

Reconstruction of diachronic changes in human fishing activity and marine ecosystems from carbon and nitrogen stable isotope ratios of Epi-Jomon to Okhotsk fish remains from Hamanaka 2, Hokkaido, Japan

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## **Abstract**

Stable isotope analysis is one of the most effective methods of reconstructing human fishing practices and changes in past marine ecosystems. The effectiveness of this method can be further improved when considering diachronic changes in stable isotope ratios of archaeological remains of several different fish species that exhibit different behavioral or ecological traits. In this study, diachronic changes in human fishing practices and marine ecosystems were investigated for Epi-Jomon (2300–260 BC) and Okhotsk (489–1200 AD) periods in prehistoric Hokkaido, northern Japan, by utilizing the stable isotope analysis of archaeological fish bone collagen. Carbon and nitrogen stable isotope ratios of 242 fish bone samples, representing 12 taxa, excavated from the site of Hamanaka 2 on Rebun Island revealed significantly lower ( $p < 0.05$ ) nitrogen isotope ratios in cod from the Okhotsk period. This difference could be related to the development of fishing gear and/or to changes in fishing strategies in the Okhotsk period, as well as to changes in the behavior of cod because of the rapid cooling climate event separating the two periods. Our results demonstrate that some aspects of past human fishing practices and marine ecosystem change can be reconstructed by considering diachronic changes in the stable isotope ratios of several fish species together.

## **Keywords**

climate change; cod; fishing practices; Hokkaido; stable isotope analysis

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## 50 **1. Introduction**

51     Alongside more traditional studies of species composition and fishing gear, stable isotope  
52     analysis of fish remains provides the opportunity for reconstructing aspects of past fishing  
53     activities and changes in marine ecosystems. Carbon and nitrogen stable isotope ratios  
54     systematically differ by the organisms' diet and habitat and have been used as tracers of food  
55     sources or proxies for geolocation (Hobson 1999; McMahon et al. 2013; Newsome et al.  
56     2010; Schoeninger et al. 1984). Fish diets differ both within but particularly between species,  
57     with food items including plankton, benthos, crustaceans/molluscs, and fish, and changes in  
58     the marine food web and isotopic baseline can be estimated from the stable isotope ratios of  
59     fish because of their great variety of food sources. Furthermore, fish remains excavated from  
60     archaeological sites were obtained and "filtered" through fishing activities and can be  
61     regarded as a record of past human behavior (Bas et al. 2020; Barrett et al. 2011; Guiry et al.  
62     2020; Orton et al. 2011; Pestle 2013; Szpak et al. 2013).

63     Separating the effects on stable isotope ratios of fishing practices and ecosystem changes is  
64     often challenging. However, they can be investigated more in detail by considering diachronic  
65     change in stable isotope ratios of archaeological remains of several different fish species that  
66     have different behavioral or ecological traits. There is great diversity in diet and habitat use of  
67     different fish species, which provides a useful resource to reconstruct past human behaviors  
68     and marine ecosystems from diverse aspects. Such a reconstruction is not possible when  
69     either a single species or a single time period is considered.

70     In this study, these potential diachronic changes are investigated by applying carbon and  
71     nitrogen stable isotope analysis to archaeological fish bones. The study site of Hamanaka 2,  
72     Rebun Island, Hokkaido, northern Japan, was used by Epi-Jomon hunter-gatherer-fishers and

Okhotsk fishers between 400 cal BC and 950 cal AD, encompassing a series of climatic events (e.g., the Medieval Warm Period and the Little Ice Age) (Mann et al. 2009). There are also differences in technology and culture between the two periods that might result in changes to fishing practices and fishing intensity. Both these and potential climate-related changes in marine food webs can be examined through the stable isotope ratios of fish bones originating from a broad range of taxonomic groups with different foraging and migratory patterns. Thus, stable isotopic evidence of various ancient fish species from two time periods with different ecological conditions, as well as contextual evidence from the archaeological records, can provide a multifaceted understanding of human fishing practices and marine ecosystems in the past.

#### 1.1 Hokkaido prehistory and Hamanaka 2

Marine organisms were important food sources for humans in Hokkaido, northern Japan, since at least the beginning of the Holocene (Figure 1). A large amount of excavated bones of marine fish and mammals, diverse fishing gear (e.g., fish hooks, harpoons, and net sinkers), stable carbon and nitrogen isotope ratios of human skeletons, and lipid residues in pottery all indicate a reliance of marine food sources in prehistoric Hokkaido people from the Jomon to Ainu periods (e.g., Junno et al. 2020; Lucquin et al. 2018; Naito et al. 2010a, 2010b; Nomura & Utagawa 2003; Robson et al. 2020; Takase 2020; Tsutaya et al. 2013, 2014). The Epi-Jomon and Okhotsk periods witnessed particularly high reliance on marine foods, and so potentially had more pronounced effects on nearshore marine ecosystems, compared with previous time periods in Hokkaido. Therefore, they provide the ideal target of this study.

Epi-Jomon people were directly descended from Jomon hunter-gatherer-fishers in Hokkaido, and they are characterized by a high reliance on marine foods. Populations in

Hokkaido continued hunting-gathering-fishing even after the introduction of rice agriculture in mainland Japan (Yayoi period), which did not reach Hokkaido during the Epi-Jomon period (450 BC–650 AD). Stable isotope analysis suggests that Epi-Jomon people obtained most of their dietary protein through the consumption of marine mammals and fish as well as terrestrial animals (Tsutaya et al. 2013). A wealth of fishing tools, such as fishhooks, harpoons, and net sinkers, suggest that marine mammals and fish were important food sources during the Epi-Jomon (Nomura & Utagawa 2003). A meta-analysis showed that 44.5% of Epi-Jomon archaeological sites are located within 2 km of the modern coastline (Abe et al. 2016). However, the quantity and composition of excavated fish and marine mammal bones suggest nearshore, but not pelagic, and rather small-scale fishing activities at this time (Nishimoto 1985; Takase 2020).

Ancient DNA and morphological analyses indicate that the origins of the Okhotsk (400–1200 AD) was through immigrant fishers from the region around the lower Amur River and Sakhalin to the northeastern coast of Hokkaido (Hudson 2004; Ishida 1996; Sato et al. 2007, 2009). The Okhotsk culture is again characterized by a heavy reliance on marine food sources. A meta-analysis showed that 88.7% of Okhotsk sites are located within 2 km of the modern coastline (Abe et al. 2016). There were developments in fishing gear compared with the previous periods, such as the increase in the size of net sinkers, and figures depicted on bone tools suggest a presence of several types of ocean-going vessels (Amano 1977; Nomura & Utagawa 2003; Oba 1955). Although Okhotsk people had domesticated dogs and pigs, stable isotopic studies of human skeletons suggested that  $\geq 80\%$  of dietary protein was obtained from marine fish and marine mammals (Naito et al. 2010b; Tsutaya et al. 2014). All such evidence, as well as the quantity and composition of excavated fish and marine mammal bones (Nishimoto 1978, 1985), suggests that, while the Okhotsk still relied primarily on an

inshore fishery, it was practiced on a larger scale than previous periods including the Epi-Jomon. During their immigration from north to east along the northeastern coastline of Hokkaido, the main dietary protein sources changed from marine fish to marine mammals, partly because the floating ice on the east coast of Hokkaido prevented fishing but facilitated marine mammal hunting during winter (Naito et al. 2010b; Ono 1996a, b). The Okhotsk culture was merged into Epi-Jomon and Satsumon cultures to become the historically documented Ainu culture (Hudson 2004; Nomura & Utagawa, 2003).

Rebun Island is located approximately 60 km northwest of the Hokkaido mainland, and its total area is 81 km<sup>2</sup> (Figure 1). The island has yielded numerous archaeological sites spanning the Jomon to Ainu periods (Kato 2015). Among those dating to the Okhotsk period, Kafukai has an exceptionally large amount of excavated faunal remains. Zooarchaeological analysis of Kafukai remains, which includes over hundreds of individual specimens for each category, suggested that  $\geq 80\%$  of the caloric contribution was obtained from marine fish, despite the presence of a diverse fauna including marine mammals, marine shellfish, sea urchins, birds, and terrestrial mammals (Nishimoto 1978; Oba & Ohyi 1981). Migrant fish species coming closer to the coast, i.e., Pacific herring (*Clupea pallasii*) in spring, Okhotsk atka mackerel (*Pleurogrammus azonus*) in autumn, and cod in winter, were the most important food sources at Kafukai, supplemented by various benthic fish, marine molluscan, crustacean, and echinoderm species when they were easily available (Nishimoto 1978; Oba & Ohyi 1981).

Hamanaka 2 is a multi-component sand dune site located on Rebun Island's north coast, and, unlike other sites on the island, contains a continuous cultural sequence from the Late/Final Jomon to historic Ainu periods (Table 1). Several excavation campaigns have been conducted (e.g., Rebun Town 1992; Nishimoto 2000) with materials from the most recent excavations since 2011 at the Nakatani location (45°43'26"N, 141°00'96"E) forming the

focus of this study (e.g., Kato 2015; Center for Ainu and Indigenous Studies 2017; Leipe et al. 2017, 2018; Lynch et al. 2018; Müller et al. 2016; Okamoto et al. 2016; Tsutaya et al. 2019). The Nakatani location of Hamanaka 2 yielded thin occupation layers dating to the Late/Final Jomon and Epi-Jomon periods (layers VII and VIII, dated to 299–258 cal BC: Junno et al. 2021) and thick fish bone layers in the Okhotsk period, separated by a thick sand layer with few cultural remains (Center for Ainu and Indigenous Studies 2017). Okhotsk layers at Hamanaka 2 can be divided further into three phases: Initial, Middle, and Final. There was limited human activity during the Initial Okhotsk (489–573 cal AD: Junno et al. 2021) and the amount of excavated remains including fish bones was less than for the later phases (Center for Ainu and Indigenous Studies 2017; Sato et al. 2015). The thick sand layers IV, V, and VI can be assigned to the Initial Okhotsk and yield Towada pottery. The quantity of excavated remains increase and a thick fish bone layer was formed during the Middle Okhotsk, corresponding to layer III (573–850 cal AD: Center for Ainu and Indigenous Studies 2017; Junno et al. 2021; Sato et al. 2015). This layer yields Kokumon, Chinsenmon, and Motochi pottery. Human activity appears to have decreased during the Final Okhotsk (850–1200 AD), which corresponds to layer II. Layer II yields Motochi and Satsumon pottery. Although the latter relates to the Satsumon culture rather than the Okhotsk culture, remains excavated from the layer II were assigned to Final Okhotsk in this study. It is difficult to separate the Motochi and Satsumon sublayers in layer II due to the disturbance (Junno et al. 2021). The previously published radiocarbon dates of charred plant materials from the Nakatani location of Hamanaka 2 (Junno et al. 2021; Leipe et al. 2017, 2018; Müller et al. 2016) show generally consistent ages for each period, compared with the ages assigned by pottery typology.

## 1.2 Factors affecting stable isotope ratios of fish

Carbon and nitrogen stable isotopes are used as naturally occurring tracers of food sources, and their abundance ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, respectively) further vary systematically due to changes in the marine ecosystem (Hobson 1999; McMahon et al. 2013; Newsome et al. 2010; Schoeninger et al. 1984). Relevant factors affecting carbon and nitrogen stable isotope ratios of fish in the context of Epi-Jomon and Okhotsk periods in Rebun Island are inshore/pelagic habitats, trophic position, temperature, long-term baseline change, and origin of the water mass, e.g., the influence of major currents (Figure 1). These factors can affect fish stable isotope ratios at both organismal and ecological levels. Details of these factors are explained below, and should be considered when interpreting the stable isotopic results obtained from the Hamanaka 2 fish remains. It is expected that diachronic changes in human fishing activities and in the marine ecosystem can be reflected in various fish species that have different diets and habitat use, according to these factors.

Higher nutrient concentrations and thus higher productivity can be typically seen in inshore and benthic systems resulting in enriched  $^{13}\text{C}$  for biota compared to pelagic systems (France 1995). Such inshore/pelagic differences can be seen in modern fish species in the Okhotsk Sea and Pacific Ocean (Hiwatari et al. 2011; Misarti et al. 2009). This provides the basis for differentiating between inshore and offshore fishing using  $\delta^{13}\text{C}$  values.

The  $\delta^{15}\text{N}$  values of marine organisms increase with trophic level because  $^{15}\text{N}$  shows bioenrichment due to the preferential excretion of nitrogen in the form of  $^{14}\text{N}$  (Chikaraishi et al. 2014; Minagawa & Wada 1984; Schoeninger et al. 1984). Therefore, the  $\delta^{15}\text{N}$  values of fish species typically increase from planktivores to molluscivores to piscivores. Trophic level, and therefore  $\delta^{15}\text{N}$  values, of some fish species, such as cod and rockfish, also increase with growth in body size, while that of other species, such as herring and plaice, decrease



(Jennings et al. 2002). A more nuanced analysis, therefore, can compare trophic level within as well as between species, taking into account body size differences.

Ambient marine temperature affects the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of fish. Ocean bottom temperature shows a significant positive correlation with scallop  $\delta^{13}\text{C}$  values in the northeast Atlantic because temperature affects the dissolution of atmospheric  $\text{CO}_2$  and the ecological dynamics of phytoplankton (Barnes et al. 2009). A significant proportion of spatial variation in  $\delta^{15}\text{N}$  values of scallops was explained by salinity, depth, and temperature in the northeast Atlantic, with higher temperature corresponding to higher  $\delta^{15}\text{N}$  values (Jennings et al. 2003). Palynological studies have shown that there were several cooling events affecting Rebutia Island during the period under consideration here (Leipe et al. 2018; Müller et al. 2016), and these climatic changes may have directly affected the stable isotope ratios of marine fish.

The Okhotsk Sea and the Sea of Japan (East Sea) experienced long-term changes in baseline  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values during the Late Holocene. Analysis of marine sediment cores revealed baseline  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  changes on the order of hundreds or thousands of years. There were only minor changes in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, within 1‰, in sediment cores from the Sea of Japan during the Late Holocene (Khim et al. 2008). There were also few changes in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in sediment cores from the Okhotsk Sea during most of the Late Holocene, but  $\delta^{15}\text{N}$  values increased by approximately 1.5‰ during the last ~2000 years possibly due to the decrease in palaeoproductivity in the central region of the Okhotsk Sea (Khim et al. 2012; Ternois et al., 2001). Environmental conditions should be considered when interpreting long-term changes in fish  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values because stable isotope ratios of marine organisms are directly affected by changes to the baseline isotope system (Ostrom et al. 2017).

Fish living in waters with varying oceanographic origins can show different isotope ratios. Nutrient sources of organisms may differ in marine regions with different ecological and oceanographical characters, especially as regards  $\delta^{15}\text{N}$ . For example,  $\delta^{15}\text{N}$  values of nitrate ( $\text{NO}_3^-$ ), the major nutrient source for plankton, vary across different marine regions due to denitrification, assimilation by plankton, and influence of upwelling deep water (Montoya, 2007; Trueman et al., 2012). The  $\delta^{15}\text{N}$  values of marine organic matter decrease due to nitrogen fixation by plankton in the oligotrophic zone (Montoya, 2007; Trueman et al., 2012). These differences in  $\delta^{15}\text{N}$  values are reflected in organisms in higher trophic levels, including fish. The  $\delta^{15}\text{N}$  values of body tissue of migratory pelagic fish may differ if they traverse water masses with different baseline isotope ratios of marine organic matter (Richert et al., 2015). The other way in which this can occur is if the waters themselves move via large currents, such as those running past northwest Hokkaido, with the East Sakhalin Current bringing waters from the north and the Kuroshio Current bringing waters from the south past Rebun Island (Figure 1).

## **2. Materials and Methods**

### **2.1 Fish bone samples**

A total of 285 fish bones from 12 taxonomic groups excavated from 2011 to 2016 from the Nakatani location of Hamanaka 2 was used in this study (Supplementary Table 1). Fish bones excavated from layers VIII–VII, VI–IV, III, and II were assigned to the Epi-Jomon period and to the Initial, Middle, and Final phases of the Okhotsk period, based on the pottery typology and radiocarbon dating (Table 1; Junno et al. 2021). Fish bones were collected via water flotation using 9.52, 4, and 2 mm meshes and then air-dried. Species identification was done by an experienced zooarchaeologist (Tomonari Takahashi), and samples for stable isotope

analysis were randomly selected from the identified bones. The resolution of species identification in some taxa is low; possible fish species derived from morphological traits of the samples and geographic distribution of the living species are shown in Table 2. There was no evident difference in the general composition of fish taxa excavated from each archaeological period, with Okhotsk atka mackerel, Pacific herring, and cod being the dominant species (Sato et al. 2015; Supplementary Figure 1). Elements retaining at least half of their whole size were used to avoid replicate sampling from the same element. While there is a possibility of duplicate measurements of the same individual when using vertebrae, no samples were obtained from an articulated fish skeleton. The sheer number of fish bones from the site also mitigates against this possibility.

The vertebra was used for most fish species. Fish vertebrae grow incrementally (Matsubayashi et al. 2017) and thus were cut longitudinally when sub-sampling to avoid a bias caused by growth-related dietary change. Maxillae/premaxillae and spines were sampled for pufferfish and rockfish. Previously published stable isotopic data on 30 fish bone samples (Tsutaya et al. 2017) were also included in this study (see Supplementary Table 1).

## 2.2 Stable isotope analysis

Collagen was extracted from fish bones weighing 6–360 mg using the method described in Tsutaya et al. (2017, 2018). Briefly, bones were washed with water and then 0.2 M NaOH to remove exogenous matters and humic substances. Bone samples were then decalcified in 0.25 N or 0.5 N HCl at 4°C for 2–4 days. The decalcified samples were gelatinized and filtered using a glass fiber filter (Whatman GF/F) to remove noncollagenous substances. The filtered samples were then freeze-dried. Approximately 350 µg of the resultant collagen was used for carbon and nitrogen stable isotope analysis. Lipid extraction was not performed, and NaOH

treatment was performed before decalcification in this study, since a previous study demonstrated experimentally that these treatments do not affect the stable isotope ratios of collagen extracted from fish bones specifically at Hamanaka 2 (Tsutaya et al. 2018).

Carbon and nitrogen stable isotope ratios were measured using elemental analyzer–isotope ratio mass spectrometry (Thermo Flash 2000 elemental analyzer, Finnigan ConFlo III interface, and Thermo Delta V mass spectrometer) at the University Museum, University of Tokyo, Japan. The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were calibrated against the laboratory working standard (L-alanine:  $\delta^{13}\text{C} = -19.6 \pm 0.2\text{‰}$ ;  $\delta^{15}\text{N} = 8.7 \pm 0.2\text{‰}$ ) provided by SI Science (Saitama, Japan), whose values were determined by the NBS 19 and the International Atomic Energy Agency (IAEA) Sucrose ANU (calibrated against Pee Dee Belemnite and IAEA N1 and IAEA N2 (calibrated against AIR) international standards, respectively. Based on repeated measurements of the calibration standards, precision was determined to be less than  $\pm 0.1\text{‰}$  standard deviation (SD) for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . The accuracy or systematic error was not determined (Szpak et al. 2017).

### 2.3 Data analysis

Data analysis and statistical tests were performed using R, version 4.0.2 (R Core Team 2020). Distributions of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were depicted with standard ellipses using the functions of Stable Isotope Bayesian Ellipses in R (SIBER) in the R package “siar”, version 4.2 (Parnell et al., 2010; Jackson et al., 2011). Bee swarm plots were drawn using the R package “beeswarm”. Diachronic trends were investigated only for five fish species having sufficient sample sizes from at least three periods/phases, comprising cod, flatfish, Okhotsk atka mackerel, Pacific herring, and rockfish. Zooarchaeological studies have shown that these

species, except for flatfish, were the most important food sources for Okhotsk communities on Rebun Island (Nishimoto 1978; Oba & Ohyi 1981; Sato et al. 2015).

### **3. Results**

#### **3.1 Bone preservation and outliers**

Of the total of 285 bone samples analyzed, 242 samples provided reliable stable isotope ratios (Supplementary Table 1). An insufficient amount of collagen for measurement by EA-IRMS was obtained from 23 bone samples. Atomic C/N ratios outside the acceptable range of 2.9–3.6 (DeNiro 1985) were seen in 13 samples, seven of which also had collagen yields lower than the acceptable limit of 1% (van Klinken 1999). These 13 samples were excluded. After this initial screening by C/N ratio and yield, leave-one-out cross-validation was applied to detect outliers. Mean and standard deviation (SD) for every fish species was calculated by excluding the target sample, and if either the  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  value of the target sample was outside the mean  $\pm$  3SD range, this sample was regarded as an outlier. A total of seven samples were classified as outliers and were further excluded from the dataset, as we are primarily interested in the central tendencies of the datasets, rather than in outliers. These outliers might be a result of misidentification, measurement error, or fish deriving from locations with different isotopic baselines.

#### **3.2 Stable isotope ratios of fish bones**

The  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  niches for fish species of different time periods are shown in Figure 2, with mean values for different species provided in Table 2, and those for different time periods provided in Supplementary Table 2. Fish species represented by  $\geq 3$  individuals can be divided into three different groups: A) lower  $\delta^{13}\text{C}$  and higher  $\delta^{15}\text{N}$  values for cod, B) higher

$\delta^{13}\text{C}$  and middle  $\delta^{15}\text{N}$  for flatfish, pufferfish, rockfish, and sculpin, and C) lower  $\delta^{13}\text{C}$  and lower  $\delta^{15}\text{N}$  for Pacific herring and Okhotsk atka mackerel (Figure 2). While  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values are possibly biased due to small sample size ( $n < 3$ ), Pacific halibut (*Hippoglossus stenolepis*) falls between groups A and C, salmon falls between groups B and C, tuna has higher  $\delta^{13}\text{C}$  and lower  $\delta^{15}\text{N}$ , and yellowtail can be classified with group C (Figure 2).

Mann-Whitney U-tests were applied first to investigate the isotopic difference between fish remains excavated from the Epi-Jomon and Okhotsk periods, with the latter considered as a single group (Table 3; Figure 3). No significant differences in  $\delta^{13}\text{C}$  between the two periods were found for any fish species. Epi-Jomon  $\delta^{15}\text{N}$  values of cod and Pacific herring were significantly higher (by 1.1‰ and 0.4‰, respectively) than those in the Okhotsk period, with no significant difference in the  $\delta^{15}\text{N}$  values of the other fish species.

Subsequently, Kruskal–Wallis tests were applied to investigate chronological differences further, breaking the Okhotsk period down into its three phases. The results indicate significant chronological differences in the  $\delta^{13}\text{C}$  values of rockfish and  $\delta^{15}\text{N}$  values of cod and Pacific herring, but not for other fish species (Table 4; Figure 3). Post-hoc Mann–Whitney U-tests with corrected p-values of 0.0083 ( $= 0.05/6$ ) for rockfish and Pacific herring and 0.0167 ( $= 0.05/3$ ) for cod, according to the Bonferroni method (Bland and Altman, 1995), confirmed that the difference was statistically significant (Table 5). The  $\delta^{13}\text{C}$  values of rockfish from the Initial Okhotsk phase were significantly lower than those from the Middle Okhotsk phase by 0.6‰ (Supplementary Table 2). The  $\delta^{15}\text{N}$  values of cod from the Epi-Jomon period were significantly higher than those from the Initial and Middle Okhotsk phases, by 0.9‰ and 1.3‰, respectively (Supplementary Table 2; no cod were included from the Final Okhotsk due to the limited and fragmentary nature of the remains). The  $\delta^{15}\text{N}$  values of Pacific herring

from the Epi-Jomon period were on average significantly higher than those from the Middle Okhotsk phase by 0.6‰ (Supplementary Table 2).

## **4. Discussion**

### 4.1 Inter-species differences

Inter-species differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values are consistent with the species-specific diet and habitat of the analyzed fish with  $\geq 3$  individuals. Migrating fish species that seasonally come near the coast, such as cod, Okhotsk atka mackerel, and Pacific herring (Table 2; Fisheries Agency 2019, 2020), exhibit lower  $\delta^{13}\text{C}$  values, consistent with more time spent feeding in offshore waters (Bas et al. 2020; France 1995; Hiwatari et al. 2011; Misarti et al. 2009). The  $\delta^{15}\text{N}$  values of these species can be classified into higher (i.e., cod) and lower (i.e., Pacific herring and Okhotsk atka mackerel) groups, reflecting their diets (Table 2; Chikaraishi et al. 2014; Minagawa & Wada 1984; Schoeninger et al. 1984). The main prey of adult cod are fish, crustaceans, and molluscs resulting in a relatively high trophic level with elevated  $\delta^{15}\text{N}$  values, while adult Pacific herring and adult Okhotsk atka mackerel focus on plankton, small fish, and crustaceans from relatively low trophic levels and hence exhibit lower  $\delta^{15}\text{N}$  values (Table 2; Fisheries Agency 2019, 2020). Fish species living in the inshore benthic system (i.e., flatfish, pufferfish, rockfish, and sculpin) show higher  $\delta^{13}\text{C}$  values, a signature of the inshore/benthic ocean (Bas et al. 2020; France 1995; Hiwatari et al. 2011; Misarti et al. 2009; Szpak et al. 2013). The typical  $\delta^{15}\text{N}$  values of these species are intermediate between the higher and lower groups, suggesting that their prey are mainly from the middle trophic levels. Typical food sources of these fish species during adulthood are fish, crustaceans, molluscs, and plankton, which is consistent with the isotopic result (Fisheries Agency 2019, 2020).

#### 4.2 Chronological trends in cod

Cod showed the largest diachronic  $\delta^{15}\text{N}$  changes (0.9‰ and 1.3‰ higher in the Epi-Jomon than in the Okhotsk Initial and Middle phases, respectively) among the five fish species (Table 3–5; Figure 3). Since trophic level of cod increases with their growth (Jennings et al. 2002), higher  $\delta^{15}\text{N}$  values in the Epi-Jomon period suggest that larger individuals were caught compared with the Okhotsk period. This explanation is supported by preliminary results showing a significantly larger diameter of Epi-Jomon ( $13.0 \pm 4.2$  mm,  $n = 14$ ) compared with Okhotsk ( $8.7 \pm 3.2$  mm,  $n = 22$ ) cod vertebra and a significant positive correlation between diameter and  $\delta^{15}\text{N}$  values (Supplementary Text; Supplementary Table 2–5; Supplementary Figure 2 and 3). Although the bone samples identified as “cod” include several possible species (Table 2), most cod bone samples analyzed in this study were expected to be derived from Pacific cod (*Gadus macrocephalus*) because of their relatively larger vertebra diameters ( $10.4 \pm 4.2$  mm,  $n = 36$ ; Supplementary Table 1).

Alternatively, the higher  $\delta^{15}\text{N}$  values of cod in the Epi-Jomon compared with the other periods/phases (Table 3–5; Figure 3) could be attributed both to cultural changes in fishing practices and/or to behavioral changes in the fish themselves due to the cooling climate event occurring between the Epi-Jomon period and Initial Okhotsk phase (Leipe et al. 2018). There was a development in fishing gear, such as increased size in net sinkers and the appearance of several types of boats in the Okhotsk period (Amano 1977; Nomura & Utagawa 2003; Oba 1955), and this development might have enabled the Okhotsk people to catch smaller cod more efficiently. It is also possible that the conscious fishing effort of Epi-Jomon communities was biased toward large cod. Excavated fishing gear and faunal remains in the Epi-Jomon period suggest that capture of fish swimming near the ocean surface and small-



scale net-catching near the shore were the dominant types of fishing activities (Nishimoto 1985). If fish were mainly caught individually by the fisher's observation, rather than non-selectively by fixed nets or long lines as suggested for later periods, including the Okhotsk (Amano 1977; Nishimoto 1985), the size distribution of the caught fish would be biased toward larger individuals. A meta-analysis of excavated faunal remains and fishing tools in prehistoric Hokkaido indicates that larger halibut were selectively targeted particularly during the Epi-Jomon period, possibly as a status-building activity (Takase 2020), but such evidence is absent for cod.

It is possible that cod reflect the effect of changing cultural practices more prominently than other fish species. Pacific cod are opportunistic feeders and have no strong prey selectivity (Yamamura et al. 1993), and the fact that their average  $\delta^{15}\text{N}$  values were the highest among the analyzed five fish species (Figure 2) suggests higher trophic level prey compared with other fish species in lower trophic levels. Therefore, cod would have a more pronounced  $\delta^{15}\text{N}$  spectrum according to their body size as a result of greater availability of prey species at higher trophic levels.

The cooling climate event between the Epi-Jomon and Initial Okhotsk is another possible reason for the observed difference in cod  $\delta^{15}\text{N}$  values. Pollen records revealed a rapid cooling event affecting Rebun Island around 400 cal AD (Leipe et al. 2018), which marks the transition from the Epi-Jomon to the Initial Okhotsk and this might affect growth patterns, habitat use, and spawning behavior of cod. Previous studies indicated that ambient water temperature affects the availability of prey species and biomass in Pacific cod (Kihara & Shimada, 1988; Barbeaux et al. 2020), and growth rate and spawning habitat in Atlantic cod (Brander 1995; Pedersen & Jobling 1989; Sundby & Nakken 2008). Knowledge of behavioral changes in cod – and any concomitant isotopic changes – in response to change in water

temperature and how long the effect lasts in cod populations is lacking for the waters around Hokkaido specifically. However, it is possible that large cod no longer came close to the north Rebun shore during the spawning season due to changes in water temperature, making them less accessible to Okhotsk communities. Such an ecological change would decrease the  $\delta^{15}\text{N}$  values of cod caught. Also, possible changes in the migration route of cod due to the cooling event might result in lower  $\delta^{15}\text{N}$  values reflecting the isotopic signatures of different water mass with different nitrogen cycles (Montoya, 2007; Richert et al. 2015; Trueman et al., 2012). Sequential stable isotope analysis of fish vertebra for the reconstruction of migration routes in the marine isoscape (Matsubayashi et al. 2020) would be a useful method to investigate this possibility further.

Intensive human exploitation of marine resources, such as modern commercial fishing, sometimes alters marine food webs and decreases trophic level in higher predators (Ostrom et al. 2017). This may even be possible with small human populations intensively exploiting near-shore environments (Pestle 2013; Schulting et al. 2021). This phenomenon has been termed ‘fishing down the food web’ (Pauly et al. 1998). However, anthropogenic fishing pressure is unlikely to be the cause of the  $\delta^{15}\text{N}$  differences in cod observed in this study. Although the significant decrease in cod  $\delta^{15}\text{N}$  values already occurs in the Initial Okhotsk phase (Table 5), the amount of deposited fish bone during this phase appears to be substantially lower than in the Middle Okhotsk (Sato et al. 2015; Supplementary Figure 1). Furthermore, pollen records from Rebun Island show a noticeable deforestation and opening of the landscape started from ca. 480 cal AD and reached a maximum ca. 650–700 cal AD (Junno et al. 2021; Leipe et al. 2018), which corresponds to the archaeological layers of the Initial and Middle Okhotsk phases, respectively (Table 1). This evidence suggests relatively low human activity during the Initial phase compared with the Middle Okhotsk phase, at least

at this location. Therefore, differences in fishing practices and the cooling climate between the Epi-Jomon and Initial Okhotsk, as indicated by the archaeological and palynological evidence, respectively, provide a more plausible explanation.

#### 4.3 Chronological trends in Pacific herring

A similar diachronic trend of significantly higher  $\delta^{15}\text{N}$  values in the Epi-Jomon period can be seen in Pacific herring (Table 3–5; Figure 3). But, unlike cod, previous studies suggests that the trophic level, and thus  $\delta^{15}\text{N}$  value, of Atlantic herring (*C. harengus*) *decreases* with growth (Jennings et al. 2002). Thus, it could be that on average smaller Pacific herring were caught during the Epi-Jomon compared to the Middle Okhotsk phase. This difference in herring size can result both from changes in human fishing activities and Pacific herring's behavioral change due to the cooling climate event, as was the case with cod. Previous studies suggest that reproductive behaviors and migration patterns of Pacific herring can change due to changes in the marine environment, including water temperature (Hay et al. 2008; Tojo et al. 2007), though how these would affect stable isotope values is unknown. In fact, Pacific herring around Hokkaido experienced a large change in population and migration patterns in the 20th century due to changes in the marine ecosystem likely caused at least in part by intensive modern commercial fishing (Kobayashi et al. 2002; Nagasawa 2001). However, no significant difference in  $\delta^{15}\text{N}$  values of Pacific herring was evident between the Epi-Jomon and Initial or Final Okhotsk, and the  $\delta^{15}\text{N}$  difference between the Epi-Jomon and Middle Okhotsk is relatively small (0.6‰) compared with that seen in cod (1.3‰) (Table 5; Figure 3). Also, preliminary analysis revealed there was no significant chronological difference in the body size of Pacific herring inferred from the vertebral diameter (Supplementary Text; Supplementary Table 2–4; Supplementary Figure 2). Therefore, it is not clear whether larger

herring individuals were caught during the Middle Okhotsk phase compared with the Epi-Jomon period. Further research is needed to understand the cause of the significantly lower  $\delta^{15}\text{N}$  values of Pacific herring in the Middle Okhotsk phase.

#### 4.4 Chronological trends in rockfish

Although the  $\delta^{13}\text{C}$  values of rockfish from the Initial Okhotsk phase were significantly lower (0.6‰) than those from the Middle Okhotsk phase, no consistent chronological trend was seen. This result would be an artifact of taphonomic or sampling biases in the composition of rockfish species excavated. Since it was not possible to identify the species of rockfish solely from the morphological traits, it is possible that diverse rockfish species were included from each period. The influence of such a bias would be greatest in this group because it includes the greatest number of possible fish species that potentially show different stable isotope ratios (Table 2). It is essential to identify the rockfish taxa at greater resolution using DNA or proteomics (Bas et al. 2020; Richter et al. 2011, 2020) for further investigation of the observed difference in  $\delta^{13}\text{C}$  values of rockfish in this study.

#### 4.5 Other possible reasons for the isotopic difference

Other factors, such as changes in fishing location (i.e. inshore vs. offshore), isotopic baseline change, taphonomy, seasonal occupation, and the cooling event *per se*, can affect the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of fish bones, but they would not be the cause of the significant  $\delta^{15}\text{N}$  difference seen in cod and Pacific herring.

First, it seems that fishing locations did not change between the Epi-Jomon and Okhotsk periods, as there was no significant chronological difference in the  $\delta^{13}\text{C}$  values of the five fish species, except for rockfish from the Initial Okhotsk phase (Table 4; Figure 3). The  $\delta^{13}\text{C}$

values of inshore fish are typically higher than those of offshore or pelagic fish (Bas et al. 2020; France 1995; Hiwatari et al. 2011; Misarti et al. 2009), but no difference between the time periods was seen here. Although the Okhotsk had ocean-going vessels (Amano 1977; Nomura & Utagawa 2003; Oba 1955), and zooarchaeological evidence that suggests that Okhotsk communities did fish somewhat further from the coast than in the Epi-Jomon, relatively speaking both can still be considered as inshore fisheries (Nishimoto 1985).

Second, the baseline change in the  $\delta^{15}\text{N}$  value of the Sea of Japan during the Late Holocene was less evident in marine sediment cores (Khim et al. 2008) while that of the Okhotsk Sea shows the opposite direction of change (i.e., an increase in more recent periods: Khim et al. 2012).

Third, preservation of cod bones is typically poorer than that of other fish in several burial environments compared with plaice, herring, and whiting (Nicholson 1996), and it is possible that smaller cod bones, which would be expected to show lower  $\delta^{15}\text{N}$  values, were more prone to destruction in the older Epi-Jomon layers. However, this scenario does not explain the absence of cod bones showing higher  $\delta^{15}\text{N}$  values in the Okhotsk period (see Figure 3) and so is not a plausible explanation.

Fourth, occupation of Hamanaka 2 was more seasonal during the Epi-Jomon period, but more year-round occupation in the Okhotsk period (Kato 2015; Center for Ainu and Indigenous Studies 2017; Sakaguchi 2007), which might result in an exaggerated representation of seasonal isotopic variability (Gorbatenko et al. 2014). However, the lack of archaeological evidence for deeper water fishing suggests that Epi-Jomon and Okhotsk people opportunistically caught fish species that either migrated nearer the coast seasonally or were present year-round (Nishimoto 1978; Oba & Ohyi 1981). Since the season of fish migration does not drastically differ, seasonality of occupation should have no essential effect on

available fish populations for the Epi-Jomon and Okhotsk communities. Nonetheless, although the larger Pacific cod come closer to the coast during winter (Fisheries Agency 2019, 2020), archaeological evidence suggested that Hamanaka 2 was used mainly in summer and spring during the Epi-Jomon period (Kato 2015; Sakaguchi 2007). Therefore, seasonal occupation in this case would result in an opposite effect on the size of cod caught.

Finally, the rapid cooling event affecting Rebun Island during the transition period from the Epi-Jomon to the Initial Okhotsk (Leipe et al. 2018) might directly affect the stable isotope ratios of marine organisms through decreasing marine temperatures. However, no decrease in  $\delta^{13}\text{C}$  value – the expected signature of decreased water temperature (Barnes et al. 2009) – was found in any fish species, suggesting that the cooling event around 400 cal AD did not affect stable isotope ratios of fish caught off Rebun Island. While lower water temperature is correlated with a decrease in  $\delta^{15}\text{N}$  values (Jennings et al. 2003), the correlation between water temperature and stable isotope ratios is stronger in carbon than nitrogen (Barnes et al. 2009; Jennings et al. 2003). Therefore, the lack of any significant change in  $\delta^{13}\text{C}$  values argues strongly against the possibility of the cooling event *per se* as the cause of the observed significant change in cod  $\delta^{15}\text{N}$  values. It is also worth emphasising that the cooling trend was detected in a terrestrial pollen record (Leipe et al. 2018), whereas the region's marine system may have been buffered by the Kuroshio Current bringing warmer waters from the south.

#### 4.6 Implications

Stable isotope analysis employed in this study suggest that more cod from lower trophic levels and/or a lower  $\delta^{15}\text{N}$  environment were caught during the Okhotsk period compared with the Epi-Jomon period, and that this phenomenon was probably related to changes in fishing practices and/or to changes in cod behavior because of the climate cooling event

separating these periods. To validate these explanations further, future research might undertake: i) compound-specific stable isotope analysis of individual amino acids for more accurate estimation of trophic level (e.g., Chikaraishi et al. 2014; Ostrom et al. 2017); ii) comparison of body size of fish in different periods by collecting bone elements more suited as a body size proxy; iii) comparison of the number of individual fish caught in different periods by counting the number of identified specimens; iv) investigation of the impact of the terrestrial cooling trend on the marine environment. There was no conclusive chronological difference in the stable isotope ratios of other fish taxa, implying that fishing practices and the marine ecosystem were isotopically similar between Epi-Jomon and Okhotsk periods for these taxa.

This study shows that human fishing activities and marine ecosystem changes can be investigated more in detail by considering diachronic trends in carbon and nitrogen stable isotope ratios of several different fish species. Combining this framework of bulk stable isotope analysis with other zooarchaeological methods, such as estimation of the number of individual specimens, body size reconstruction, taxonomic identification using genomics or proteomics (Bas et al. 2020; Richter et al. 2011, 2020), and compound-specific stable isotope analysis (Chikaraishi et al. 2014; Matsubayashi et al. 2020; Ostrom et al. 2017) to estimate trophic levels more accurately can further elucidate the complex interplay between past fishing practices and changes in marine ecosystems. Such a study can be done on any archaeological sites that yield large fish bone deposits from different chronological periods.

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#### **Author contributions**

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Visualization: TTs

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810

811 **Figure captions**

812 **Figure 1.** Location of Rebun Island and major currents. Warm and cold currents are shown  
813 with red solid arrows and blue dotted arrows, respectively. Locations of the sediment cores  
814 mentioned in the main text are also shown with brown rectangles (GGC-5: Ternois et al. 2002;  
815 GH99-1239: Khim et al. 2008; GC9A: Khim et al. 2012).

816

817 **Figure 2.** Scatter plot and SIBER (Jackson et al. 2011) showing the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of  
818 fish species from different time periods: a) Epi-Jomon, b) Initial Okhotsk, c) Middle Okhotsk,  
819 and d) Fianl Okhotsk periods/phases. The standard ellipse ranges include approximately 40%  
820 of the data regardless of the sample size for each fish species (Jackson et al., 2011).

821

822 **Figure 3.** Boxplot and bee swarm plot showing the chronological difference in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
823 values of a) cod, b) flatfish, c) Okhotsk akta mackerel, d) Pacific herring, and e) rockfish.  
824 Significant differences were shown with an asterisk. Outlier is shown with gray points.

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