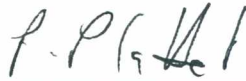


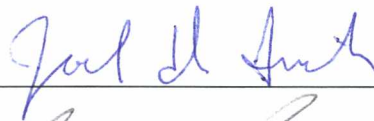
REGIONAL VARIATION IN MANDIBULAR MORPHOLOGY IN THE
PREHISTORIC JAPANESE POPULATIONS OF THE JŌMON AND OKHOTSK

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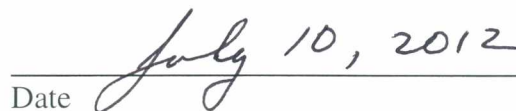
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REGIONAL VARIATION IN MANDIBULAR MORPHOLOGY IN THE
PREHISTORIC JAPANESE POPULATIONS OF THE JŌMON AND OKHOTSK

A
THESIS

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By

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ABSTRACT

Examination of 11 metric mandibular traits was conducted on data collected from several Jōmon and Okhotsk sites for the purpose of analyzing potential impacts of dietary differences on mandibular morphology for these groups. Based on the dietary history of the populations and their respective regions, Middle Jōmon (5,000 - 3,000 BP) sites would share comparable robusticities across all regions based on social and economic continuity as a stable climate resulted in abundant dietary resources which fostered a growth in population in the Japanese islands of Honshu and Hokkaido. As the climate cooled in the Late/Final Jōmon (4,000 - 2,000 BP), the population of the two islands crashed coinciding with reduced carrying capacity of the environment due to a reduction in available food resources. Late/Final Jōmon were expected to show mandibular reduction in the Honshu interior which had engaged in plant cultivation and emergent agriculture as opposed to populations on the Hokkaido and Honshu coast which engaged in marine subsistence. The success of agriculture resulted in an expansion across Honshu, pushing marine subsistence communities northeastward to Hokkaido where the tradition persisted as the Epi-Jōmon until the arrival of immigrant populations of the Okhotsk (1,000-600 BP). The Epi-Jōmon and Okhotsk would share comparable robusticities based on their shared practice of marine subsistence. The Late/Final Jōmon and Epi-Jōmon/Okhotsk hypothesis were not supported citing the presence of more diversified and complex subsistence practices than was initially anticipated.

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Preface

Before engaging in the discourse central to this thesis, clarification of key points regarding its composition is necessary. This thesis will draw heavily from theories and findings on the Jōmon as founded in Japanese anthropological literature. On a theoretical basis, Japanese anthropology differs in some ways from its American counterpart. While American anthropology tends to lean more on the scientific and deductive, Japanese anthropology is generally practiced as a form of history (Habu, 2004). This regionally specific sentiment perhaps is tied to the modern Japanese socio-cultural identity as heavily invested in a specific interpretation of prehistoric Japan (Habu, 2004). Generally in anthropology, the subject of study is viewed as outside the context of the one performing the study, either in terms of time or in a perceived socio-cultural context. The Japanese, on the other hand, have a strong sense of identity, whether substantiated or perceived, tied to the prehistoric populations that once lived within the archipelago that is now modern day Japan.

Of the prehistoric populations that occupied Japan, one is popularly given credence over the others: the Yayoi are accepted as being the ancestral population of modern day Japanese, while the Jōmon and Ainu are not. The Jōmon refers to the people and culture of the pre-agricultural period of Japan from 10,000 -500 BP. By 2,300BP, immigrants from mainland Asia brought and established the practice of wet rice agriculture in the islands marking the beginning of the Yayoi. The Ainu resided in Hokkaido, descended from the Epi-Jōmon, the displaced Jōmon populations that

persisted in the practice of hunting and fishing while agriculture was spreading through the southern island of Honshu.

While the argument on Japanese origins may seem teleological, the topic is embedded with a strong sense of identity and pride that is questionably unique. This is not to say that this perceptual difference negates the consistency or validity of Japanese anthropology so much as to say that the respective goals and the context to which they are applied differ within the practice of Japanese anthropology and those from the United States. Therefore, anthropologists from differing schools may share differing contexts and view data under different sets of assumptions.

Accessibility to published data is particularly difficult to non-Japanese speaking anthropologists because most materials on prehistoric Japan are written in Japanese. Compilations such as *Prehistoric Japan* by Keiji Imamura and the *Jōmon of Japan* by Junko Habu increase accessibility but introduce an epistemological third party bias by funneling information and data through the same handful of mediators. This has changed considerably within recent years with an increase in anthropologists studying Japanese prehistory and publishing in English, but many of the original studies and projects still remain inaccessible to non-Japanese readers.

For the purposes of this project, I focus on materials published in English when available. I have done my best in retrieving sources in English when available and cite any specific findings to those sources. In situations where a specific conclusion or

observation was made by an original publication that is inaccessible, I will refer to the authors of such publication while referring to the second-hand material that referenced it.

Chapter 1 Introduction

When studying past populations, one of the most significant and revealing biological markers found in skeletal remains are those related to diet. Observable markers on the odonto-skeletal remains of individuals may reflect dietary behaviors in life as well as any nutritional and mechanical consequences of the behavior. Studying these biological markers allows for extrapolation of information about diet and behaviors related to acquisition and maintenance. While diet related markers can be found throughout the body (i.e. nutritional stressors or subsistence practice traumas), several significant ones can be found in the skull, specifically within the mandible.

The pre-agricultural Jōmon period of pre-historic Japan is marked by variation in subsistence patterns and diet coinciding with periodic fluctuations in climate from 10,000-500 BP. Populations peaked during the Middle Jōmon, between 5,000-3,000 BP, in response to a more stabilized climate and consistent food sources. During this time of population growth, an increase in cultural homogeneity occurred between sites along with more instances and degrees of sedentism and social stratification and more intricate material goods not related to subsistence. By the Final Jōmon, populations decreased in number and became more isolated, fragmenting into pockets of diverging cultural, economic, and dietary systems (Habu, 2004). Through differences in regional occupation and cultural exposures, the Jōmon adapted different patterns of subsistence, ranging from marine exploitation in the northeast coastal areas and plant cultivation and gathering in the inland regions (Akazawa, 1981, 1982a).

Following the Jōmon, subsequent exposure to immigrants from mainland Asia (who originally migrated to the southern island Kyushu by at 2,300 BP) initiated the widespread adoption of wet rice agriculture, a practice that marks the beginning of the Yayoi (Aikens and Higuchi, 1982). By 1,000 BP, the immigrant population of the Okhotsk from Sakhalin would settle along the coasts of Hokkaido, an island north of mainland Honshu. Okhotsk subsistence was heavily and nearly exclusively marine dependent, evidenced by coastal habitation and tools specialized for fishing and hunting marine mammals (Aikens and Higuchi, 1982). At this point, subsistence patterns throughout Japan were fragmented based on regional resource availability, cultural predispositions, and external influences (i.e. immigrant wet rice agriculturalists). These differences would remain until 600 BP, when agriculturalists from Honshu would push northward bringing with them their practice of wet rice agriculture and displacing coastal populations into Hokkaido (Akazawa, 1982b).

Mandibular development and characteristics have been described extensively and demonstrate morphological plasticity influenced by diet. The mandible, like all bones, remodels in response to mechanical stresses-- becoming more robust in response to increased stresses and more gracile in response to reduced stresses. The mandible is unique in that changes in its robusticity serve two purposes: to dissipate pressures on the crania and to maintain occlusion (Enlow, 1975). The mandible's form, like most boney processes, follows the idiom of increased robusticity to harsher diets and gracility in response to more processed foods (Hinton and Carlson, 1979). This notion has served as a line of evidence for inferring the nature of diet and the environment based on skeletal

remains. Given the Jōmon's complex subsistence patterns, the relationship of mandibular robusticity and diet presents an interesting case.

Biomechanics during growth and development of the mandible provides a context in which to explore possible ambiguities in the relationship between Jōmon diet and mandibular morphology. Assuming that the primary forces applied to the mandible are related to mastication, measurements of the mandible can be used to infer diet quality as well as extrapolate the sort of diet that would contribute to its development. In conjunction with bioarchaeological findings, human behavioral ecology can assist in reconstructing the sort of behaviors and diet that would contribute to the sorts of findings in the record. Since the acquisition of food and the sustenance of diet have been one of the fundamental necessities governing an organism's behavior, applying models of resource distribution, acquisition, and processing can assist interpreting findings in the mandibular data by suggesting the sort of diets and behaviors that would result in measurements observed.

Multiple factors such as diet, environment, social structure, and cultural practices are likely to contribute to the mandibular form of the Jōmon and the Okhotsk. Research has shown that one of the most influential factors in determining mandibular robusticity is diet consistency, which can often be determined by available resources and subsistence economy (Hinton and Carlson, 1979). One well documented phenomenon is the overall craniofacial reduction that follows the adoption of agriculture as a result of reduced masticatory forces due to softer, processed foods (Hinton and Carlson, 1979). Subsistence

and diet changes that occurred between the Middle and Late/Final Jōmon is likely to be evident in osteological remains from those periods. To examine and test the relationship between diet and robusticity, multiple mandibular measurements will be compared by period and region.

The Middle Jōmon was a period of climatic stability, marked by increased carrying capacity that resulted in large, culturally continuous populations with comparable diets across all regions occupied by the Jōmon. Middle Jōmon sites are expected to display comparable mandibular morphology despite spatial/regional differences under the assumption that similar diets would result in comparable robusticities. The hypothesis is that Middle Jōmon sites will show no significant difference in mandibular robusticity among regions.

By the Late/Final Jōmon, cultural and economic splintering occurred among the Jōmon, with coastal populations specializing in marine subsistence and interior sites in Honshu specializing in plant cultivation, which would subsequently lead to the ready adoption of agriculture at the start of the Yayoi. The hypothesis is that interior Honshu sites during the Late/Final Jōmon will differ significantly from coastal Jōmon sites from the Late/Final Jōmon. Specifically, this hypothesis is founded on the prediction that plant cultivation and emergent agriculture in southwest, interior Honshu would result in a reduction in mandibular morphology based on food processing and consistency.

The Epi-Jōmon reflect persistence of Jōmon culture and traditional subsistence economy in Hokkaido after the expansion of agriculture across Honshu (Imamura, 1996).

They shared temporally proximal yet socially isolated occupation of the Hokkaido coast with the Okhotsk, an immigrant population from mainland Asia via Sakhalin that settled along the coast of Hokkaido. The Okhotsk were culturally distinct from the Jōmon and heavily specialized in marine subsistence (Aikens and Higuchi, 1982). Based on both the Epi-Jōmon and Okhotsk engaging in marine subsistence, the hypothesis is that there is no significant difference in mandibular morphology between the Epi-Jōmon and the Okhotsk.

In order to comprehensively address the question, this thesis incorporates models and theories from different disciplines to clarify the relationship between mandibular robusticity and diet and to characterize the human behaviors attributed to observed changes in mandibular morphology. Chapter 2 discusses relevant components from established knowledge of biomechanics and how forces attributed to the masticatory process shape the mandible and its surrounding processes. Chapter 3 briefly discusses important factors in human behavioral ecology related to diet and how the environment influences the decisions to consume or exploit specific resources. Chapter 4 discusses the biocultural context of the Jōmon, Epi-Jōmon, and Okhotsk focusing specifically on biomechanical and human behavioral models and theories discussed in previous the preceding chapters. The chapters that follow discuss the materials used in the study (Chapter 5), the procedures and statistics used to analyze the data (Chapter 6), and the results of the analysis (Chapter 7). Chapter 8 examines the results and incorporates biomechanics and human behavioral ecology to contextualize the findings to Jōmon, Epi-Jōmon, and Okhotsk mandibular robusticities and subsistence practices. Chapter 9

concludes the thesis by revisiting previously discussed topics and their applicability to the experiment and its results.

Chapter 2 Biomechanics

2.1 Mastication and plasticity

Biomechanics applies the principles of physics to the living form by fundamentally envisioning the body as a complex system of simple machines working cooperatively to produce the spectra of motions and functions capable by the overall form (Spencer and Demes, 1993). In humans, the synergistic connections of bone, muscle, and connective tissue that span the body provide the function of structure, stability, and mobility. With respect to diet, the focus of biomechanical analysis is centered on the craniofacial complex.

The craniofacial complex consists of the bones of the crania including the mandible and teeth and associated muscles. Mastication involves the processing of food and the stabilization of other functions of the craniofacial complex, such as providing sufficient protection to the organs from applied forces while still maintaining the ability to chew (Thomason and Russell, 1986). This interplay between function and stabilizing form has resulted in one of the highest degrees of plasticity in the human body. Plasticity is the ability of a component to adapt to pressures within the environment in order to optimize both its respective and overall function (Petrovic et al., 1975; Pritchard et al., 1956). In doing so, an organism achieves an optimal balance between improved mastication and protection of critical organs, such as the brain, from bite force (Thomason and Russell, 1986).

In biomechanical terms, the mandible serves as a simple lever that generates the necessary force to produce a bite through the occlusion of its teeth with those of the maxilla (Enlow, 1975). The muscles of the masseter are associated with tensile forces while the temporalis is associated with compressive forces and provide the motions and force necessary to operate the lever (Endo, 1970). As greater force is placed on these muscles, one can find evidence of strain and compensation for additional loading based on the muscle attachments and processes in the skull (Endo, 1970). Likewise, the bones of the mandible and maxilla may become more robust to diffuse these forces (Lieberman, 1996). What becomes evident then is a cooperative response to chewing forces that results in changes to mitigate the strain of these forces.

At the heart of the masticatory process is the mandible which serves as the lever within the biomechanical schematic. A lever is a simple machine which provides increased input of force via the location of its fulcrum, or the point through which the mechanism pivots (Enlow, 1975; Ricketts, 1975). The force of the lever can be adjusted through plastic means within the form of the mandible, through its bone, joint, cartilage, and muscle attachments. Teeth of the mandible, although not possessing the plasticity of bone, play a significant role in the masticatory process through chewing, produced through the occlusion when in contact with the teeth of the maxilla (Enlow, 1975). Therefore, in order to understand the mechanism of the lever, one must look at both the mandible and its corresponding teeth.

While the joint provides the fulcrum for the lever, the cartilage of the mandibular condyle serves as a proxy of growth. As the center of growth and ossification for the mandible, the condylar cartilage is responsive to various pressures and is the center of growth in response to muscular forces in order to maintain consistent articulation (Durkin et al., 1973). Therefore, mandibular condylar cartilage grows in response to changes that occur with the articular fossa with said growth providing structural support and function of the temporomandibular joint (Durkin et al., 1973). Horizontal development of the mandible results in vertical development of the face while vertical development of the mandible results in more horizontal growth of the face. The overall process is controlled by the angle of the mandible (Ricketts, 1975). The mechanism for the condylar cartilage growth results from evolution of the temporomandibular joint from a secondary joining of the squamosal and dentary bones (McNamara et al., 1975; Petrovic, 1972).

2.2 Biomechanical mandibular microevolution

The human lineage has displayed general trends with regards to the craniofacial complex leading to the human form. The evolutionary path to modern humans has seen the gracilization of the crania (Baab et al., 2010). The mandible is the component most associated with diet and has displayed variation in ramus angle and size based on factors such as age and population affinity. Most variation in the mandible is associated with the degree of molar wear in individuals and compensation for occlusion (Oettle et al., 2009). Modern humans display a gracilization of the mandible with a more obtuse angle in the ramus although a full explanation can be difficult due to fragmentary nature of mandibular remains in the record (Wolpoff, 1975). Cortical robusticity of the crania

shows a reduction in robusticity as the human lineage progresses (Lieberman, 1996). While there may be a genetic component, most of this variation is likely an environmental effect (Lieberman, 1996). Geographical variation in craniofacial form may be attributed to the environment (Hanihara, 1996; Hennessey and Stringer, 2002). Overall, despite the trend towards gracility in modern humans and potential reflection on dietary changes, the plasticity of craniofacial complex is limited within the confines of its predisposed genetic variation (Arya et al., 1973; Lahr and Wright, 1996). In order to understand the environmental forces at work in pronouncing the plastic components of the craniofacial complex, one must understand the functions each component serves and how forces apply to them.

The temporomandibular joint has shown a general trend of reduction in size in conjunction with reduction in muscle robusticity as observed in living populations (Hinton and Carlson, 1979). This may be attributable to a reduction in chewing force coincident with a shift from hunter-gatherer to agricultural subsistence (Hinton and Carlson, 1979). This subsistence transition is associated with a reduction in fossa depth and reduced sloping of the ramus with greater wear placed on teeth (Hinton, 1981). This pattern is the result of not only softer food quality but pre-masticatory processing and cooking that also decreases loading strain on the muscles of the craniofacial complex (Lieberman et al., 2004). Studies of human populations have shown reduction to be a general and pervasive trend among populations in transition although dietary context has had an impact on localized areas of reduction (Paschetta et al., 2010). For instance, in response to softer or harder food types, reduction tends to be more localized closer to the

plane of occlusion and results in adjustments along the temporal fossa that corresponds with displacement of the temporal muscle (Paschetta et al., 2010). Likewise, studies on the contributions of softer foods over harder foods have shown a smaller impact on the robusticity of the mandibular bone itself (McFadden and McFadden, 1986). Any changes in the bone were localized mostly within the ramus of the mandible, the component that serves as the fulcrum, in the lever mechanism (McFadden and McFadden, 1986). The composition of mandibular bone has shown little increase in cortical bone density resulting in thinner cortical bone along the ramus (Bresin et al., 1999). The thinner form maintains the effectiveness of bone per unit (Bresin et al., 1999).

The effects of occlusal loading can also be observed in the maxilla and evidenced by studies of intermaxillary sutures. Facial and cranial sutures also demonstrate a degree of plasticity and can remodel to compensate for increased dietary forces (Pearson, 1973; Pritchard et al., 1956). Changes in loading forces have demonstrated increased activity in intermaxillary sutures of secondary cartilage, like those found in the condyle of the mandible (Hinton, 1988). This change results in more fibrous connections providing higher flexibility and plasticity that may serve the purpose of diffusing occlusal forces (Hinton, 1988). While studies in lab environments with rats have shown less impact due to non-dietary environmental components, how these can play out in human populations within natural environments is uncertain (Beecher and Corruccini, 1981; McFadden and McFadden, 1986; Pearson, 1973).

The process of maintaining the craniofacial form is susceptible not only by the increase in pressure, but in its reduction as well. Food processing and softer diets, as found urbanized societies, have displayed much higher degrees of malocclusion than that found in hunter-gather societies (Beecher and Corruccini, 1981). While nutritionally-based studies show differences in mandibular development and dental eruption, most evidence suggests the impact of dietary consistency is more important: softer or processed diets are associated with less tooth wear, smaller muscle attachments, and reduced thickness in the buccolingual thickness of the mandible (Beecher and Corruccini, 1981; Corruccini et al., 1985). Malocclusion is multifaceted in etiology and results in disruption of the circular order of growth (Beecher and Corruccini, 1981; Enlow, 1975). The phenomenon has been confirmed in multiple groups in transition in which those subsisting on modern soft diets have displayed higher rates of malocclusion (Corruccini et al., 1983).

Chapter 3 Theory: Human Behavioral Ecology

An interdisciplinary field by nature, human behavioral ecology is not a new science, so much as a new paradigm by which many old questions are readdressed within the context of the subject's relationship to the environment (Joseph, 2000). For instance, topics such as the study of subsistence, economic patterns, or social organization are not new to the field, but from a human ecological perspective, are studied in light of how these very same institutions have been formed either in response to or in the influence of the environment. In its simplest form, human behavioral ecology can be said to be the study of the relationships of an individual or population with respect to the environment and the subsequent behavioral adaptations (Bird and O'Connell, 2006).

The individual is not the sole player in this dynamic, as typically this response is the result of an intricate interplay between three main agents: the individual, the population, and the environment (Jones, 2004). These three components are assumed to be in equilibrium unless under the pressure of extraneous forces resulting in ecological shifts that can potentially lead to multiple causative or correlative feedback pathways or changes to the overall system (Burger et al., 2005). Tracing these changes can become very complex even when focusing on a single element. For instance, an individual adopting a set of behaviors improving its respective fitness and in turn contributing to the fitness of the population to which the individual belongs would also apply pressure to the environment which can either support the added strain or fail to support the additional needs of the adjusted behavior. The response from the environment can in turn place

pressures on the population to reinforce or change its behavior, establishing framework of individual subsistence. This interplay is dynamic and often occurs in more subtle ways that can change by day, or seasonally, or for the long term. With so many factors and variables at work, direct and concrete deduction can be nearly incalculable (Bassett et al., 2002). As a result, in order to make sense of all these variables, various models are used to describe the particular mechanics of an ecological event or phenomenon.

Ecological models are open-ended-- not pertaining to any one particular environment-- and are more generalized as they are intended to describe relationships and responses of individuals to that environment (Bassett et al., 2002). Behavioral ecology is not so much a testable concept as a conditional relationship between multiple elements within the environment (Bird and O'Connell, 2006). Through repeated observations, models are refined or rejected. Depending on the focus of the study, particular variables are selected and serve as surrogates which are representative of the particular phenomenon under observation (Bassett et al., 2002). For example, one cannot profile the whole of an environment or comprehensively chart the interactions of its resources and agents, rather models such as carrying capacity can estimate an environment's ability to sustain a population based on variables known to be of significance (i.e. initial population size, resource growth rate, resource distribution) (Bassett et al., 2002).

Although behavior can be influenced by the nature and frequency of a food source, an organism is also constrained by the capacity of the environment to mitigate exploitation of its resources. Resilience can be termed as the capacity of an environment

to return to equilibrium after it has been disturbed (Holling, 1973). If the environment can withstand pressures at little cost to the dynamic of the system as a whole, the environment can be considered resilient. Although disturbances may be stochastic events (i.e. wild fire or floods) disturbances can also be continuous and systemic. As there are multiple contributors to a system's equilibrium as well as many possible perturbations, resilience is best envisioned as a status quo to which an environment can return (Folke et al., 2004). The resilience of an environment is determined by multiple biotic and abiotic factors resulting in different resilience "types" ranging from immediate to long-term restoration of equilibrium and those susceptible to crashing at the slightest deviation. As a result, behavior is regulated not only by the interplay of an organism and a resource, but the reliability of the system as a whole. Depending on the environments resilience, a behavior's optimality may vary based on the current conditions of the environment. Behavioral ecology is more a spectrum of behaviors than a singular action and should represent a repertoire of responses available under specifying conditions.

The need for these models further confirms the complexity of behavioral ecology as measurements are defined either through comparison with other existing measurements or through some set of qualifiers and criteria (Peterson et al., 1998). As a result, subjectivity in interpretations can be high. Most observations that are made can only be inductive by nature, often making it difficult to establish a baseline or standard by which an environment can be observed without the support of analogy (Peterson et al., 1998). These behavioral ecology models may work well for other species but capture only part of the picture when applied to humans: no other species has been known to

manipulate and respond to the environment in the same manner and to the same extent as human beings, a species which has gone as far as to develop biocultural toolkits as to allow for the proliferation of the species in ecosystems outside of its own evolutionary niche (Binford, 1979).

The depth and breadth of human adaptation is what makes human behavioral ecology such a challenging study. While the models discussed previously may apply to humans, we have developed the capacity to mitigate, circumvent, or overcome the fundamental components that define the parameters of these models. Our cultural adaptation shifts the equilibrium to our favor and makes it difficult to follow and observe the extent to which the concepts play out, if at all (Bird and O'Connell, 2006). One can find among humans examples that both support and deviate from the fundamental tenets of behavioral ecology (Rodes et al., 1999). Although examples can be cited that support optimal foraging theory, there are many potential practices that counter this, such as the pursuit of "luxury" foods that serve the purpose of novelty (Pyke, 1984). Others cases may sometimes even seem borderline mal-adaptive, such as the overexploitation of a resource to the point of depletion or extinction, such as the conjectural argument of human's contribution to the extinction of various megafauna (Burney and Flannery, 2005; Pyke 1984). In examples where the environment would have typically placed a constraint on the population size of an organism, humans have manufactured alternative subsistence means to circumvent these pressures, such as the classic example of the development of agriculture (Hawkes et al., 1993; Higgs and Jarman, 1969). As a result,

the implementation of classic ecological models and theory do not always apply when studying humans and their behavior with regard to a particular ecosystem.

These limitations, among others, make reconstruction of a paleo-environment and the study of human adaptations in response to that environment complicated. More often than not, studies in human behavioral ecology are conducted by studying extant populations (O'Connell, 1995). While contemporary ethnographic studies of hunter-gatherers are useful in understanding human's relationship with the environment, they are limited in their ability to reveal the relationship between humans and the environment in a prehistorical context. In terms of the environment, contemporary population studies do little to tell us about the response of prehistoric populations to environmental changes (O'Connell, 1995). They overlook issues such as the relatively unstable and ever-fluctuating nature of the paleo-environment, the different expectations or perceptions of the stability of the environment by the population, or the context of a hunter-gatherer population free and independent from the influence of a greater socioeconomic system that is often in place despite these smaller scale practices (Bird and O'Connell, 2006; David-Bird, 1990; O'Connell, 1995). To assume subsistence practices like hunting-gathering have remained static since they were first adopted is problematic. Even if the methods remain the same, the presence of interactions with other populations engaging in different subsistence practices would have influenced the tools and resources available to the smaller group (David-Bird, 1990, 1992). Therefore, despite the wealth of information regarding human ecology in modern populations, these data are insufficient in understanding human behavioral ecology in a prehistoric context.

Piecing together the prehistoric past involves the implementation and cooperation of various methodologies such as archaeology, bioarchaeology, paleoethnobotany, zooarchaeology, geophysics, climatology and like disciplines, each contributing a facet of our understanding of the paleo-environment (Bettinger, 1987; Schiffer, 1996). The primary problem regarding behavioral ecological studies in a prehistoric context is the lack of behavioral "artifacts" (Bird and O'Connell, 2006). Conjecturally, some behavioral adaptations may not leave a trace or may have lost their meaning overtime.

According to Bird, the research of past behavior is a two part process that involves reconstruction of the past and accounting for the process by which the reconstruction is made (Bird and O'Connell, 2006). Although archaeological data provide us with physical materials by which we can reconstruct past behavior, the process by which this behavior is reconstructed is often subjective as the reconstruction is based on the comparison of past populations with contemporary extant populations (Bird and O'Connell, 2006). In other words, determinations are heavily influenced by our comprehension and impression of contemporary behaviors and assume the responses in the past would have been comparable. In this case, our study of contemporary populations is useful, but in another sense, it may also be limiting or confounding actual prehistoric events, in which organization, structure, and behavior may have had a context completely different from any that of a contemporary population.

Conjecturally, in order for the Jōmon to have developed such a rich and diverse culture while still practicing hunter-gatherer subsistence, the Jōmon would have lived in a

relatively rich environment abundant in most food sources both nutritionally and seasonally. Such an environment would also be more than capable of sustaining large human populations. This notion has been substantiated through the analysis of middens and tools, but also through the presence of sedentary settlements (Imamura, 1996; Habu, 2004). Jōmon semi-sedentary habitations suggest that the Jōmon were collector-foragers (Habu et al., 2001; Habu, 2004). Collectors remained in more sedentary communities, bringing necessary resources back to camp from the surrounding area-- the radius between which is termed the foraging zone. Foragers on the other hand are characterized by higher mobility, following new sources as others become overly exploited (Binford, 1979). Although excavations of several Jōmon settlements have provided substantial evidence that the Jōmon were sedentary, the Jōmon most likely did not engage in strictly either system, but rather a mixture of the two, although the predisposition to semi-sedentary habitations is more focused on a collecting strategy or reflective of a resource rich environment (Habu, 2004).

Archaeological excavations, especially those conducted within middens and storage pits show a rich dietary background composed of flora and fauna from various niches (Habu, 2004). From these data, Kobayashi synthesized what is termed as the "Jōmon calendar" which covers the seasonal cycles and foci of Jōmon subsistence. The calendar is split into four main components comprising plant gathering, terrestrial hunting, shell fish collecting, and fishing. Study of floral assemblages found in storage pits show that foraging centered on the collection of acorns and other nuts (Habu, 2004; Matsui and Kanehara, 2006). In conjunction with lithic analysis, the Jōmon engaged in

small scale plant cultivation which comprised the core nutrition of the population. This is termed informally as the "plant cultivation hypothesis" and has found strongest support in sites in western Japan, mainly inland regions (Habu, 2004; Matsui and Kanehara, 2006). Others propose "the salmon hypothesis" as the core source of nutritional and caloric intake of the Jōmon, which has been supported by fish bones comprising the majority of faunal remains found in middens (Habu, 2004). Likely, discrepancies in interpretation of the archeological record indicate the existence of regional variation in diet. Evidence of marine subsistence has been particularly strong within eastern Japan (Akazawa, 1982a). Isotopic analysis demonstrates that marine subsistence was a significant staple but there is no evidence to support whether it served as the core source for caloric intake in western Japan (Habu, 2004). Western regions engaged in limited marine subsistence, deriving most of their protein from terrestrial mammals. Likely, fishing was more a secondary food source, serving as a protein supplement, in western Japan (Akazawa, 1982a; Koyama, 1978). In either case, the investment placed in the storage and processing of foraged goods suggest that plants and nuts were a common resource of the Jōmon across all regions (Habu, 2004).

Recent isotopic analysis has provided more detail to the subsistence patterns of the Jōmon. While older models such as the Jōmon calendar are sufficient in following Jōmon seasonality in subsistence, stable isotope analysis of ^{13}C and ^{15}N have provided the scaffold by which one can reconstruct the Jōmon diet and contextualize the trophic levels of Jōmon subsistence. Study of inland remains showed a higher degree of dependence on terrestrial plants with occasional reliance, most likely seasonal, on marine

resources (Yoneda et al., 2002). Remains from the Middle Jōmon along the south western coast of Hokkaido differed with ^{15}N analysis suggesting that 74% of protein intake was derived from marine proteins, both fish and marine mammals (Naito et al., 2010).

Jōmon success, as characterized by the growth and stability of the Middle Jōmon period across all regions of Japan, is reflected in this diverse subsistence pattern.

Likewise, the rich environment and abundance of resources allowed for the development of rich material culture and relative sedentism despite hunter-gatherer practices (Habu, 2004). The differential exploitation of maritime resources overall seemed to show a proliferation more along eastern Japan than along the western regions, with dramatic abundance observed in Hokkaido which had access to marine mammals. The environment during the Middle Jōmon period proved quite resilient to the exploitation of various niches to an extensive degree.

One of the most interesting behavioral adaptation lies within the Late Jōmon, at which point one can observe a shift among subsistence patterns between eastern and western Japan. For multiple reasons ranging from a change in climate to the pressure on the carrying capacity of the ecosystem, the environment lost its resiliency and was no longer able to sustain the same population under the same subsistence practices. The Late and Final Jōmon saw an environmental strain that resulted in a drop in population and cultural divergence between the eastern and western regions of Japan, especially within the realm of subsistence practices (Habu, 2004). In response to cooling temperatures and changing coastlines, coastal populations in Hokkaido and the eastern coast of Honshu

began to specialize in marine subsistence. Cooling temperatures did not impact the southwest interior of Japan to the same extent and populations were able to continue broad spectrum foraging although not to the extent of maintaining the population size as seen in the Middle Jōmon (Akazawa, 1982a; Akazawa, 1987).

The technological and cultural predispositions that resulted from this divergence in subsistence practices set the foundation for future environmental responses. The maintained practice of broad spectrum foraging in the Honshu interior had fostered specialization in the practice of plant cultivation (Akazawa, 1981, 1982,a,b, 1986a,b,c, 1987). The predisposition to plant cultivation had facilitated the adoption of wet-rice agriculture when the practice was brought to the island from the southern island Kyushu where it was introduced via migration from mainland Asia. Wet-rice agriculture did not develop among the Jōmon of eastern Japan given their relative success with marine subsistence and resistance to contact with agricultural groups (Akazawa, 1986b). The inability of the Jōmon of eastern Honshu to adapt wet-rice agriculture resulted in their subsequent displacement as the practice expanded across the island (Higgs and Jarman, 1969; Akazawa, 1986a; Habu, 2004).

The events of the Final Jōmon demonstrate the sort of difficulties in studying human behavioral adaptations in past populations. For instance, in contrast to optimal foraging theory, each region displayed a predisposition to adopting practices that were not necessarily optimal so much as readily accessible based on technological predispositions and receptivity to practicing populations (Akazawa, 1982a). The

southwest Honshu, which had been so heavily dependent on plant gathering, readily adopted wet-rice agriculture when it was introduced, while the eastern, coastal regions of Honshu resisted this subsistence strategy in lieu of the marine practices for which they were already specialized and invested (Akazawa, 1981, 1982a, 1982b). The adoption of agriculture provided a means by which the population growth could circumvent impositions on size as placed by the environment due to the reduction in available food source; those that relied exclusively on marine subsistence were unable to adjust to the changes in the environment. As a result, the Late to Final Jōmon saw an overall drop in population size which was followed by a steady increase in population as agriculture spread as well as through the immigration of other populations from the mainland.

The contribution of human behavioral ecology to the study of the Jōmon is twofold. First, human behavioral ecology as applied to the Jōmon demonstrates how the environment shaped population behavior and responses within a complex interplay of pressures and forces resulting in the continuous move to either a state of equilibrium or persistent perturbation of one component to compensate to the pressures of the other. Second, generalized models from human behavioral ecology helped explain ecological phenomenon and revealed variation in the ability of human populations to circumvent or instigate some of these pressures.

Chapter 4 Biocultural Context of the Jōmon, Epi-Jōmon, and Okhotsk

4.1 Jōmon

The term Jōmon is a Japanese word meaning "cord markings." It refers to the pattern of pottery that was discovered in Japan dating to the period from which it derives its namesake (Habu, 2004). The Jōmon period spanned from 14,000 BCE to 300BCE through the four main islands of Japan: Hokkaido, Honshu, Shikoku, and Kyushu. The Jōmon are characterized as complex hunter-gatherers displaying intricate settlements and material culture atypical of most hunter-gatherers (Habu, 2004). Despite most subsistence was derived from hunting and gathering, the Jōmon also engaged in seasonal and supplementary practices of plant cultivation and fishing (Habu, 2004).

The Jōmon period is broad and demarcated by pottery technology (Aikens and Higuchi, 1982). These phases progressed in chronological order as follows: Incipient Jōmon, Initial Jōmon, Early Jōmon, Middle Jōmon, Late Jōmon, Latest Jōmon, and Final Jōmon (Imamura, 1996). Study of the phases are often focused on those characteristics which define them, and therefore are often viewed in perspective of their transition whereby they are often referred to by the adjoining two periods, i.e. Initial-Early, Middle-Late, Late-Final, etc. (Imamura, 1996). Simplified, these phase transitions represent shifts in pottery, stylistically and functionally, in which the Incipient was emergent, the Early rudimentary, the Middle more complex and decorated, and by the Final reduced again in form (Aikens and Higuchi, 1982).

Despite the fact that the Jōmon period is split into phases based on archaeological criteria, the fluctuations in technology overtime suggest that Jōmon phases also coincided with changes that were also environmental, behavioral, and cultural (Aikens and Higuchi, 1982). This correlation between technology and other changes is no mere coincidence as material goods often have a strong relationship to the ecological niche and demands of the population. From material findings, one can derive information ranging from subsistence practices, settlement patterns, and population dynamics. As a result, one can undertake a study examining the behavior underlying certain findings and extrapolate the sort of environment that would be conducive to such practices.

With initial occupation dating as recent as 14,000 BCE, the Jōmon's presence on the Japanese archipelago spanned over 10, 000 years. (Habu, 2004). Foremost, as a hunter-gatherer society, they showed a degree of complexity atypical of small societies, displaying characteristics such as social structure, rich material culture, and population sizes typical of larger scale societies (Habu, 2004). As complex hunter-gatherers. they possessed semi-sedentary habitations that comprised communities that could number in the thousands (Habu, 2004). The degree of Jōmon cultural complexity explains makes them a unique hunter-gatherer population to study.

During the Early to Middle Jōmon period, the Jōmon population was characterized by population growth and diversification, maintained mostly through foraging as the core subsistence pattern (Pearson, 2006). In fact, regional variation is a very common theme when discussing the Jōmon and is often split among various lines

ranging from East and West, North to South, Interior to Coastal, and site by site.

Temporally, periods are often arranged by Early, Middle, Late and Final Jōmon.

The Incipient Jōmon dates from 14,000 BCE to 9250 BCE. Incipient Jōmon is prefaced by a point in time known as the pre-ceramic period, an amalgamous period of time covering the dates prior to the estimated dates of the emergence of Jōmon pottery (Imamura, 1996). The Incipient Jōmon is marked by the presence of stone tools and microblades derived from mainland Indo-China and brought into the islands of Japan via land bridges formed along the straits to due lower sea levels during cooler periods (Imamura, 1996). Subsistence was small scale and opportunistic as evidenced through the presence of stone tools attributed mostly to hunting (Imamura, 1996). Settlements at this time were small and dependent mostly on already existing natural structures such as caves (Imamura 1996). The Incipient designation serves more as a source of distinction, separating the period of the pre-ceramic with that of subsequent Jōmon phases. There are only the most fragmentary of human remains from this period. Regardless, discussion of the Incipient and subsequent Initial Jōmon is of importance for the purposes of establishing perspective on the time frame and corresponding populations.

The transition to the Early Jōmon was marked by a general warming in climate. This resulted in the replacement of coniferous forests with nut-bearing trees, a trend that progressed slowly from southern to northern Japan (Imamura, 1996; Pearson, 2006). The Early Jōmon saw a rise in population due to the availability of abundant foraging resources (Pearson, 2006). Settlements became larger and more structured with organized

pit dwellings (Imamura, 1996). Subsistence practices became more pluralistic as evidenced by the presence of more specialized tools such as those for plant gathering and fishing (Matsui and Kanehara, 2006). The practice of hunting becomes more specialized with the development of pit traps (Imamura, 1996). The increase in population has typically been attributed to the increase in nutrition and caloric intake through diversification in food sources (Habu, 2004; Pearson, 2006). This shift led to the development of sedentary habitations with larger populations (Pearson, 2006). Population growth, food variety, and sedentism are traits that positively impacted health (Pearson, 2006). While there is an increase in population during this period, the end of the Early Jōmon is marked by a decrease in population (Imamura, 1996). This decrease is significant as the Middle Jōmon is followed by a dramatic upsurge in population, estimated as being hundreds if not thousands of times greater than that of the Early Jōmon (Imamura, 1996).

The Middle Jōmon showed much greater prosperity, which can be seen in the development of larger settlements, richer, more artistic materials goods, and expansion into typically uninhabited regions (Imamura, 1996). The sudden increase in population is attributed to a phenomenon in the Early Jōmon of pit storage, in which gathered foods such as plants and nuts were kept and stored for extended periods of time and could be used to supplement variability in food collection (Imamura, 1996; Habu, 2004). The increased carrying capacity has been attributed to the change in climate which had produced stable environments that could sustain larger populations (Habu, 2004; Imamura, 1996; Pearson, 2006). Subsistence patterns at this time are multi-faceted and

include specialized plant cultivation, hunting of terrestrial animals, and fishing (Imamura, 1996; Habu, 2004).

The Late to Final Jōmon saw a sharp decrease in population size. This decrease has been attributed to a change in the environment linked to a cooling climate that resulted in a decrease in the quantity of food sources that could be collected (Imamura, 1996). Resource shortage resulted in isolation of communities and the subsequent splintering into at least two distinct cultural groups as evidenced by material culture and subsistence technology: the northeast in Hokkaido and southwest in northern Honshu (Akazawa, 1986a,b,c).

Differences in material culture coincide with the emergence of differing subsistence economies by region. Groups in the northeast along the coast specialized in marine subsistence, maintaining a smaller but stable population. Populations from the inland southwestern regions in Honshu specialized in plant-based subsistence and were able to sustain larger, complex populations. By the end of the Final Jōmon, a significant increase in trade and contact with mainland Asia occurs as does the introduction of wet-rice agriculture to the southern island of Kyushu (Imamura, 1996). Agriculture developed readily in southwest inland regions of Honshu where specialization in plant-cultivation had already been predominant (Akazawa, 1986a). Northeastern coastal groups maintained a marine subsistence economy until they were displaced by the agricultural expansion from Honshu (Akazawa, 1986b,c).

Multiple lines of evidence show the beginning of a new period, the Yayoi, which saw the immigration of individuals from the Asian mainland (via the land bridge to Kyushu), the introduction of wet rice agriculture, metal technologies, and the introduction of local clans with stratified social systems (Imamura, 1996). The changing landscape of the environment was conducive to settlements based on agriculture, specifically wet rice agriculture (Akazawa, 1982a,b,c). The Yayoi demonstrated lower frequencies of linear enamel hypoplasia and cribra orbitalia than the Jōmon at the time (Temple, 2010). This has been attributed to the introduction of a predictable food source and the lower frequency of stress markers associated with rice agriculture. The Yayoi also display higher frequencies of dental caries as is typically attributed to agricultural practice (Fujita, 1993; Temple, 2007; Todaka et al., 2003).

Typically, the ready adoption of agriculture is reasonable considering the massive reduction of the Jōmon population by the Final Jōmon; however, Hoover and Matsumura (2008) show that enamel hypoplasia frequency and fluctuating asymmetry indexes are not significantly different among the Jōmon periods. Thus, although resources diminished and the population crashed from the Middle to the Late/Final Jōmon, population health did not change significantly. The disruptions from climate change and the population crash at the beginning of the Late Jōmon may not have had the severity anticipated. The shifting population dynamics of each region and response to specialization may serve as a compensatory mechanism mitigating the impacts of dietary disruptions, as evidenced by the adjusting population sizes and social structure (Hoover and Matsumura, 2008)

The sudden change in population dynamics between periods has brought into question what happened to the Jōmon following the arrival of the Yayoi. Different models have been proposed ranging from complete replacement to dual origins (Hanihara, 1991). According to dual origins model, modern Japanese derive from the immigrants from southeastern Asia that gave rise to the Jōmon and the immigrants from northeastern Asia that gave rise to the Yayoi. Both populations intermixed within varying degrees throughout the Japanese islands-- the degree to which can be observed in cultural differences between eastern and western Japan and differing distributions of domesticated floral and faunal species (Hanihara, 1991).

4.2 Epi-Jōmon and Okhotsk

The end of the Final Jōmon saw much change throughout the Japanese archipelago. The term Epi-Jōmon refers to persistent hunter-gatherer populations on Hokkaido during the Yayoi period. The Epi-Jōmon possessed similar trends in material goods to the Final Jōmon. The period of the Epi-Jōmon coincided with various changes in the population composition and subsistence practices throughout the Japanese archipelago. Separations began to occur with subsistence patterns based on differential environmental responses to optimal food resources and the introduction of wet rice agriculture from mainland southeastern Asia. This event saw the rise of the Yayoi period, a multi-cultural and migratorily dynamic period that saw the intermixing of various populations that theoretically would lead to the modern day Japanese people. Despite this, the Epi-Jōmon retained a cultural complex that was distinctly theirs and differed

from those of surrounding populations and founded migrating groups, such as the Okhotsk (Hudson, 1999; Matsumura et al., 2006).

The Okhotsk comprise a population of immigrants who arrived in Hokkaido via the land bridge from Sakhalin at 1,000-600 BP. In comparison to the Epi-Jōmon, the presence and existence of the Okhotsk represent a sort of enigma, with their occupation of the Japanese archipelago only representing a fraction, both spatially and temporally (1200-500 BP) of that of the Jōmon (Imamura, 1996). They possessed a cultural identity that has been determined to be distinctly their own in both material goods, cultural practices, and possibly language (Hudson, 1999; Matsumura et al., 2006). Their settlements remained almost exclusively along the coast of Hokkaido with inhabitants engaging in fishing and hunting of marine mammals for subsistence (Imamura, 1996). While they did engage in interactions with neighboring groups, the Okhotsk resisted merging with other Asian groups based on differences in political economy. As a result, Hokkaido became a peripheral system compared the developing systems in Honshu and remained relatively isolated to surrounding populations (Hudson, 2004).

The populations of the Epi-Jōmon and the Okhotsk serve as a good source of comparison to the Jōmon considering their subsistence adaptations and the relationship they have to subsequent Japanese populations. Following the Final Jōmon, as climate started to cool, the decrease in available resources resulted in population crashes among the Jōmon and changes within settlement patterns and subsistence practices. Jōmon expansion which had moved northeastward into Hokkaido during warmer climates began

to recede southwest back into Honshu or cluster along the coasts. Settlements that developed along the coastlines of Hokkaido developed subsistence patterns that were heavily based on marine resources (Aikens and Higuchi, 1982). Material evidence shows a decrease in the frequency and quality of pottery remains and increased investment in fishing and marine mammal hunting technologies such as hooks and harpoons (Aikens and Higuchi, 1982). Concurrently, in Honshu, the predisposition to engaging in small scale wet rice agriculture supplanted hunting and gathering as the primary source of subsistence (Akazawa, 1982a).

Chapter 5 Materials

The data used for this study consist of metric mandibular measurements taken by Kara C. Hoover in individuals from 18 Jōmon, Epi-Jōmon, and Okhotsk sites on Hokkaido and Honshu (Table 1). The total sample contains individuals that are male, female, or unsexed. Subadults were removed from the sample due to their exclusive presence in specific sites and periods. The age of all remaining individuals were either adult or were not aged. Individuals that are not aged could include subadults but were kept due to their large frequency in specific sites, such as Yoshigo.

Four sites in this study are dated to the Middle Jōmon period: Ebishima, Kitakogane, Kotan-onsen, and Ohta. Kitakogane and Kotan-Onsen share spatial proximity along the southwest Hokkaido coast. Ebishima and Ohta are located in the interior of Honshu. Despite these regional differences, the Middle Jōmon population is marked by cultural and economic continuity among regions and relatively homogenous material culture (Imamura, 1996; Habu, 2004).

The Late/Final Jōmon is marked by a division of the homogenous culture of the Middle Jōmon into distinct material styles, mainly between the islands of Honshu and Hokkaido. A total of six sites dated from the Late/Final Jōmon: Funadomari, Irie, and Takasago from Hokkaido and Miyano-kaisuka, Ikawazu, and Yoshigo from Honshu. Cultural splintering coincided with climatic cooling which had placed a strain on the available food sources resulting in specialized subsistence practices as opposed to the generalized, pluralistic practices of the Middle Jōmon. Extensive study of material

culture dated from this time shows a clear cultural and economic distinction between southwest and northeast regions in Japan, centralized between Honshu and Hokkaido (Akazawa, 1981, 1982,a,b, 1986a,b,c, 1987). Ikawazu, Miyano-kaisuka, and Yoshigo are sites that reflect southwestern groups that specialized tools for plant-based subsistence and maintained a greater level of social complexity than the northeastern groups which had concentrated on a fishing subsistence economy along the coast and maintained socially simpler and smaller populations. Funadomari, Irie, and Takasago are located along the coast of Hokkaido and reflect the specialization in marine subsistence based on the increase in frequency and complexity of fishing implements (Akazawa, 1981, 1982,a,b, 1986a,b,c, 1987).

Samples from the Epi-Jōmon are from four sites along the southwestern and northeastern coasts of Hokkaido: Bouzuyama, Minami-usu, Onkoromanai, and Rebunge. The Epi-Jōmon, between 100 BC to 800 AD, marks the persistence of Jōmon culture and subsistence practice during the emergence and expansion of agriculture at the start of the Yayoi. All sites are located along the coasts of Hokkaido having been displaced northeastward by the expanding agricultural practice of the Yayoi. Despite being a more recent period than the earlier Jōmon, few materials good have been uncovered to differentiate any finer discrepancies in Epi-Jōmon culture. The samples from all the Epi-Jōmon sites totaled only seven individuals, with Bouzuyama and Onkoromanai only having a single useable individual. Due to the sample sizes, all Epi-Jōmon sites have been grouped together into a single Epi-Jōmon unit.

Four archaeological sites are dated to the Okhotsk: Hamanaka, Ohmisaki, Pirikatai, and Utoro-jinjayama. The Okhotsk period started at approximately 800 AD following the arrival of immigrant groups from Sakhalin. The Okhotsk specialized heavily on marine subsistence centered along the northern Hokkaido coast. Okhotsk culture flourished concurrently with the agricultural societies in Honshu that had developed from the Yayoi. Despite interactions, the Okhotsk remained isolated from the rest of Japan due to social and economic differences. By the end of the Okhotsk, there is diminished archeological evidence of Okhotsk presence in Japan, with populations in Hokkaido most likely returning to Sakhalin (Aikens and Higuchi, 1982). Due to the cultural isolation, origins from different immigrant populations, and marine subsistence practices, the Okhotsk sites have been pooled together for analysis.

Table 1. Site data for samples used in study

| Period | Site | Region | n |
|--------------------------|------------------|----------------|-----|
| Middle Jōmon | Kitakogane | SW Hokkaido | 8 |
| Middle Jōmon | Kotan-onsen | SW Hokkaido | 4 |
| Middle Jōmon | Ebishima | NE Pacific | 25 |
| Middle Jōmon | Ohta | Inland sea | 21 |
| <i>Middle total</i> | | | 58 |
| Late Jōmon | Funadomari | NE Hokkaido | 8 |
| Late Jōmon | Irie | SW Hokkaido | 6 |
| Late Jōmon | Takasago | SW Hokkaido | 4 |
| <i>Late total</i> | | | 18 |
| Late/Latest Jōmon | Ikawazu | S. central bay | 18 |
| <i>Late/Latest total</i> | | | 18 |
| Latest Jōmon | Miyano-kaisuka | NE Pacific | 4 |
| <i>Latest total</i> | | | 4 |
| Final Jōmon | Yoshigo | S. central bay | 41 |
| <i>Final total</i> | | | 41 |
| Epi-Jōmon | Bouzuyama | SW Hokkaido | 1 |
| Epi-Jōmon | Minami-usu | SW Hokkaido | 3 |
| Epi-Jōmon | Onkoromanai | NE Hokkaido | 1 |
| Epi-Jōmon | Rebunge | NE Hokkaido | 2 |
| <i>Epi-Jōmon total</i> | | | 7 |
| Okhotsk | Hamanaka (1 & 2) | NE Hokkaido | 2 |
| Okhotsk | Ohmisaki | NE Hokkaido | 12 |
| Okhotsk | Pirikatai | NE Hokkaido | 1 |
| Okhotsk | Utoro-jinjayama | NE Hokkaido | 3 |
| <i>Okhotsk total</i> | | | 18 |
| <i>Overall total</i> | | | 164 |

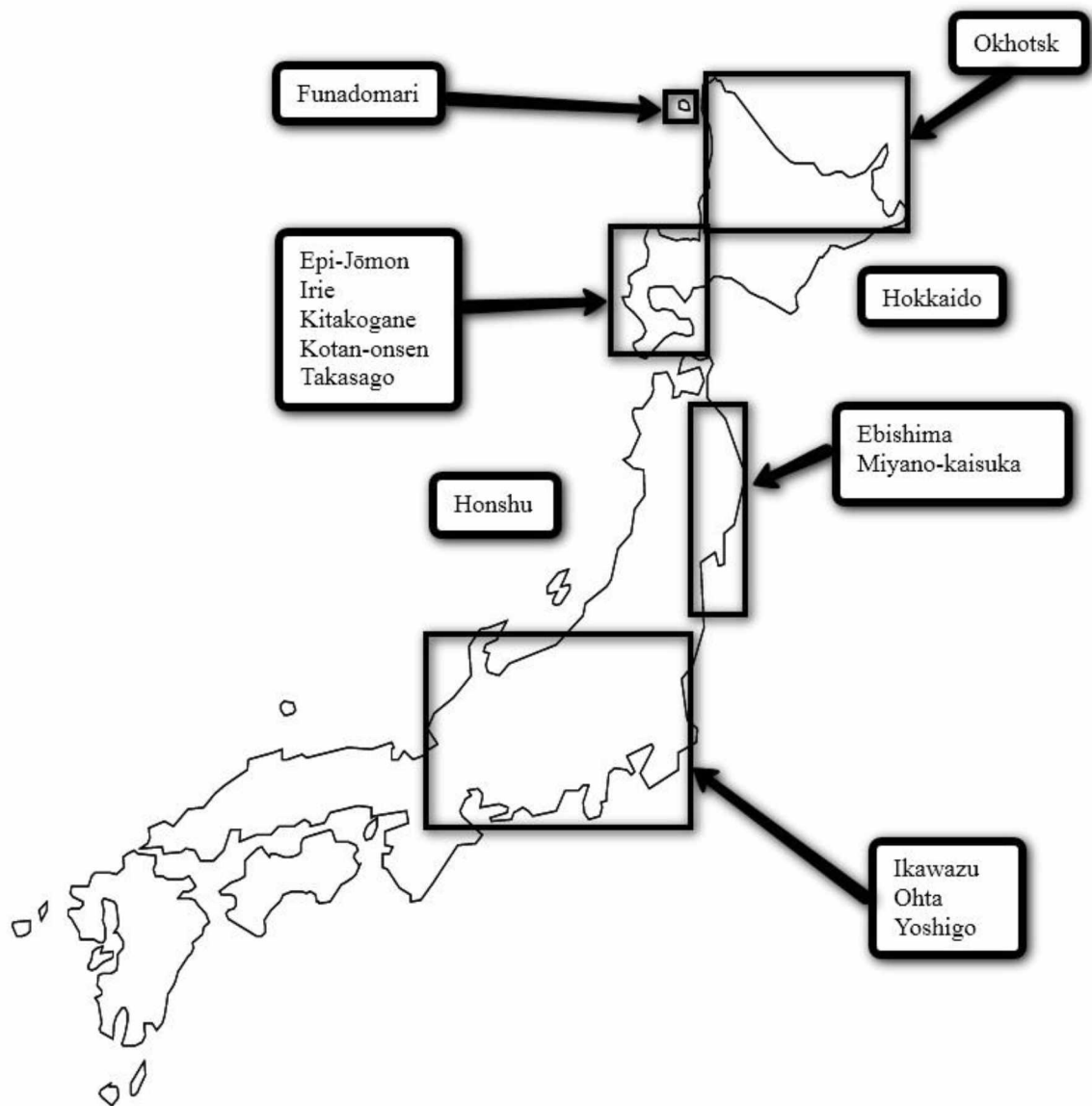


Fig. 1. Map of Japan showing the regional divisions of the samples and their respective sites.

Chapter 6 Methods

Data were collected by Kara C. Hoover in June of 2004 on 11 metric, mandibular traits according to standard osteological guidelines (Table 2)(Buikstra and Ubelakaer, 1994). Each measurement was taken twice to two decimal places using Mituyo sliding calipers (Hoover, personal communication). All analysis was conducted (Rogelio A. Arenas) using IBM SPSS Statistics 20.

Table 2. List of measurements used

| Measurement | Abbreviation |
|-------------------------------|--------------|
| Chin height | IDGN |
| Bigonial width | GOGO |
| Bicondylar breadth | CDLCDL |
| Right minimum ramus breadth | MINRBR |
| Left minimum ramus breadth | MINRBL |
| Right maximum ramus breadth | MAXRBR |
| Left maximum ramus breadth | MAXRBL |
| Right mandibular body breadth | BMANR |
| Left mandibular body breadth | BMANL |
| Right mandibular body height | HMANR |
| Left mandibular body height | HMANL |

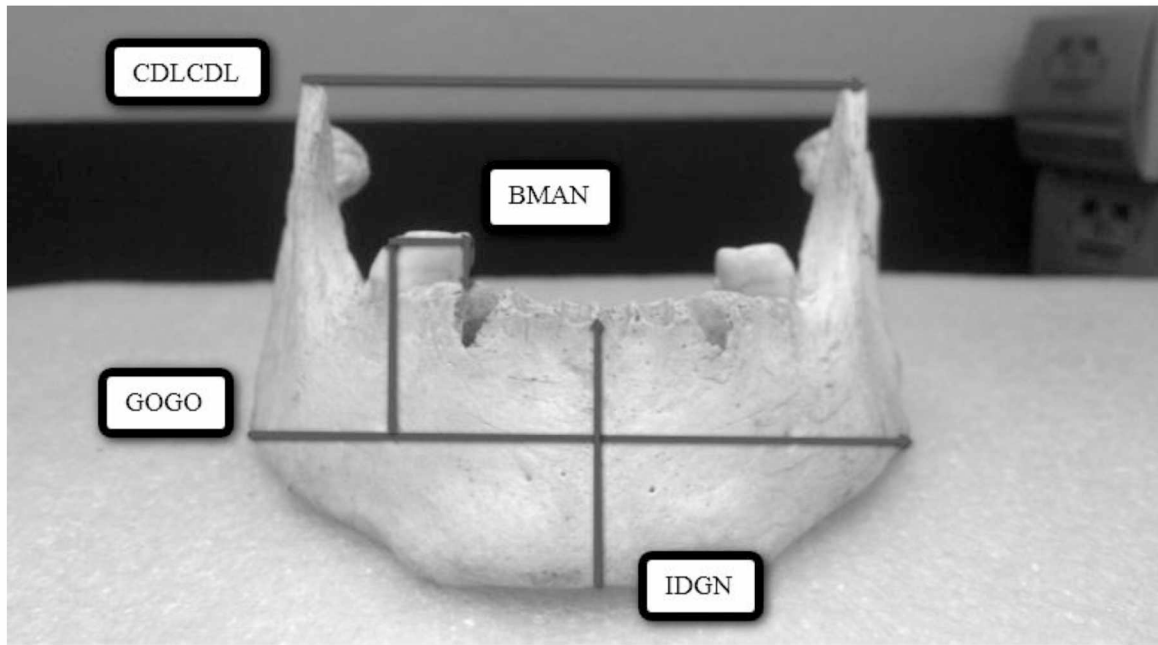


Fig. 2. Measurements on mandible, anterior view.

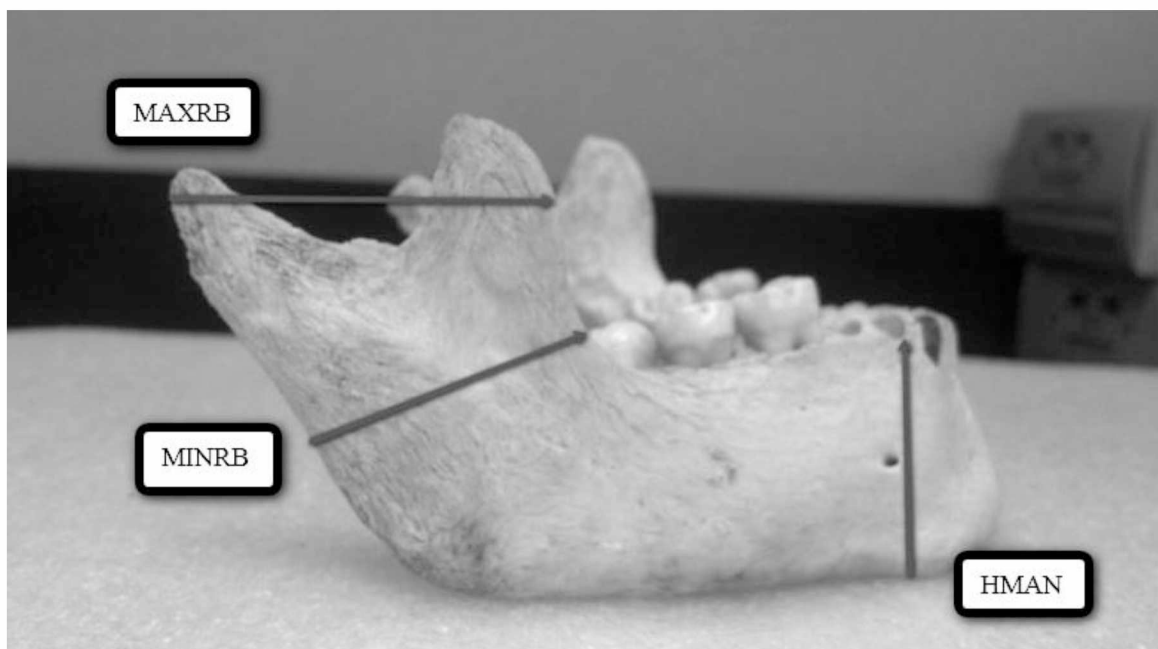


Fig. 3. Measurements on mandible, lateral view.

A normality test was conducted on the data to determine the appropriateness of using parametric tests. Samples were divided into regional/temporal populations of Middle Jōmon, Late/Final Jōmon, Epi-Jōmon, and Okhotsk for normality testing based on the work of Akazawa (Akazawa, 1981, 1982a,b, 1986a,b,c, 1987). A Shapiro-Wilk ($\alpha = 0.05$) test was performed on these categories to test for the normal distribution of the data. If applicable, parametric hypothesis testing would provide more robust analysis of the data.

Before conducting hypothesis testing, the viability of pooling together the ages and sexes at each site was tested through an F-test. The distributions of unknown sex and age were disproportionate by site with some sites consisting entirely of individuals of unknown sex or age. Since the majority of the data were comprised of individuals whose sex and age were unknown, these samples could not simply be eliminated. Variance testing was conducted using an F-test with Levene's homogeneity statistic, on all unpaired and bilateral measurements. If pooling was a viable option, then the unknowns could be pooled together, increasing sample size, for hypothesis testing.

Because bone remodels, traits are subject to differential development resulting in one side of a bilateral trait developing disproportionately from the other. Directional asymmetry (DA) index was calculated for all bilateral traits. The process for analyzing asymmetry has been described extensively and standardized (Van Valen, 1962). There are three measures of asymmetry: antisymmetry, directional asymmetry, and fluctuating asymmetry. Both fluctuating asymmetry and antisymmetry refer to the nondirectional

change in symmetry for a trait, but both differ in their distribution. Fluctuating asymmetry possesses a normal distribution while antisymmetry is platykurtic or bimodal. Since the mandible is prone to remodeling in response to masticatory forces, directional asymmetry is a more useful measure in providing context to the nature of dietary impact on the mandible. Generally when studying asymmetry, fluctuating asymmetry is used, calculated as $|(L - R)/0.5([L + R])|$ (Van Valen, 1962). As this study is concerned with the presence of directional asymmetry, the absolute value was eliminated in favor of the directional index, which describes the presence of asymmetry with respect to the side of the bilateral plane. A negative value is indicative of asymmetry centralized along the left plane while a positive value is indicative of asymmetry favoring the right. Since DA is a directional index, a test on the normality of variables would be sufficient in determining the presence of any significance in asymmetry. If DA indexes were significant, both right and left measurements will be used for testing. If the DA indexes were not significant, then the mean of both measurements was used for testing.

Conducting a principal components analysis (PCA) is useful in determining the associations between traits as well as the traits that account for the majority of the variation. A Kaiser-Meyer-Olkin measure was calculated to determine the appropriateness of the traits overall for use in factor analysis. Since all traits are interrelated through the mandible, a correlation matrix can measure the individual associations among each trait. Selection of variables for hypothesis testing was based on the outcome of a PCA on selected metric mandibular traits. To test the hypothesis that there is no significant difference in mandibular morphology between regions during the

Middle Jōmon, sites from the Middle Jōmon were divided according to location within the interior or on the coast of Honshu and tested with an ANOVA. To test the hypothesis that mandibular morphology differed significantly between interior Jōmon sites in Honshu and coastal Jōmon sites during the Late/Final Jōmon, Late/Final Jōmon sites were analyzed by ANOVA based on their location within the interior Honshu, coastal Honshu, and coastal Hokkaido. To test the hypothesis that there is no difference in mandibular morphology between the Epi-Jōmon and Okhotsk, all Epi-Jōmon and Okhotsk sites were pooled into their respective groups and analyzed using ANOVA.

Chapter 7 Results

A Shapiro Wilk's test for normality was conducted on the population pools for all 11 metric variables (refer to Appendix: Tables A1-A4). No significance was determined for any variable or pool ($p > 0.05$).

An F-test testing incorporating Levene's statistic was calculated for each variable by site for differences in variances by sex (males, females, and unsexed) and age (adult and unknown) for all metric mandibular measurements. The only sites that required variance testing for sex were Kitakogane, Ohta, Funadomari, Irie, Takasago, and Ohmisaki (Appendix: Tables A5-A7). For all sites, there was no significant difference by sex. No significance in variance existed between adults and unknown ages at Yoshigo (Appendix: Table A6).

Sites were pooled into groups based on their regional location and period. The three sites of Ebishima, Kitakogane, Kotan-onsen from the Middle Jōmon were pooled into a coastal Middle Jōmon group. Ikawazu and Yoshigo are dated to the Late/Final Jōmon and are spatially located within the interior south central bay area and were thus pooled as interior Honshu Late/Final Jōmon. Miyano-kaisuka, Funadomari, Irie, and Takasago are coastal Late/Final Jōmon settlements and were grouped together into a coastal Honshu Late/Final Jōmon pool. Epi-Jōmon sites had few individuals for testing with the four sites of Bouzuyama, Minami-usu, Onkoromanai, and Rebunge consisting of between one to three individuals each. Due to their shared cultural background, period, and comparable location along the coast of Hokkaido, all the Epi-Jōmon sites were

grouped into an Epi-Jōmon pool. For the Okhotsk, the only site with sufficient number of sexes and ages to test was Ohmisaki. Hamanaka, Pirikatai, and Utoro-jinjayama are three sites from the Okhotsk that possessed less than three individuals with indeterminate sex. Since these sites could not be analyzed for pooling, all Okhotsk sites were pooled together into an Okhotsk group based on cultural similarities, period, and regional exclusivity to the Hokkaido coast.

To test for presence of directional asymmetry (DA), a DA index was calculated for all bilateral traits. An F-test analysis showed that there was no significance in asymmetry except for maximum ramus breadth ($P = 0.003$) (Table 3).

Table 3. F-test for DA indices

| DA index | n | Mean | SD | F | Sig |
|----------|-----|-----------|----------|-------|--------|
| BMAN | 153 | -0.009700 | 0.065565 | 0.281 | 0.890 |
| HMAN | 90 | -0.013630 | 0.058310 | 0.610 | 0.656 |
| MINRB | 94 | -0.001204 | 0.043572 | 1.691 | 0.159 |
| MAXRB | 56 | -0.011250 | 0.056450 | 4.493 | 0.003* |

*Significant at $\alpha = 0.05$

Principal component analysis was performed on eight values. The matrix used was the correlation matrix of the pooled Jōmon, Epi-Jōmon, and Okhotsk data. The next step in the analysis was to determine the associations between the traits and account for the variations in the samples. The calculated Kaiser-Meyer-Olkin measure was 0.730, showing that the overall variables are sufficiently correlated. Results of the correlation matrix reveal varying associations among traits but show the general tendency of one measure to be directionally proportional to the other even when weakly associated (Table 4). The only exception was bicondylar breadth which showed a weak inverse association.

The strongest correlations existed among minimum ramus breadth (MINRB) and left and right maximum ramus breadth (MAXRBL, MAXRBR).

Table 4. Correlation matrix for selected traits

| Measurement | IDGN | GOGO | CDLCDL | BMAN | HMAN | MINRB | MAXRBL | MAXRBR |
|-------------|--------|-------|--------|-------|-------|-------|--------|--------|
| IDGN | 1.000 | 0.382 | -0.099 | 0.146 | 0.651 | 0.587 | 0.425 | 0.502 |
| GOGO | 0.382 | 1.000 | 0.322 | 0.623 | 0.517 | 0.627 | 0.653 | 0.552 |
| CDLCDL | -0.099 | 0.322 | 1.000 | 0.317 | 0.160 | 0.067 | 0.047 | -0.041 |
| BMAN | 0.146 | 0.623 | 0.317 | 1.000 | 0.441 | 0.320 | 0.265 | 0.328 |
| HMAN | 0.651 | 0.517 | 0.160 | 0.441 | 1.000 | 0.448 | 0.376 | 0.453 |
| MINRB | 0.587 | 0.627 | 0.067 | 0.320 | 0.448 | 1.000 | 0.827 | 0.858 |
| MAXRBL | 0.425 | 0.653 | 0.047 | 0.265 | 0.376 | 0.827 | 1.000 | 0.870 |
| MAXRBR | 0.502 | 0.552 | -0.041 | 0.328 | 0.453 | 0.858 | 0.870 | 1.000 |

Overall, two factors explained 79.12% of the total variance. A rotated component matrix assigned relative labels to these factors (Table 5). For PCI, left maximum ramus breadth (MAXRBL) and minimum ramus breadth (MINRB) were the prominent traits in determining these factors. For PCII, bicondylar breadth (CDL) was the most influential resulting in negative scores for maximum ramus breadth (MAXL, MAXR). While bicondylar breadth showed weak associations in the correlation matrix, the presence of negative values, as well as the result of the component analysis, suggest that further examination is warranted.

Table 5. Component loadings of the principal component analysis

| Variables | Component loading | |
|---------------------------|-------------------|--------|
| | PCI | PCII |
| MAXRBL | 0.939 | -0.117 |
| MIN | 0.917 | -0.097 |
| MAXRBR | 0.913 | -0.219 |
| GOGO | 0.789 | 0.324 |
| IDGN | 0.575 | -0.202 |
| HMAN | 0.556 | 0.122 |
| BMAN | 0.441 | 0.370 |
| CDLCDL | 0.146 | 0.966 |
| Total contribution (%) | 59.92 | 22.2 |
| Cumulative proportion (%) | 59.92 | 79.12 |

Based on the results of the PCA, four traits were selected for hypothesis testing via ANOVA: bicondylar breadth, bigonial breadth, minimum ramus breadth, left maximum ramus breadth, and right maximum ramus breadth (Table 6). For the Middle Jōmon, there was no significant difference between the coast and interior of Honshu for either selected trait. For the regional comparison of the Late/Final Jōmon, all traits were found to be significant. Multiple comparisons analysis incorporating least squares showed that significance was exclusively centered in coastal Hokkaido Jōmon compared to interior and coastal Honshu Jōmon (Table 7). Further examination showed that coastal Hokkaido was more robust than interior or coastal Honshu for minimum ramus breadth and maximum ramus breadth for both left and right sides. Inversely, coastal Hokkaido had narrower bicondylar breadth and bigonial breadth than interior or coastal Honshu.

Results were significant for minimum ramus breadth and right maximum ramus breadth for the Epi-Jōmon and Okhotsk. For minimum and maximum ramus breadth, the Okhotsk was consistently wider than the Epi-Jōmon. Examination of the data showed that the Okhotsk samples were the source of directional asymmetry.

Table 6. ANOVA testing of selected traits for region by period

| Period | Measurement | MS | df | F | Sig. |
|-------------------|-------------|---------|----|--------|--------|
| Middle Jōmon | CDLCDL | 3.819 | 1 | 0.115 | 0.738 |
| | GOGO | 11.556 | 1 | 0.907 | 0.345 |
| | MAXRBL | 6.735 | 1 | 0.316 | 0.577 |
| | MAXRBR | 7.078 | 1 | 0.273 | 0.605 |
| Late/Final Jōmon | CDLCDL | 147.930 | 2 | 13.399 | 0.001* |
| | GOGO | 83.745 | 2 | 8.086 | 0.001* |
| | MAXRBL | 115.470 | 2 | 5.85 | 0.008* |
| | MAXRBR | 55.970 | 2 | 4.893 | 0.014* |
| Epi-Jōmon:Okhotsk | CDLCDL | 0.326 | 1 | 0.013 | 0.912 |
| | GOGO | 229.686 | 1 | 8.835 | 0.007* |
| | MAXRBL | 102.580 | 1 | 4.633 | 0.051 |
| | MAXRBR | 45.720 | 1 | 5.748 | 0.030* |

*Significant at $\alpha = 0.05$

Table 7. Multiple comparisons incorporating least squares for Late/Final Jōmon

| Measurement | Region | Honshu interior | Honshu coast | Hokkaido coast |
|-------------|-----------------|-----------------|--------------|----------------|
| CDLCDL | Honshu interior | | 0.548 | 0.001* |
| | Honshu coast | 0.548 | | 0.001* |
| | Hokkaido coast | 0.001* | 0.001* | |
| GOGO | Honshu interior | | 0.205 | 0.001* |
| | Honshu coast | 0.205 | | 0.003* |
| | Hokkaido coast | 0.001* | 0.003* | |
| MAXRBL | Honshu interior | | 0.269 | 0.002* |
| | Honshu coast | 0.269 | | 0.218 |
| | Hokkaido coast | 0.002* | 0.218 | |
| MAXRBR | Honshu interior | | 0.132 | 0.005* |
| | Honshu coast | 0.132 | | 0.846 |
| | Hokkaido coast | 0.005* | 0.846 | |

*Significant at $\alpha = 0.05$

Chapter 8 Discussion

While all variables are interrelated as parts of the mandible and through their cooperative function in the masticatory process, individual analysis of each variable suggests that not all differences are weighted by the same factors. Ramus breadth showed the most variability, while others such as mandibular height and breadth were minimal in respect. Analysis of DA index for all bilateral measurements showed that only the DA index for maximum ramus breadth was significant. While multiple traits are susceptible to asymmetry, they are often prone to disruptions to different degrees, even when part of an interconnected system (i.e. although all measurements are related to the mandible, some may be intrinsically more susceptible to disruption than others) (Palmer, 1994). The outcome of the PCA suggest that measurements of maximum and minimum ramus breadth accounted for a majority of the variation likely the result asymmetry. While other traits were also variable, associations between each component suggest that their variances are heavily directionally dependent on the variances found in maximum and minimum ramus breadth (i.e. other traits are large by way of MINRB and MAXRB being large). The hypothesis is that mandibular traits would vary by region and period under the notion that the mandible would respond differently to varied diets based on the resources accessible to the respective environment.

8.1 Middle Jōmon

For the Middle Jōmon, the relatively continuous practices of seasonal, pluralistic foraging was expected to result in comparably robust traits within the period, despite regional specificity. The results supported my hypothesis as there was no significant difference between interior and coastal population in the Middle Jōmon for any of the selected traits. This further supports the continuity that has been attributed to the Middle Jōmon populations across Japan despite regional differences that has been documented extensively in the literature. In the scope of this thesis, this gives a reliable foundation on which to document and follow any observed differences in analysis of later Jōmon populations as documented trends and expectations are supported by the samples in this portion of the analysis.

8.2 Late/Final Jōmon

The hypothesis was that the Late/Final Jōmon, marked by cultural and economic differentiation, would show regionally different mandibular robusticities based on changes in diet. Specifically, the interior populations of Honshu would show a reduction in mandibular morphology as a result of emergent agriculture, while the populations of coastal Honshu and Hokkaido would be more robust and comparable to each other as a result of their shared practice of marine subsistence. The results did not support the hypothesis, showing significant differences that were contrary to expectations. Coastal and interior Honshu had similar robusticities, while the populations of coastal Hokkaido were significantly more robust than those from Honshu for both minimum and maximum

ramus breadth. Inversely, coastal Hokkaido populations had significantly narrower bicondylar breadth from populations in Honshu.

Bicondylar breadth and bigonial breadth were of particular interest due to the negative value it derived from the PCA analysis. Generally, bicondylar breadth and bigonial breadth widens in response to increased masticatory forces and has been shown to become shorter narrower in response to softer diets like those found in agricultural populations (Hinton and Carlson, 1979). The coastal sites of Hokkaido showed the narrowest bicondylar breadth and bigonial breadth compared to coastal and interior Honshu populations. The Late/Final Jōmon sites of Hokkaido consist of Funadomari along the northeast coast of Hokkaido and Takasago and Irie along the southwest coast. Examination of three sites shows that Irie is mostly responsible for the low values from the Late/Final Jōmon.

Kaifu (1997) came across a similar discrepancy in his examination of mandibular size in response to masticatory function between the Jōmon in the Yayoi. Given the Yayoi extensive engagement in wet rice agriculture, mandible size was expected to be reduced compared to the ancestral hunter-gatherer population of the Jōmon, but analysis showed that Yayoi mandibles were significantly larger (Kaifu, 1997). Kaifu had concluded that unexpected robusticities were the result of Yayoi period populations continuing hunter-gather practices similar to their ancestral populations in mainland Asia given that adoption of wet rice agriculture was fairly recent among the Yayoi at the time (Kaifu, 1997). The Jōmon, despite their engagement in foraging, had respectively

advanced processing and preparation, giving credence to their classification as complex hunter-gathers. While they may have engaged in broad spectrum foraging, the Jōmon may have already possessed extensive means of processing their food supported by their status as one of the world's earliest pottery making traditions (Kaifu, 1997). Kaifu's (1997) explanation may explain the discrepancy in this study regarding the difference in observed mandibular morphology and diet versus the expected.

Despite the development of regionally specific specialization in subsistence tool sets, the Jōmon across all regions were still dependent on hunting and foraging as evidenced by midden remains and the presence of traditional subsistence implements (Akazawa, 1986c). While the Late/Final Jōmon is marked by climatic cooling and a drop in carrying capacity, technological innovation may reflect a mechanism by which populations mitigated the change to the environment. Studies by Hoover and Matsumura (2008) on linear enamel hypoplasia show that LEH was high in all Jōmon populations. This finding could suggest comparable nutritional stress by region, in which individual populations were capable of adapting to environmental changes respective to their own region. The ability to sustain a larger population indicates either that the population had yet to reach carrying capacity for its respective environment and is capable of increasing exploitation or an ability of said population to adaptively increase the carrying capacity of their respective niche. An explanation may lie in the environmental pressures that resulted in regional subsistence specialization in the first place.

One feature that marked the Late/Final Jōmon was the shift in coastline. The extent of the changing coastline was not uniform across Honshu and Hokkaido, and resulted in three distinct ecosystem types: forest-freshwater, forest-estuary, and forest-Pacific shelf littoral (Akazawa, 1986a,b). These distinct ecosystems would have resulted in differences in fishing methods with respective differences in technology, food source, and diet breadth (Akazawa, 1986a,b). While the diet breadth sustained by individual forest systems may have differed by region, the most influential limiting factor was the biomass and productivity of surrounding water sources (Akazawa, 1986a,b). Each system had different marine sources accessible to the Jōmon within the reach of their respective technological level.

During the Late/Final Jōmon, coastal and interior Honshu experienced an increase in forest-estuary ecosystems. Of the three types, forest-estuary offered the highest level of productivity in terms of species diversity and edible biomass (Akazawa, 1986a,b). This system provided both an abundance of terrestrial and marine resources, generally divided into seasonality of predominantly marine subsistence in the warmer seasons and terrestrial in the cooler seasons (Akazawa, 1986a,b). Although the environment of the Late/Final Jōmon may not have been as favorable as the Middle Jōmon, the environment was more favorable for Honshu than Hokkaido in terms of diversity, quantity, and quality of food resources. Climatic cooling had resulted in a drop in the carrying capacity across Japan in the Late/Final Jōmon, but Honshu had remained the most stable, not just in the extent of their subsistence practice, but in the relative abundance of resources that remained available compared to Hokkaido. In accordance, while populations decreased

overall after the Middle Jōmon, population centers in Honshu remained high while those along the coast in Hokkaido were generally smaller with less social stratification (Habu, 2004).

Coastal Hokkaido in contrast experienced a transition between estuary and Pacific shelf littoral which had the lowest productivity as fishing was impeded by rocky shores and fewer marine species readily accessible (Akazawa, 1986b). Of the three groups, the coastal Jōmon of Hokkaido were the most technologically adapted to handle marine subsistence. This presents a potential fallacy in the assumptions made in this thesis: specialization in a subsistence practice translated into more effective exploitation of resources from its respective source. Rather, the evidence would suggest that fishing specialization may have been the result of a need to invest in specialization due to resource constraints. If the environment on the Hokkaido coast had the lowest level of productivity, then more technological investment would be necessary to meet the needs of the population. Since the new coastal ecosystem had produced obstacles to once easily accessible resources, technological specialization may reflect the need to overcome these impairments as previously non-specialized fishing implements were no longer sufficient in supporting the return rate associated with that level of investment. As a result, Hokkaido populations would likely have a broader diet breadth than those in Honshu due to fewer and less diverse food resources. Broadening of their diet breadth could result in dependence on tougher and less processed food items than those which would be readily available to populations in Honshu. This would also support presence of the low coastal population densities in Hokkaido while populations in Honshu were relatively larger.

While populations in Honshu may have differed in regional specializations, they both shared the advantage of a an environment that was favorably denser and diverse in edible food resources compared to the populations in Hokkaido. While Hokkaido Jōmon managed to sustain themselves nutritionally, the degree of their specialization in marine subsistence may reflect the need to specialize as a result of increasing difficulty in acquiring marine resources than was previously experienced before the change in ecosystem for that region.

8.3 Epi-Jōmon and Okhotsk

The hypothesis that mandibles from the Okhotsk and the Epi-Jōmon would be morphologically similar to each other due to their shared practice of engaging in marine subsistence. The results did not support this hypothesis as Okhotsk samples were significantly more robust in minimum and maximum ramus breadth. The Okhotsk sample is also the source of asymmetric variation found in the data. If diet is a factor in this variation, this could reflect an Okhotsk diet that was tougher than those of the Jōmon, even those engaged in marine subsistence.

The Epi-Jōmon have been difficult to describe in full given the paucity of osteological and material remains in comparison to other groups and periods in Japan. As a result, the closest approximations to the details of their social and economic practices are often inductively deduced from the Jōmon populations that preceded it and the Satsumon that followed. Material remains that have been attributed to the Epi-Jōmon are comparable to the types found for the Late/Final Jōmon in Hokkaido and are

predominantly found in the southwest coast where the Epi-Jōmon were most centralized (Imamura, 1996). Data from midden excavations suggest a diet based in foraging, with marine resources reflecting the traditional shell fish and salmon as seen in previous Jōmon periods (Imamura, 1996). This evidence suggests that like their predecessors, the Epi-Jōmon had engaged and specialized in marine subsistence but did not practice it exclusively. Rather, they had retained subsistence practices materially comparable to those seen in Honshu and Hokkaido during the Late/Final Jōmon.

One distinct difference that has been found with regard to the Epi-Jōmon is the possibility that unlike their Late/Final Jōmon predecessors in Hokkaido, the Epi-Jōmon had begun to practice limited plant cultivation. While the environment did not facilitate the adoption of wet rice agriculture, the Satsumon that arose later had grown rice in dry fields and expanded on this practice, diversifying into the cultivation of buckwheat, barley, sorghum, beans, and millet (Imamura, 1996). Plant cultivation to this extent is unlikely for the Epi-Jōmon given the discernible gap in material evidence regarding the practice of extensive plant cultivation in southwest Hokkaido, but enough is present to suggest the possibility that the Epi-Jōmon may have engaged in the practice to a limited degree, and if so, most likely restricted to buckwheat and barley (Imamura, 1996). Based on this evidence, Epi-Jōmon subsistence was in sharp contrast to Okhotsk subsistence, despite both engaging in marine subsistence. Winter sea ice extended out along the eastern coast of Hokkaido had provided access to marine resources that would not have been accessible to the Epi-Jōmon given their location along the warmer southwest; an example is the Okhotsk exploitation of sea mammals as evidenced by stable isotope

analysis and the quantity and specialization of harpoons found in the material record (Chisholm et al, 1992; Imamura, 1996; Hudson, 2004).

The Epi-Jōmon may have smaller mandible sizes because they were better adapted to mitigating changes in the environment and food resources based on the comprehensive social and material toolset they possessed and that dated to the earlier Jōmon periods. Evidence suggest that the time of the Early Okhotsk/Epi-Jōmon (when the immigrant population arrived via Sakhalin land bridge) was particularly harsh compared to the warmer temperatures of the Late Okhotsk/Middle Satsumon. The initial arrival and later expansion of the Okhotsk into Japan has been attributed to environmental pressures that required the increased mobility to buffer issues of food scarcity and increasing population density (Hudson, 2004). To compensate for food scarcity, the Okhotsk engaged in limited domestication of pigs, a practice which could not be sustained (Hudson, 2004). Later adaptations, as seen in the Middle Okhotsk, suggest that the Okhotsk may have begun limited practice of plant cultivation, although never to the extent of supplanting their marine-based subsistence practices (Hudson, 2004). Evidence from pits and graves suggest that barley, millets, and buckwheat were part of the Okhotsk repertoire and were resources that had been brought with them as these plants are not native to Hokkaido and their remains were localized solely within the perimeter of Okhotsk settlements (Hudson, 2004).

While coastal Jōmon may have been resistant to adopting emergent agricultural practices during the Late/Final Jōmon, they adopted limited plant cultivation to

supplement their diet, a practice that is expanded upon in the Satsumon. The limited evidence of the extent of this practice raises an interesting question if the details of cultivation can be substantiated. If emergent Epi-Jōmon horticulture involved cultivation of plants that were not native to Hokkaido, then why did the Epi-Jōmon experiment with these plants while the Okhotsk did not attempt the practice until the Late Okhotsk, at which point the Satsumon had already specialized in the practice? The harsh climate associated with the Early Okhotsk resulted in groups across Hokkaido developing different strategies to mitigate the change in carrying capacity as a result of limited resources. The Epi-Jōmon responded by experimenting and successfully dabbling with new resources while the Okhotsk struggled with domestication and resorted to mobility to mitigate the impact of scarce resources rather than attempt to cultivate plant materials. Perhaps receptivity to cultivation practices were based on social and technological differences, the heavy exploitation of plant resources made cultivation more accessible to the Epi-Jōmon than to the Okhotsk, but the implications extend beyond the actual practice and reflect a predisposition by the Epi-Jōmon to adapt more readily or with more flexibility to environment changes than the Okhotsk.

In terms of the Okhotsk, the presence of significant directional asymmetry may reflect the initial difficulty in adapting marine subsistence to the harsher winters during the Early Okhotsk. While directional asymmetry can often indicate preferential sidedness, it can also indicate the presence of heavy and prolonged masticatory pressures as can be the result of consistent exposure to tough diets (Scheuer and Black, 2000). The Okhotsk marine-based diet, especially sea mammals, is already tough, but the significant strain

observed in the Okhotsk sample may reflect the need to engage in available food resources as well as the lack of processing these food items. Epi-Jōmon subsistence was marine-based but focused primarily on fishing and broad spectrum foraging. Their diet was not exclusively marine-based; terrestrial food sources may have mitigated malnutrition during times of scarcity. The Epi-Jōmon likely possessed a history of food processing like their predecessors, which made exploitation of terrestrial resources more accessible and placed less masticatory strain on the mandible. The very same predisposition made experimental plant cultivation feasible while the Okhotsk could not exploit or process the resource to the same degree. Exposure of the Okhotsk to tougher and unprocessed food items, on top of their already tough marine diet, may explain the particularly robust mandibles as well as the significant presence of directional asymmetry.

Chapter 9 Conclusion

As climate stabilized, the resources became abundant and reliable leading to the population explosion that marked the Middle Jōmon (5,000 - 3,000 BP). This led to the formation of a continuous cultural group that occupied the two northern islands of Honshu and Hokkaido. As the climate cooled by the Late and Final Jōmon (4,000 - 2,000 BP), the reduced carrying capacity of the two islands resulted in a population crash and fracturing of the continuous Jōmon population into distinct groups with differing economies and material cultures. Populations within the interior specialized in hunting and plant cultivation while those populations along the coast specialized in marine subsistence. The arrival of agriculture from immigrant populations led predisposed plant cultivation populations of interior Honshu to readily adopt the practice while coastal populations were more resistant, maintaining their marine economy. The Epi-Jōmon populations in Hokkaido reflect this cultural persistence, temporally and spatially proximal to the Okhotsk, and immigrant population from Sakhalin that exclusively occupied the Hokkaido coast.

This thesis sought to relationship of masticatory forces of diet on the mandible within the context of regional differences in diet within prehistoric Japan, from the Jōmon and the Okhotsk. Based on the work that has been conducted on Jōmon and Okhotsk diet, the hypothesis was that Middle Jōmon sites would possess comparable mandibular robusticities based on their shared cultural and dietary continuity. For the Late/Final Jōmon, the hypothesis was that there would be a reduction in mandibular form in interior

Honshu sites, coinciding with the emergence of wet-rice agriculture and the incorporation of processed food items, while coastal populations in Honshu and Hokkaido would be comparably more robust. The coastal populations of the Epi-Jōmon and Okhotsk would possess comparable mandibular morphologies under the assumption that both populations possessed similar marine subsistence economies.

Eleven measurements from 16 different sites dating from the Middle Jōmon, Late/Final Jōmon, Epi-Jōmon, and Okhotsk were used to test for dietary differences in mandibular robusticity by region and period. Based on the outcome of preliminary variance analysis, individuals within sites were pooled together for further testing on the regional and period level based on spatial, temporal, cultural, and material similarities. This resulted in the pooling of sites from the Middle Jōmon into separate groups based on their location within the interior island of Honshu or the coast and the Late/Final Jōmon by interior Honshu, coastal Honshu, and coastal Hokkaido. Epi-Jōmon and Okhotsk sites were grouped into Epi-Jōmon and Okhotsk pools, respectively.

Since bone is susceptible to remodeling in response to changes in pressure, directional asymmetry was calculated and tested for the presence of significant difference between sides for a bilateral trait. Results showed that there was a significant difference between the right and left side for maximum ramus breadth, resulting in the two measurements being tested separately while the average of all other bilateral traits were tested. A PCA was then conducted to determine the variables most influential in describing the majority of the variation.

The results showed that minimum ramus breadth and both left and right ramus breadth were responsible for 79.92% of the variation. Bicondylar breadth and bigonial breadth was the only trait showing weak reduction as other traits became more robust. Hypothesis testing was conducted using an ANOVA.

The results supported the hypothesis that there was no significant difference in mandibular morphology by region in the Middle Jōmon. This supported the idea that mandibular morphologies were comparable as a result of cultural and economic continuity as broad spectrum foragers among regions.

For the hypothesis that mandibular form was reduced in interior Honshu populations in the Late/Final Jōmon, the results did not support the hypothesis showing that there was no difference between the coastal and interior regions of Honshu. In contrast to predictions, coastal Hokkaido populations were significantly more robust for minimum and maximum ramus breadth but displayed a narrower bicondylar breadth than the populations in Honshu. The results suggest that broad spectrum foraging was still a substantial practice in Honshu and Hokkaido during the Late/Final Jōmon. Specialization in marine subsistence may reflect a need to compensate for the low productivity of the surrounding coastline and may be indicative of a broader diet breadth which would incorporate harsher foods than those accessible through the diversity and quantity seen in Honshu.

The Okhotsk was the source of the significant asymmetry for maximum ramus breadth and was significantly more robust for these measures and minimum ramus

breadth compared to all. Possible explanations for the observed differences are differences in marine subsistence diets. Access to resources and diet breadth may have differed based on the coastline and thus resulted in different diets despite groups shared practice of marine subsistence. The Epi-Jōmon may have begun to engage in small scale plant cultivation as is evidenced by material goods and seen on a greater scale in the subsequent Satsumon populations. While the Epi-Jōmon engaged in marine subsistence, likely they did not practice to the same exclusivity as the Okhotsk.

The findings are significant not only for the study of Japanese prehistory but in the study of human behavioral ecology as well. The relationships between morphology and diet have been sufficiently substantiated in anthropological study, but determination of specific environmental factors and behavioral adaptations through extrapolation is a less accurate. Complex hunter gatherer's such as the Jōmon have a history of processing that may potentially mitigate the results that would typically be expected from populations engaged in seemingly equivocal subsistence practices. As a result, examination may be limited in scope and restricted in application without contextual knowledge of pre-existing practices pertaining to a particular population.

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Appendix

Table A1. Normality test for traits for the Middle Jōmon

| Site | Mean | S.D. | df | W | p |
|--------|--------|------|----|-------|-------|
| IDGN | 31.33 | 3.17 | 6 | 0.873 | 0.238 |
| GOGO | 84.64 | 2.97 | 6 | 0.943 | 0.687 |
| CDLCDL | 127.78 | 3.8 | 6 | 0.285 | 0.883 |
| BMANL | 16.75 | 2.72 | 6 | 0.876 | 0.249 |
| BMANR | 17.39 | 2.64 | 6 | 0.961 | 0.824 |
| HMANL | 30.13 | 1.55 | 6 | 0.921 | 0.515 |
| HMANR | 30.57 | 1.74 | 6 | 0.906 | 0.409 |
| MINRBL | 35.75 | 2.92 | 6 | 0.907 | 0.415 |
| MINRBR | 35.26 | 3.18 | 6 | 0.811 | 0.073 |
| MAXRBL | 47.97 | 2.36 | 6 | 0.827 | 0.101 |
| MAXRBR | 47.88 | 2.69 | 6 | 0.842 | 0.134 |

*Significant at $\alpha = 0.05$

Table A2. Normality test for traits for the Late/Final Jōmon in Honshu

| Site | Mean | S.D. | df | W | p |
|--------|--------|------|----|-------|-------|
| IDGN | 31.81 | 3.17 | 5 | 0.966 | 0.852 |
| GOGO | 84.93 | 2.97 | 5 | 0.866 | 0.252 |
| CDLCDL | 127.13 | 3.8 | 5 | 0.988 | 0.972 |
| BMANL | 15.76 | 2.72 | 5 | 0.928 | 0.583 |
| BMANR | 16.01 | 2.64 | 5 | 0.799 | 0.080 |
| HMANL | 29.76 | 1.55 | 5 | 0.814 | 0.105 |
| HMANR | 30.19 | 1.74 | 5 | 0.904 | 0.433 |
| MINRBL | 33.86 | 2.92 | 5 | 0.877 | 0.294 |
| MINRBR | 34.06 | 3.18 | 5 | 0.839 | 0.162 |
| MAXRBL | 44.37 | 2.36 | 5 | 0.821 | 0.120 |
| MAXRBR | 45.07 | 2.69 | 5 | 0.858 | 0.222 |

*Significant at $\alpha = 0.05$

Table A3. Normality test for traits for the Late/Final Jōmon in Hokkaido

| Site | Mean | S.D. | df | W | p |
|--------|--------|------|----|-------|-------|
| IDGN | 31.82 | 2.73 | 4 | 0.907 | 0.467 |
| GOGO | 81.35 | 1.20 | 4 | 0.846 | 0.214 |
| CDLCDL | 115.51 | 4.95 | 4 | 0.881 | 0.345 |
| BMANL | 15.06 | 0.48 | 4 | 0.822 | 0.148 |
| BMANR | 15.60 | 0.26 | 4 | 0.930 | 0.592 |
| HMANL | 27.39 | 1.24 | 4 | 0.866 | 0.283 |
| HMANR | 27.54 | 1.45 | 4 | 0.940 | 0.655 |
| MINRBL | 34.29 | 0.44 | 4 | 0.999 | 0.937 |
| MINRBR | 35.47 | 1.21 | 4 | 0.817 | 0.136 |
| MAXRBL | 45.19 | 2.88 | 4 | 0.875 | 0.317 |
| MAXRBR | 49.19 | 3.92 | 4 | 0.841 | 0.199 |

*Significant at $\alpha = 0.05$

Table A4. Normality test for traits for the Okhotsk

| Site | Mean | S.D. | df | W | p |
|--------|--------|------|----|-------|-------|
| IDGN | 36.25 | 1.27 | 7 | 0.876 | 0.211 |
| GOGO | 91.53 | 2.8 | 7 | 0.986 | 0.962 |
| CDLCDL | 125.21 | 4.98 | 7 | 0.920 | 0.466 |
| BMANL | 18.61 | 0.96 | 7 | 0.830 | 0.106 |
| BMANR | 18.12 | 1.56 | 7 | 0.962 | 0.836 |
| HMANL | 32.5 | 2.58 | 7 | 0.946 | 0.691 |
| HMANR | 33.21 | 1.79 | 7 | 0.980 | 0.960 |
| MINRBL | 41.73 | 1.47 | 7 | 0.864 | 0.165 |
| MINRBR | 43.49 | 3.23 | 7 | 0.834 | 0.087 |
| MAXRBL | 54.19 | 4.75 | 7 | 0.823 | 0.070 |
| MAXRBR | 53.07 | 1.83 | 7 | 0.965 | 0.860 |

*Significant at $\alpha = 0.05$

Table A5. F-test for male, female, and unsexed in Middle Jōmon sites

| Site | Trait | MS | df | F | p |
|------------|--------|--------|----|--------|-------|
| Kitakogane | IDGN | | | | |
| | GOGO | 0.384 | 1 | 0.040 | 0.848 |
| | CDLCDL | | | | |
| | BMANL | 1.622 | 1 | 0.446 | 0.529 |
| | BMANR | 0.104 | 1 | 0.084 | 0.783 |
| | HMANL | 9.856 | 1 | 1.001 | 0.391 |
| | HMANR | 12.059 | 1 | 0.266 | 0.641 |
| | MINRBL | 8.311 | 1 | 1.415 | 0.288 |
| | MINRBR | 38.813 | 1 | 4.254 | 0.175 |
| | MAXRBL | 16.95 | 1 | 0.951 | 0.385 |
| | MAXRBR | 27.405 | 1 | 16.714 | 0.055 |
| Ohta | IDGN | 17.541 | 2 | 2.993 | 0.115 |
| | GOGO | 7.421 | 2 | 0.914 | 0.421 |
| | CDLCDL | 26.225 | 2 | 0.708 | 0.521 |
| | BMANL | 2.375 | 2 | 0.885 | 0.431 |
| | BMANR | 4.682 | 2 | 0.995 | 0.390 |
| | HMANL | 1.557 | 2 | 0.160 | 0.853 |
| | HMANR | 1.878 | 2 | 0.189 | 0.830 |
| | MINRBL | 4.341 | 2 | 0.668 | 0.534 |
| | MINRBR | 2.458 | 2 | 0.516 | 0.612 |
| | MAXRBL | 11.834 | 2 | 0.772 | 0.503 |
| | MAXRBR | 2.248 | 2 | 0.189 | 0.831 |

*Significant at $\alpha = 0.05$

Table A6. F-test for male, female, and unsexed in Late/Final Jōmon sites

| Site | Trait | MS | df | F | p |
|------------|--------|--------|----|--------|-------|
| Funadomari | IDGN | | | | |
| | GOGO | 3.182 | 1 | 0.474 | 0.541 |
| | CDLCDL | | | | |
| | BMANL | 2.456 | 1 | 1.913 | 0.242 |
| | BMANR | 3.773 | 1 | 0.962 | 0.443 |
| | HMANL | 15.611 | 1 | 5.618 | 0.098 |
| | HMANR | | | | |
| | MINRBL | 4.629 | 1 | 4.170 | 0.290 |
| | MINRBR | 1.92 | 1 | 0.408 | 0.551 |
| | MAXRBL | 0.342 | 1 | 0.029 | 0.881 |
| | MAXRBR | | | | |
| Irie | IDGN | | | | |
| | GOGO | 0.394 | 2 | 0.175 | 0.851 |
| | CDLCDL | 0.001 | 1 | 0.031 | 0.889 |
| | BMANL | 0.618 | 2 | 0.323 | 0.746 |
| | BMANR | 1.372 | 2 | 0.376 | 0.715 |
| | HMANL | | | | |
| | HMANR | 16.58 | 2 | 0.080 | 0.325 |
| | MINRBL | 7.758 | 2 | 0.326 | 0.754 |
| | MINRBR | 11.586 | 2 | 1.779 | 0.360 |
| | MAXRBL | 39.869 | 2 | 4.384 | 0.186 |
| | MAXRBR | 36.308 | 2 | 6.502 | 0.133 |
| Takasago | IDGN | | | | |
| | GOGO | 20.839 | 1 | 2.656 | 0.245 |
| | CDLCDL | | | | |
| | BMANL | 0.093 | 1 | 0.063 | 0.825 |
| | BMANR | 0.757 | 1 | 0.677 | 0.497 |
| | HMANL | 10.349 | 1 | 3.780 | 0.302 |
| | HMANR | 3.11 | 1 | 29.299 | 0.116 |
| | MINRBL | 12.355 | 1 | 1.522 | 0.434 |
| | MINRBR | 71.741 | 1 | 9.298 | 0.093 |
| | | MAXRBL | | | |
| | MAXRBR | | | | |

*Significant at $\alpha = 0.05$

Table A7. F-test for male, female, and unsexed in Okhotsk sites

| Site | Trait | MS | df | F | p |
|----------|--------|--------|-------|-------|-------|
| Ohmisaki | IDGN | 3.986 | 1 | 2.394 | 0.160 |
| | GOGO | 34.693 | 1 | 1.043 | 0.331 |
| | CDLCDL | 37.076 | 1 | 2.104 | 0.197 |
| | BMANL | 6.275 | 1 | 3.998 | 0.081 |
| | BMANR | 3.224 | 1 | 0.953 | 0.358 |
| | HMANL | 16.538 | 1 | 2.158 | 0.176 |
| | HMANR | 11.722 | 1 | 4.198 | 0.075 |
| | MINRBL | 0.049 | 1 | 0.016 | 0.904 |
| | MINRBR | 10.778 | 1 | 1.115 | 0.322 |
| | MAXRBL | 9.563 | 1 | 0.627 | 0.454 |
| MAXRBR | 4.977 | 1 | 2.916 | 0.126 | |

*Significant at $\alpha = 0.05$

Table A8. F-test for adult and unknown age Yoshigo

| Site | Trait | MS | df | F | p |
|---------|--------|--------|----|-------|-------|
| Yoshigo | IDGN | 34.135 | 1 | 1.646 | 0.209 |
| | GOGO | 17.723 | 1 | 1.651 | 0.208 |
| | CDLCDL | | | | |
| | BMANL | 0.662 | 1 | 0.160 | 0.692 |
| | BMANR | 1.019 | 1 | 0.320 | 0.575 |
| | HMANL | 13.749 | 1 | 1.387 | 0.255 |
| | HMANR | 31.11 | 1 | 2.883 | 0.102 |
| | MINRBL | | | | |
| | MINRBR | | | | |
| | MAXRBL | | | | |
| MAXRBR | | | | | |

*Significant at $\alpha = 0.05$