounds in the Middle Jōmon and their increasing prevalence by the Late Jōmon. The intensity of shellfish gathering activities varied in response to the availability of other food resources (Takahashi et al., 1998). Fish species recovered from shell middens are

temporally and spatially variable. The primary species in coastal sites of northern Japan are herring, scorpion fishes, greenlings, flounders, and salmon (Takahashi et al., 1998). Species in southern Japan are broad but yielded in low quantity and include sea breams, sea bass, puffers, sardines, mackerel, and horse mackerel (Takahashi et al., 1998). Species in northern Japan are fewer but larger in quantity; such a tendency accords well with the north-south difference in fish species inhabiting the coastal areas of the country. In the shell midden sites located in river mouths or inland estuaries, on the other hand, fresh water and brackish water species such as crucian (huna), carp (koi), minnow (ugui), catfish (namazu) and eel (unagi) predominate (Takahashi et al., 1998).

Plant exploitation reconstructed from macrobotanical analysis of archaeological sites suggests a reliance on nuts. Eastern Japan exploited nuts from deciduous broadleaf forest (e.g., chestnuts, walnuts, horse chestnuts and acorn). Western Japan exploited evergreen broadleaf forest (e.g., chinquapin and evergreen oak). Inland estuaries exploited water chestnuts also. Across sites and based on historical evidence, tubers (e.g., lily bulbs, arrow root and Japanese yam) were likely exploited. The spread of rice cultivation began during the beginning of the Final Jōmon Period. While Western Japan adopted wet rice agriculture from continental immigrants, Eastern Japan was more resistant to rice cultivation evidenced by the scarcity of rice remains and agricultural tools associated with cultivation; this resistance extends the Final Jōmon period in the east while the west had already entered the middle phase of the Early Yayoi Period. Rice cultivation was, at most, a minor component of eastern subsistence economies (Takahashi et al., 1998).

Environmental and cultural changes played a role in temporal changes in diet. Between 6,500-5,000 BP, marine transgression further isolated the archipelago from Asia and transformed the coast (Umitsu, 1991); changes in ocean currents transformed the coastline and the northward expansion of warm water species of shellfish and coral reefs (Matsushima, 1984). Changes to resource extraction across time may reflect internal cultural changes (e.g., social relationships, sedentism and kinship) or response/adaptation to environmental change. For example, fish bone assemblages from Pacific coast shell mounds shift from offshore to coastal fishes. This change in fishing technology reflects alterations in subsistence patterns from individual activities (angling and spear fishing) to collective fishing activities (fish netting and trapping) (Takahashi et al.,

1998). The collective activities are productively stable and contributed to residential stability of later Jōmon populations.

On Honshu, the Middle Jōmon (5,000-4,000 BP) is characterized by significant population expansion (increased pottery and domestic dwellings), cultural complexity (social stratification and sedentism), and cultural continuity (Imamura, 1996; Habu, 2004); strontium evidence indicates no signature for migration in western Honshu, suggesting that the expansion resulted from an increase in indigenous groups (Kusaka et al., 2012). Abundant woodland flora and terrestrial fauna provided an adequate diet, and lowered sea levels extended settlement areas along the coast (Habu, 2004). By the Late and Final Jōmon, cultural continuity fractured, a less stable environment upset the resource base, and population declined. In South/West Honshu, heavy concentrations of plant-based subsistence tools dominate artifact assemblages suggesting populations were engaged in broad spectrum foraging (e.g., terrestrial and maritime fauna, tubers and vegetables) while the Pacific Coast Jōmon in the northeast increasingly specialized in maritime resources (Akazawa, 1981, 1982a, 1982b, 1986a, 1986b, 1986c, 1987).

On Hokkaido, the pre-agricultural period extends beyond the Later Jōmon periods into the Epi-Jōmon (2,000-1,000 BP), a period paralleling the wet-rice agricultural period (Yayoi) on Honshu, and the Okhotsk (1,000-600 BP), which resembles the Honshu proto-historic period and is named for immigrants from the land bridge between Sakhalin and Hokkaido (Mitsunashi and Yamaguchi, 1961; Aikens and Higuchi, 1982; Ishida, 1988, 1991, 1994, 1996; Yamaguchi, 1991; Ishida et al., 1993, 1994; Imamura, 1996; Habu, 2004; Hudson, 2004; Sato et al., 2007, 2009; Naito et al., 2010; Tsutaya et al., 2014).

Environmental factors were relatively constant on Hokkaido enabling dietary consistency with a primary focus on marine mammals (Imamura, 1996; Habu, 2004; Tsutaya et al., 2014). Northern Hokkaido is part of the subarctic and this is reflected by local diet which consists largely of marine resources (fish and marine mammals) (Tsutaya et al., 2014). The temperate areas to the south exploited mostly terrestrial resources inland and a mix of both terrestrial and marine resources in coastal areas (Takahashi et al., 1998; Tsutaya et al., 2014). Main marine resources in the north included seals (commonly fur seals) and sea lions. In Honshu, some specialized coastal fisher groups also hunted dolphin and small whale, remains of which have been found at Shomyoji (Late Jōmon, Kanagawa) and Mawaki (Final Jōmon, Ishikawa) (Takahashi et al., 1998). Across the archipelago, terrestrial resources were mainly deer and boar

as well as medium-bodied mammals (e.g., badger and hare); some inland mountain cave sites also yielded bear, serow (a goat-like *Capricornis* genus), and macaque bones suggesting a specific local hunting tradition that differed from the lowland areas (Takahashi et al., 1998).

3. Materials and Methods

Samples are from 21 archaeological sites distributed across Honshu and Hokkaido (Fig. 2) and include three time periods: Middle Jōmon, Late/Final Jōmon and Epi-Jōmon (Hokkaido). Contact among sites was largely limited to trade in non-food resources (e.g., jade, amber, obsidian, asphalt and pottery); in the Middle to Final Jōmon period, there is some evidence that salt and perhaps shellfish were also traded to a limited extent (Takahashi et al., 1998).

3.1 Site descriptions (see Table 1 for sample details)

3.1.1 North Hokkaido

North Hokkaido is a subarctic region and contains 2 sites included in this research. Subarctic adaptations in Hokkaido and resulting health patterns of the Hokkaido Jōmon have been linked to Alaska populations, especially those in Kodiak who also exploit a maritime diet (Oxenham and Matsumura, 2007). Although Eastern Hokkaido and Northern Hokkaido have been shown to differ in stable isotope profiles of amino acids (glutamic acid and phenylalanine) reflecting different contributions from seal to the diet (Naito et al., 2010), the heavy exploitation and main focus on maritime resources links them into one region for the purposes of our analysis.

Rebun Island. Funadomari is located on the northern shore of Rebun Island, the northernmost island off the coast of Hokkaido (Nishimoto, 2000a). Funadomari has Late Jōmon components and has been linked morphologically to Jōmon populations in the southwest of Hokkaido with some support for possible biological and cultural exchange between the two groups (Matsumura et al., 2001). Ancient DNA analysis indicates that Funadomari individuals are more closely linked to Okhotsk (associated with the Okhotsk period following the Epi-Jōmon period on Hokkaido) and Siberian populations than Honshu Jōmon (Adachi et al., 2009, 2011).

Wakkanai. Onkoromanai is a shell mound in Wakkanai near the Cape of Soya. Onkoromanai contains Epi-Jōmon and Okhotsk period remains (Ishida, 1996).

3.1.2 Southwest Hokkaido

Western Hokkaido. Bozuyama is located 23 km northeast of Sapporo and is associated with the Epi-Jōmon period via pottery remains recovered at the site; cranial metric affinity suggests a close relationship with Onkoromanai to the north and shows similarities also to Hokkaido and Kuril Ainu but differences from southern Hokkaido (Yamaguchi, 1963).

Kitakogane, Irie, Takasago, and Minami-Usu-6 shell midden sites are coastal sites in southwestern Hokkaido along Volcano Bay. At Minami-Usu, Esan culture, the early cultural complex of the Zoku-Jōmon (Japanese expression for “Epi-Jōmon”) period was found (Yoneda et al., 2001). Kitakogane and Irie have Early Jōmon cultural components with Kitakogane containing Early Jōmon culture pottery; Irie also has Middle and Late Jōmon phases while Takasago is associated with Late and Final Jōmon culture (Nishimoto, 2000b). Rebunge is an Epi-Jōmon site (via pottery, stone and bone tools) on Hokkaido on the north coast of Volcano Bay (Matsuda and Aono, 2003); the individual from this site is affinal (via cranial metrics) to other southwestern groups (Hanihara, 1998; Dodo and Kawakubo, 2002).

Kotan-Onsen and Usujiri are more distant than the other southwestern sites. Kotan-Onsen is a shell midden and lies near Usujiri (Ishida et al., 1992). The archaeological site of Usujiri is located in the Hokkaido region of Oshima prefecture. The site represents a small village belonging to the Middle Jōmon period, 3,000-2,000 BC, and is important for indicating social stratification, and evidence of deer hunting.

3.1.3 Northeast Honshu (including Tokyo Bay)

Northern and eastern Honshu fishing economies are characterized by fishes from the Pacific shelf (rocky-shore species like red snapper and rock trout as well as some migratory species)—fishing in the flats required both harpoon and hooks (Akazawa, 1987). The Jōmon in this area of the Pacific Coast yield ritual objects and tool artisanship specialization which emerged with an increasing focus on specialized fishing implements (Akazawa, 1981). These specialized marine subsistence economies were comparatively socially simple and stable, and form a distinct diet group on Honshu.

Ebishima (also called Kaitori) is a shell mound located in Iwate Prefecture with remains excavated across four archaeological seasons dating to the Middle Jōmon to the Latest Jōmon (via fluorine dating); cranial nonmetrics suggest a close affinity to Eastern Honshu Jōmon (Mizoguchi and Dodo, 2001). Miyano is a coastal Pacific Coast shell mound in the Tohoku district with a maritime fishing economy (Hayashi et al., 1981). Satohama is a Late Jōmon shell

mound on Miyato Island, Miyagi Prefecture; skeletons are affinal to the Kanto area and western Jōmon populations but distinct from Hokkaido and North Honshu Jōmon (Dodo, 1981). Sanganji is a shell mound site in the Fukushima Prefecture (Tohoku district, Japan) excavated in 1952 and 1954 and dated to the Late to Final Jōmon period (4,000 to 2,500 years BP). Ancient DNA analysis of four individuals from this site indicates that the Tohoku Jōmon are genetically closer (but distinct) to Hokkaido Jōmon and Okhotsk and genetically different from Kanto Jōmon (Kanzawa-Kiriyama et al., 2013).

Wakaumi, Nishigahara-nichome and Shosenzuka are shell mounds in the Tokyo Bay, Kanto region of Japan. Wakaumi is a shell mound located in Ibaraki Japan. Nishigahara-nichome is a Jōmon shell mound located in Kita-ku, Tokyo. Shosenzuka is a shell mound located in Yokohama-shi Kanagawa.

3.1.4 South/West Honshu

In south and western Honshu, heavy concentrations of plant-based subsistence tools dominate artifact assemblages. Archaeological data indicate broad-spectrum subsistence practices. Evidence for open-sea fishing indicates economic exchanges with southern Korea (Imamura, 1996). Evidence for ritual anterior tooth ablation suggests complex social rituals through adulthood and achieved status (Harunari, 1986). This complexity contradicts decreased frequencies of ritual objects and relatively simple ceramic styles in the region. Indeed, burial styles indicate achieved status for children but little evidence of differentiation in adult burials (Habu, 2004). Habu (2004) argues that vertical social complexity emerged in the Late Jōmon as horizontal structures collapsed. Local group leaders filled the ensuing power vacuum, but intensified subsistence strategies declined. With a lack of surplus, this vertical differentiation had a minimal impact in social practices. Thus, sites from this area share a cultural continuity and diet.

Yoshigo, Ikawazu, and Hobi are shell mounds sharing a geographic area and similar subsistence adaptation (broad spectrum foraging). Ikawazu is a final Jōmon site located on the Mikawa Bay, Pacific coast. Like with many Jōmon, diet varied seasonally with a wide-range of resources exploited. Deer and boar were dietary staples except in summer when marine resources predominated (Miyata et al., 2009). Ota is a shell mound located along the coast of the Inland Sea in Hiroshima. Stable isotope data suggest marine protein consumption (shell fish and marine fish) and terrestrial resources (C_3 plants and terrestrial mammals) (Kusaka et al., 2010). Sex

differentiation in diet among the Ota may reflect gender-based labor divisions: males consumed more marine foods while females consumed more terrestrial foods (Kusaka et al., 2010). Compared to other area samples, the Sanyo region populations were more reliant on higher trophic marine fish rather than shellfish (Kusaka et al., 2010).

3.2 Methods

Measurements (Fig. 3) included: three mandibular measurements (chin height, bigonial breadth, bicondylar breadth) and four paired variables (corpus height and breadth, right and left, and minimum and maximum ramus breadth, right and left). Only mandibles with at least one well-preserved side intact were measured (KCH) following published osteological standards (Buikstra and Ubelaker, 1994). Mandibles from 21 different sites included in this study are curated at three museums in Japan (Table 1).

For paired variables, we tested for the presence of directional asymmetry due to the influence on robusticity of chewing side preference (Van Valen, 1962). Right and left sides were positively correlated and one-sample t-tests of the mean indicated there were no significant differences from zero. In the absence of directional asymmetry, sides were averaged. To increase sample size, we included metrics for individuals with only one side present (assuming they would follow the sample trends of no significant directional asymmetry). The final set of measurements included in the analysis was seven.

Samples were pooled at the regional level (Northeastern Honshu, South/West Honshu, North Hokkaido, and Southwestern Hokkaido) reflecting archaeological evidence of diet. Sample sizes per analysis were dependent on the measurement examined. We tested chin height, bigonial breadth, bicondylar breadth and average mandibular variables (corpus height, corpus breadth, minimum ascending ramus breadth and maximum ascending ramus breadth) for differences in regions using ANOVA with archaeological time period and biological sex as covariates. For highly significant ANOVA results for the covariates, separate ANOVA with Tukey's Honestly Significant Differences tests were conducted, while t-tests with sex as the grouping variable were conducted for all measurements to further identify significant differences within each region. Multivariate analyses included classification rates derived from a discriminant function analysis and canonical scores axes which were plotted with 68% sample confidence ellipses to identify differences between individuals within and across regions.

4. Results and Discussion

4.1. Univariate analyses

Descriptive statistics for each of the regions are shown in Table 2. North and Southwest Hokkaido show substantially larger measurements than the other groups for minimum and maximum ascending ramus breadth and are larger for chin height. The two Honshu dietary zones show broader bigonial and bicondylar breadths than those on Hokkaido (Table 2).

4.1.1 Analysis of Variance for region with time period as a covariate

When ANOVA was conducted to locate the presence of significant differences in region with time period as a covariate, five measurements show significance (Table 3). These include chin height, bigonial breadth, bicondylar breadth and minimum and maximum ascending ramus breadths. The F-values for the significant comparisons are uniformly high. However, the F-values for minimum and maximum ascending ramus breadth are an order of magnitude higher than those for the other measurements reflecting their highly significant p -values (Table 3). A separate ANOVA with Tukey's posthoc test of significance indicates significant distinctions in minimum ascending ramus breadth exist between North Hokkaido and Northeast ($p = 0.003$) and South/West Honshu ($p = 0.002$), as well as between Southwest Hokkaido and both Northeast ($p = 0.000$) and South/West Honshu ($p = 0.000$). Tukey's posthoc test for maximum ascending ramus breadth shows Southwest Hokkaido is significantly different from Northeast and South/West Honshu ($p = 0.000$).

Time period as a covariate of regions is associated with a significant p -value only for minimum and maximum ascending ramus breadths. For these measurements, a separate ANOVA with Tukey's post-hoc test of significance shows minimum ascending ramus breadth is significantly larger in the Middle Jōmon compared to the Later Jōmon period ($p = 0.008$).

4.1.2. Analysis of Variance for region with sex as a covariate

When an ANOVA is performed for regions with sex as a covariate, nearly all of the measurements are associated with significant p -values with the exception of corpus height (Table 3). The F-values for minimum and maximum ascending ramus breadth are an order of magnitude higher than those for the other measurements reflecting highly significant p -values (Table 3). A separate ANOVA with Tukey's post-hoc test for minimum ascending ramus breadth shows that, compared to South/West Honshu, North ($p = 0.002$) and Southwest ($p = 0.000$) Hokkaido are

significantly larger. Similarly, for maximum ascending ramus breadth, Southwest Hokkaido is significantly larger ($p = 0.000$) than South/West Honshu.

The p -values for the covariate of sex are significant for chin height, bicondylar breadth and minimum ramus breadth suggesting that sex is a significant factor in producing differences between regions. A t-test of these measurements within region show that in general females are larger, although the results are significant only for bicondylar breadth ($p = 0.012$) and minimum ramus breadth ($p = 0.009$), both within Southwest Hokkaido.

4.1.3 Additional t-tests between sexes within regions

T-tests for the other measurements with sex as the grouping variable within each region also show that females are generally larger, although the only significant differences include those for corpus height ($p = 0.005$) in Northeast Honshu and maximum ascending ramus breadth ($p = 0.025$) in Southwest Hokkaido. Males are generally larger for corpus breadth, although the results are not significant; however, males are significantly larger than females for maximum ramus breadth ($p = 0.032$) in South/West Honshu.

4.2 Multivariate analyses

4.2.1. Classification using discriminant function analysis

The classification rates are highest for North Hokkaido (100%) and Southwest Hokkaido (83%) and lowest for Northeast and South/West Honshu (78%). Jack-knifed classification rates show that the one complete individual from North Hokkaido is misclassified as Southwest Hokkaido which had a relatively low rate of classification (17%) compared to Northeast and South/West Honshu (44%).

4.2.2. Canonical scores axes

Canonical scores axes 1 and 2 together account for 96.4% of the variance (Fig. 4). On the two canonical scores axes, the 68% sample confidence ellipse for Southwest Hokkaido is entirely distinct from that representing South/West Honshu. The 68% sample confidence ellipse for Northeast Honshu partially overlaps with South/West Honshu, and only minimally with Southwest Hokkaido. The one complete North Hokkaido individual is positioned within the 68% confidence ellipse for Southwest Hokkaido. The high positive correlations between the first canonical scores axis and the loading for minimum ascending ramus breadth help explain the

positive projection of Southwest Hokkaido, while the high negative loadings of bicondylar breadth account for the placement of South/West Honshu (Table 4).

On the second axis, Northeast and South/West Honshu are imperfectly separated. The high positive scores for Northeast Honshu are accounted for by the high positive correlation between this axis and corpus height, whereas the high negative loadings of maximum ascending ramus breadth and to a lesser extent, bicondylar and corpus breadths, help explain the relatively negative scores for South/West Honshu (Table 4). Individuals of North and Southwest Hokkaido are difficult to classify on the second canonical scores axis (Fig. 4).

4. 3. Comparison to other studies

Japan has been the subject of numerous investigations of craniofacial affinity (Kaifu, 1995, 1997, 2000; Dodo and Kawakubo, 2002; Hanihara and Ishida, 2009). The Jōmon have figured heavily in discussions of affinity, particularly since they are the earliest recognizable cultural period in Japan typified by distinctive cord-marked pottery (Naito et al., 2010). In these studies, the Jōmon from the Holocene and the later Epi-Jōmon on Hokkaido have been treated as homogenous groups distinct from agricultural Yayoi peoples who are thought to have migrated from East Asia or have descended from those migrants (Nishimoto, 2000a; Oxenham and Matsumura, 2007). Mandibular and cranial functional differences have been observed between hunter-gather-fisher Jōmon and subsequent inhabitants of Japan who relied on food production such as the Yayoi (Nishimoto, 2000a). These differences have also been explored in the context of mandibular development (Fukase and Suwa, 2008). These studies demonstrate a reduction in muscle attachment areas of the jaw, attributed to distinct subsistence patterns, and with patterns of chewing stress during bone growth. A reduction in facial robusticity coincident with the adoption of agriculture characterizes other groups such as Nubians (Carlson and Van Gerven, 1977; Hinton and Carlson, 1979), the southern Levant (Pinhasi et al., 2008), the Ohio River Valley (Paschetta et al., 2010), and South America (González-José et al., 2005). A global comparison of the mandible shows a clear separation of morphology in agriculturalists and hunter-gatherers rather than by geographic or genetic groupings (von Cramon-Taubadel, 2011). Hunter-gatherers are known to utilize their anterior dentition much more than agriculturalists which involves greater loading on the temporalis and masseter muscles, and results in an increased incidence of dental chipping (Hinton and Carlson, 1979). Anterior dental loading

increases the size of the ascending ramus, mandibular condyle and coronoid process of the mandible (Hinton and Carlson, 1979; Nishimoto, 2000a).

A number of studies have found a relationship between the consumption of hard items with larger particle size and tough foods to increases in mandibular size and robusticity (Corruccini and Beecher, 1982; Larsen, 1995; Bastir et al., 2004; Sardi et al., 2006; Paschetta et al., 2010). The processing of foods, such as cooking, grinding, and mascerating, softens foods which results in decreases in the magnitude of strain on the mandible (Brace, 1979; Lieberman et al., 2004; Lucas, 2004; Paschetta et al., 2010). Differences in processing technology between Honshu and Hokkaido foragers may have been predicated on the available resources. For example, the consumption of sea mammals in North and Southwest Hokkaido may have necessitated different forms of processing than the more terrestrial and broad-based diets of Northeast, West and South Honshu, particularly if foods in Hokkaido were more often smoked increasing their toughness, perhaps accounting for the pronounced ascending ramus of the mandible noted in North and Southwest Hokkaido. An elevated chin height may also be associated with a larger mandibular ramus if anterior dental loading were involved in the mastication or preparation of foods, or perhaps the preparation of hides and tools. Environmental influences on facial robusticity are well known (Kaifu, 2000, 2010; González-José et al., 2005), and Hokkaido Jōmon have been noted previously to exhibit an expanded mandibular ascending ramus (Maeda, 2002; Arenas, 2012). The presence of significantly larger female measurements for several mandibular dimensions argues against attributing the distinctions noted between regions as the result of population differences. Fukase et al. (2012) have argued that Jōmon postcranial dimensions are progressively larger in a south-north gradient along the Japanese Archipelago; thus, an alternate explanation for the larger mandibles in prehistoric Hokkaido might be that they are attributable to a similar ecogeographic phenomenon. Subsistence patterns, diet and ecological domains may all contribute to differences in mandibular morphology observed between the Jōmon of Hokkaido and Honshu.

5. Conclusions

There is a biomechanical relationship between chewing stress and coarseness/toughness of diet such that the bones attached to muscles involved in food processing tend to become more robust in response to increased mastication, regardless of population history. This is particularly

true of the mandible which is so strongly influenced by extrinsic factors. We expected that variation in mandibular morphology would reflect regional differences in Jōmon diet. These dietary distinctions include Jōmon broad-based foragers of South/West Honshu, Jōmon hunter-gatherer-fishers of Northeast Honshu, and the Hokkaido maritime hunter-gatherers. We have shown that region has a particularly pronounced effect on differences in mandibular morphology corresponding to this variation in dietary regimens, or processing activities, such as using the teeth as tools. Regional differences are more profound than distinctions in archaeological time period and biological sex; where significant differences exist between regions, these are relatively unaffected by the time period from which the materials originate. Sex is also less important than regional differences although an interesting trend is that females are larger than males in corpus height in Northeast Honshu, and in bicondylar breadth and the dimensions of the ascending ramus breadth in Southwest Hokkaido. When multiple measurements are considered the greatest differences are between Southwest (and North) Hokkaido and South/West Honshu, which reflects the greatest geographic differences in diet based on archaeological evidence. As expected, Southwest Hokkaido is more similar to North Hokkaido due to shared maritime economies. Northeast Honshu groups are closer to South/West Honshu and may reflect less tough diets, or less strenuous dental practices by both groups. These patterns imply that regionally available diets and processing regimes fundamentally influenced variation in mandibular morphology across the Japanese archipelago.

Acknowledgments

This project was supported by a National Science Foundation-Sponsored Japan Society for the Promotion of Science Short-Term Invitational Fellowship awarded to KCH. Credit goes to Monique McGee for assistance with the production of Figures 1 and 4, Jeremy Crampton with Figure 2, and David Lukasek for the base image of the 3-D scanned mandible in Figure 3. We thank Hajime Ishida and three anonymous reviewers for their insightful comments.

References

Adachi, N., Shinoda, K-i., Umetsu, K., Matsumura, H. 2009. Mitochondrial DNA analysis of Jōmon skeletons from the Funadomari Site, Hokkaido, and its implication for the origins of Native American. *American Journal of Physical Anthropology* 138, 255-265.

- Adachi, N., Shinoda, K-i., Umetsu, K., Kitano, T., Matsumura, H., Fujiyama, R., Sawada, J., Tanaka, M. 2011. Mitochondrial DNA analysis of Hokkaido Jōmon skeletons: remnants of archaic maternal lineages at the southwestern edge of former Beringia. *American Journal of Physical Anthropology* 146, 346-360.
- Akazawa, T. 1981. Maritime adaptation of prehistoric hunter-gatherers and their transition to agriculture in Japan. In: Koyama, S., Thomas, D.H. (Eds.), *Affluent Foragers: Pacific Coasts East and West*. National Museum of Ethnology, Osaka, pp. 213-258.
- Akazawa, T. 1982a. Cultural change in prehistoric Japan: receptivity to rice agriculture in the Japanese archipelago. In: Wendorf, F., Close, A.E. (Eds.), *Advances in World Archaeology*. Academic Press, New York, pp. 151-211.
- Akazawa, T. 1982b. Jōmon people's subsistence and settlements: discriminatory analysis of the Later Jōmon settlements. *Journal of the Anthropological Society of Nippon* 90, 55-76.
- Akazawa, T. 1986a. Hunter-gatherer adaptations and the transition to food production in Japan. In: Zvelebil, M. (Ed.), *Hunters in Transition*. Cambridge University Press, Cambridge, UK, pp. 151-166.
- Akazawa, T. 1986b. Regional diversity in Jōmon subsistence and its relation to the racial history of the Japanese. In: Anderson, A., (Ed.), *Traditional Fishing in the Pacific*. Pacific Anthropological Records, Honolulu, pp. 199-213.
- Akazawa, T. 1986c. Regional variation in procurement systems of Jōmon hunter-gatherers. In: Akazawa, T., Aikens, C.M. (Eds.), *Prehistoric Hunter-Gatherers in Japan*. University of Tokyo Press, Tokyo, pp. 73-92.
- Akazawa, T. 1987. Variability in the types of fishing adaptation of the Later Jōmon people, ca. 2,500-300 B.C. In: Bailey, G., Parkington, J. (Eds.), *The Archaeology of Prehistoric Coastlines*. Cambridge University Press, Cambridge, pp. 78-92.
- Aikens, C.M., Higuchi, T. 1982. *Prehistory of Japan*. Academic Press, New York.
- Arenas, R.A. 2012. Regional variation in mandibular morphology in the prehistoric Japanese populations of the Jōmon and Okhotsk. Unpublished MA Thesis, University of Alaska, Fairbanks.
- Bastir, M., Rosas, A., Kuroe, K. 2004. Petrosal orientation and mandibular ramus breadth: evidence for an integrated petroso-mandibular developmental unit. *American Journal of Physical Anthropology* 123, 340-350.

- Brace, C.L. 1979. Krapina, "Classic" Neanderthals, and the evolution of the European face. *Journal of Human Evolution* 8, 527-550.
- Buikstra, J.E., Ubelaker, D.H. 1994. Standards for Data Collection from Human Skeletal Remains: Proceedings of a Seminar at the Field Museum of Natural History. Arkansas Archeological Survey, Fayetteville, AR.
- Carlson, D.S., Van Gerven, D.P. 1977. Masticatory function and post-Pleistocene evolution in Nubia. *American Journal of Physical Anthropology* 46, 495-506.
- Corruccini, R. 1991. Anthropological aspects of orofacial and occlusal variations and anomalies. In: Kelley, M., Larsen, C.S. (Eds.), *Advances in Dental Anthropology*. Wiley-Liss, New York, pp. 295-323.
- Corruccini, R.S., Beecher, R.M. 1982. Occlusal variation related to soft diet in a non-human primate. *Science* 218, 74-76.
- Dodo, Y. 1981. Prehistoric Jōmon skulls from the Satohama shell-mound in Miyato Island Japan. *Journal of the Anthropological Society of Nippon* 89, 283-302 (in Japanese with English summary).
- Dodo, Y., Kawakubo, Y. 2002. Cranial affinities of the Epi-Jōmon inhabitants in Hokkaido, Japan. *Anthropological Science* 110, 1-32.
- Enlow, D.H., Hans, M.G. 1996. *Essentials of Facial Growth*. W.B. Saunders Co, Philadelphia.
- Fukase, H., Suwa, G. 2008. Growth-related changes in prehistoric Jōmon and modern Japanese mandibles with emphasis on cortical bone distribution. *American Journal of Physical Anthropology* 136, 441-454.
- Fukase, H., Wakebe, T., Tsurumoto, T., Saiki, K., Fujita, M., Ishida, H. 2012. Geographic variation in body form of prehistoric Jōmon males in the Japanese Archipelago: its ecogeographic implications. *American Journal of Physical Anthropology* 149, 125-135.
- González-José, R., Ramírez-Rozzi, F., Sardi, M., Martínez-Abadías, N., Hernández, M., Pucciarelli, H.M. 2005. Functional-cranial approach to the influence of economic strategy on skull morphology. *American Journal of Physical Anthropology* 128, 757-771.
- Habu, J. 2004. *Ancient Jōmon of Japan*. Cambridge University Press, Cambridge, UK.
- Hanihara, K. 1998. Reanalysis of local variations in the Ainu crania. *Anthropological Science* 106, 1-15.

- Hanihara, T., Ishida, H. 2009. Regional differences in craniofacial diversity and the population history of Jōmon Japan. *American Journal of Physical Anthropology* 139, 311-322.
- Hanunari, H. 1986. Rules of residence in the Jōmon period based on the analysis of tooth extraction. In: Pearson, R.L., Barnes, G.L., Hutterer, K.L. (Eds.), *Windows on the Japanese Past: Studies in Archaeology and Prehistory*. Center for Japanese Studies, Ann Arbor, MI, pp. 293-310.
- Hayashi, K., Yamaguchi, B., Dodo, Y., Hiramoto, Y. 1981. Miyano Kaizuka B-, C-chiku Chosa Gaiyo: Tokuni Maiso Jinkotsu wo Chushin to shite (A Preliminary Report of the Survey of Localities B and C in the Miyano Shell-Mound: with Reference to the Human Skeletal Remains). Report of the research supported by the Grant-in-Aid for Scientific Research of the Ministry of Education, Science and Culture, Japan (in Japanese with English summary).
- Hinton, R.J., Carlson, D.S. 1979. Temporal changes in human temporomandibular joint size and shape. *American Journal of Physical Anthropology* 50, 325-333.
- Holmes, M.A., Ruff, C.B. 2011. Dietary effects on development of the human mandibular corpus. *American Journal of Physical Anthropology* 145, 615-628.
- Hudson, M.J. 2004. The perverse realities of change: world system incorporation and the Okhotsk culture of Hokkaido. *Journal of Anthropological Archaeology* 23, 290-308.
- Imamura, K. 1996. *Prehistoric Japan: New Perspectives on Insular Asia*. University of Hawai'i Press, Honolulu.
- Ishida, H. 1988. Morphological studies of Okhotsk crania from Ōmisaki, Hokkaido. *Journal of the Anthropological Society of Nippon* 96, 17-45.
- Ishida, H. 1991. An Okhotsk cranium from Oshonnai site, Rebun Island, Hokkaido. *Memoires of the Natural Science Museum, Tokyo* 24, 149-154 (in Japanese with English summary).
- Ishida, H. 1994. A human skeleton of the early phase of the Okhotsk culture unearthed at the Hamanaka-2 Site, Rebun Island, Hokkaido. *Anthropological Science* 102, 363-378.
- Ishida, H. 1996. Metric and nonmetric cranial variation of prehistoric Okhotsk people. *Anthropological Science* 104, 233-258.
- Ishida, H., Dodo, Y., Hanihara, T., Ohshima, N., Kida, M., Matsumura, H. 1992. Jōmon skeletal remains from Kotan-Onsen site, Yakumo, Hokkaido. In: *Kotan-Onsen Site*. Yakumo Educational Board, Yakumo, pp. 403-421.

- Ishida, H., Kida, M., Dodo, Y., Takayama, H. 1993. Human skeletal remains of the Okhotsk culture from Jinjaya point at the Utoro site. *Bulletin of the Shiretoko Museum* 14, 73-80.
- Ishida, H., Hanihara, T., Kondo, O. 1994. Human skeletal remains of the Okhotsk culture from Jinjaya point at the Utoro site in 1990. *Bulletin of the Shiretoko Museum* 15, 13-26.
- Kaifu, Y. 1995. Differences in mandibular morphology of the Jōmon people from Kantō and Yayoi people from Northern Kyūshū and Yamaguchi. *Anthropological Science* 103, 291-308.
- Kaifu, Y. 1997. Changes in mandibular morphology from the Jōmon to modern periods in Eastern Japan. *American Journal of Physical Anthropology* 104, 227-243.
- Kaifu, Y. 2000. Temporal changes in corpus thickness of the Japanese mandibles. *Bulletin of the National Science Museum Tokyo, Series D* 26, 39-44.
- Kaifu, Y. 2010. Mandibular morphological variation in the Jōmon people of Japan. *Bulletin of the National Science Museum Tokyo, Series D* 36, 39-44.
- Kanazawa, E., Kasai, K. 1998. Comparative study of vertical sections of the Jōmon and modern Japanese mandibles. *Anthropological Science* 106, 107-118.
- Kanzawa-Kiriyama, H., Saso, A., Suwa, G., Saitou, N. 2013. Ancient mitochondrial DNA sequences of Jōmon teeth samples from Sanganji, Tokoku district, Japan. *Anthropological Science* 121, 89-103.
- Kusaka, S., Hyodo, F., Yumoto, T., Nakatsukasa, M. 2010. Carbon and nitrogen stable isotope analysis on the diet of Jōmon populations from two coastal regions of Japan. *Journal of Archaeological Sciences* 37, 1968-1977.
- Kusaka, S., Nakano, T., Morita, W., Nakada, M. 2012. Strontium analysis to reveal migration in relation to climate change and ritual tooth ablation of Jōmon skeletal remains from western Japan. *Journal of Archaeological Sciences* 31, 551-563.
- Larsen, C.S. 1995. Biological changes in human populations with agriculture. *Annual Review of Anthropology* 24, 185-213.
- Lieberman, D.E., Krovitz, G.E., Yates, F.W., Devlin, M., St. Claire, M. 2004. Effects of food processing on masticatory strain and craniofacial growth in a retrognathic face. *Journal of Human Evolution* 46, 655-677.

- Lucas, P. 2004. Dental Functional Morphology: How Teeth Work. Cambridge University Press, Cambridge, UK.
- Maeda, T. 2002. Mandibular ramus morphology of the Jōmon people from Hokkaido. *Anthropological Science* (Japanese series) 110, 27-40.
- Matsuda, K., Aono, T. 2003. A reconsideration of the pottery from the Rebunge Site. *Journal of the Anthropological Society of Nippon* 10, 93-110.
- Matsumura, H., Anezaki, T., Ishida, H. 2001. A morphometric analysis of Jōmon skeletons from the Funadomari Site on Rebun Island, Hokkaido, Japan. *Anthropological Science* 109, 1-21.
- Matsushima, Y. 1984. Shallow water marine molluscan assemblages of the postglacial period in the Japanese Archipelago: temporal and spatial variation induced by environmental changes. *Kanagawa-ken-ritsu hakubutsukan kenkyu hokoku (sizen kagaku)* 15, 37-109 (in Japanese).
- Mitsubishi, K., Yamaguchi, B. 1961. Anthropological studies on the human remains from Omisaki, Hokkaido I. Mandible. *The Sapporo Medical Journal* 19, 268-276 (in Japanese with English summary).
- Mizoguchi, K., Dodo, Y. 2001. Metric and non-metric characters of the Jōmon skulls from the Ebishima Shell-Mound in Northeastern Honshu, Japan. *Anthropological Science* 109, 23-56.
- Naito, Y., Chikaraishi, Y., Ohkouchi, N., Mukai, H., Shibata, Y., Honch, N.V., Dodo, Y., Ishida, H., Amano, T., Ono, H., Yoneda, M. 2010. Dietary reconstruction of the Okhotsk culture of Hokkaido, Japan, based on nitrogen composition of amino acids: implications for correction of ^{14}C marine reservoir effects on human bones. *Radiocarbon* 52, 671-681.
- Nishimoto, T. (Ed.). 2000a. Rebun Cho Funadomari Iseki Hakkutsu Chosa Hokokusho (Report on the Excavation at the Site of Funadomari). Rebun Cho Kyoiku Iinkai, Rebun (in Japanese).
- Nishimoto, T. (Ed.). 2000b. Hamanaka 2 Iseki Hakkutsu Chosa Hokokusho (Report on the Research Excavation at the Site of Hamanaka 2). *Bulletin of the National Museum of Japanese History* 85, Sakura (in Japanese).

- Oxenham, M.F., Matsumura, H. 2007. Oral and physiological paleohealth in cold adapted peoples: Northeast Asia, Hokkaido. *American Journal of Physical Anthropology* 135, 64-74.
- Paschetta, C., de Azevedo, S., Castillo, L., Martínez-Abadías, N., Hernández, M., Lieberman, D.E., González-José, R. 2010. The influence of masticatory loading on craniofacial morphology: a test case across technological transitions in the Ohio valley. *American Journal of Physical Anthropology* 141, 297-314.
- Pinhasi, R., Eshed, V., Shaw, P. 2008. Evolutionary changes in the masticatory complex following the transition to farming in the southern Levant. *American Journal of Physical Anthropology* 135, 136-148.
- Sardi, M.L., Novellino, P.S., Pucciarelli, H.M. 2006. Craniofacial morphology in the Argentine Center-West: consequences of the transition to food production. *American Journal of Physical Anthropology* 130, 333-343.
- Takahashi, R., Toizumi, T., Yasushi, K. 1998. Archaeological studies of Japan: current studies of the Jōmon archaeology. *Nihon Kokogaku: Journal of the Japanese Archaeological Association* 5, 47-72.
- Tsutaya, T., Naito, Y.I., Ishida, H., Yoneda, M. 2014. Carbon and nitrogen isotope analyses of human and dog diet in the Okhotsk culture: perspectives from the Moyoro site, Japan. *Anthropological Science* 122, 89-99.
- Umitsu, M. 1991. Holocene sea-level changes and coastal evolution in Japan. *Daiyonki Kenkyu* 30, 187-196 (in Japanese with English summary).
- Van Valen, L. 1962. A study of fluctuating asymmetry. *International Journal of Organic Evolution* 16, 125-143.
- von Cramon-Taubadel, N. 2011. Global human mandibular variation reflects differences in agricultural and hunter-gatherer subsistence strategies. *Proceedings of the National Academy of Science, U.S.A.* 108, 19546–19551.
- Yamaguchi, B. 1963. The human skeletal remains from Bozuyama in Central Hokkaido. *Journal of the Anthropological Society of Nippon* 71, 55-71.
- Yamaguchi, B. 1991. Skeletal remains of the Okhotsk people from the Koetoi and Pirikatai shell mounds in Wakkanai, Hokkaido. *Memoirs of the National Science Museum* 24, 141-148 (in Japanese).

Yoneda, M., Hirota, M., Uchida, M., Uzawa, K., Tanaka, A., Shibata, Y., Morita, M. 2001. Marine radiocarbon reservoir effect in the western North Pacific observed in archaeological fauna. *Radiocarbon* 43, 465-471.

Figure captions

Fig. 1: Relationship between diet, mastication, and mandibular robusticity. Mandibular robusticity is greatly influenced by the foods consumed and the degree of preparation involved. Sexual dimorphism also contributes to morphological differences, with males generally exhibiting larger and more rugose mandibles compared to females, although a gendered division of labor with females heavily utilizing their teeth as tools, for example, to process hides, may result in greater robusticity. During development, increased recruitment of the temporalis, masseter and pterygoid muscles results in a larger, more robust mandible in adulthood.

Fig. 2: Site locations. 1-Funadomari, 2-Onkoromanai, 3-Bozuyama, 4-Kitakogane, 5-Minami-Usu, 6-Takasago, 7-Irie, 8-Rebunge, 9-Kotan-Osen, 10-Usujiri, 11-Ebushima, 12-Miyano, 13-Satohama, 14-Sanganji, 15-Wakaumi, 16-Nishigahara-nichome, 17-Shosenzuka, 18-Yoshigo, 19-Ikawazu, 20-Hobi, 21-Ota.

Fig. 3: Metric variables.

Fig. 4: Canonical Scores Axis 1 and 2 with 68% sample ellipses for each region. Abbreviations for regions include N = North, SW = Southwest, NE = Northeast and S/W = South/West.

Figure 1

Figure 2

Figure 3

Figure 4

Table 1

Materials

Region	Site	Period	Museum^b	n
Hokkaido-North (n=10)	Onkoromanai	Epi-Jōmon	SMU	1
	Funadomari	Later Jōmon	SMU	9
Hokkaido-Southwest (n=30)	Bozuyama	Epi-Jōmon	SMU	2
	Minami-Usu-6	Epi-Jōmon	SMU	3
	Rebunge	Epi-Jōmon	SMU	2
	Irie	Later Jōmon	SMU	4
	Takasago	Later Jōmon	SMU	5
	Usujiri	Later Jōmon	SMU	2
	Kitakogane ^a	Early Jōmon	SMU	9
	Kotan-Onsen	Middle Jōmon	SMU	3
	Ebishima	Middle Jōmon	NMNS	28
	Nishigahara-nichome	Middle Jōmon	NMNS	1
Honshu-East North (n=37)	Wakaumi	Middle Jōmon	NMNS	1
	Miyano	Later Jōmon	NMNS	4
	Sanganji	Later Jōmon	NMNS	1
	Satohama	Later Jōmon	NMNS	1
	Shosenzuka	Later Jōmon	NMNS	1
	Ota	Middle Jōmon	KUM	26
	Hobi	Later Jōmon	NMNS	1
	Ikawazu	Later Jōmon	NMNS	20
	Yoshigo	Later Jōmon	KUM	41
Total				165

^a Kitakogane is included within the Middle Jōmon time period in the analysis.

^b SMU = Sapporo Medical University; NMNS = National Museum of Nature and Science; KUM = Kyoto University Museum.

Table 2Descriptive statistics by region^a

	N Hokkaido			SW Hokkaido			NE Honshu			S/W Honshu		
	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD
Chin height	4	32.64	5.23	12	32.75	2.97	18	31.12	4.20	61	27.42	4.54
Bigonial breadth	8	82.47	2.18	28	82.35	3.17	34	84.59	3.87	70	85.22	3.22
Bicondylar breadth	3	121.35	1.78	10	117.98	13.24	18	125.53	6.79	19	126.75	4.89
Corpus height	9	27.65	2.20	28	29.63	3.70	22	30.34	2.43	67	28.10	3.10
Corpus breadth	9	15.05	1.71	30	14.86	1.56	35	15.70	2.23	87	15.69	1.90
Minimum ramus breadth	10	37.74	1.64	29	38.54	3.03	36	34.33	2.91	69	34.35	2.62
Maximum ramus breadth	9	49.07	2.34	24	51.63	4.02	30	45.71	3.89	50	46.28	3.94

^a Abbreviations for regions include N = North, SW = Southwest, NE = Northeast and S/W = South/West

Table 3

Analysis of Variance results comparing dietary region with covariates

	Time Covariate				Sex Covariate			
	n	F	<i>p</i> (Region)	<i>p</i> (Time)	N	F	<i>p</i> (Region)	<i>p</i> (Sex)
Chin height	95	8.464	0.000 ^a	0.094	62	5.226	0.008	0.001
Bigonial breadth	140	6.498	0.000 ^a	0.160	90	7.755	0.000 ^a	0.119
Bicondylar breadth	50	4.029	0.013	0.121	28	6.893	0.004	0.005
Corpus height	126	2.095	0.104	0.576	89	0.820	0.486	0.369
Corpus breadth	161	1.277	0.284	0.062	104	3.488	0.019	0.604
Minimum ramus breadth	144	23.96	0.000 ^a	0.006	91	21.497	0.000 ^a	0.047
Maximum ramus breadth	113	18.02	0.000 ^a	0.001	73	11.614	0.000 ^a	0.334

^a Significant at $\alpha \leq 0.0001$

Table 4

Canonical discriminant functions scores standardized by within variances

	Axis 1	Axis 2
Chin height	0.204	0.114
Bigonial breadth	-0.339	-0.129
Bicondylar breadth	-0.745	-0.217
Corpus height	-0.045	1.253
Corpus breadth	-0.046	-0.209
Minimum ramus breadth	1.226	0.010
Maximum ramus breadth	-0.396	-0.534