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Spatio-temporal distribution of hunter–gatherer archaeological sites in the Hokkaido region (northern Japan): An overview

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Abstract
The spatio-temporal distribution of archaeological sites in the Hokkaido region reveals hunter–gatherer population dynamics from the Upper Palaeolithic (>14,000 cal. yr BP) through the Neolithic/Jomon and Epi Jomom period (*c.* 14,000–1300 cal. yr BP) to the historic Ainu period (*c.* 700–100 cal. yr BP). It appears that most cultural transitions coincide with periods of climate and environmental change. However, this observation does not automatically mean causality and, therefore, other potential driving factors must be checked. The data support the hypothesis that Palaeolithic subsistence was (at least partly) based on terrestrial hunting. Paralleled by lateglacial climate amelioration, rising sea levels and a change in marine currents, this strategy shifted towards marine resources and plant exploitation at the beginning of the Jomon period. Along with continuous Holocene climate warming, Hokkaido's Neolithic Jomon population increased culminating in the Middle Jomon period (5000–4000 cal. yr BP). Simultaneously, Jomon subsistence underwent a process of diversification and intensification in exploitation of food resources. This practice probably allowed the persistence of the Middle Jomon culture beyond the Holocene temperature optimum (around 5000 cal. yr BP). Thereafter, the population decreased until the end of the Jomon culture accompanied by a trend towards cooler climate conditions and a shift in subsistence towards a more narrow range of food resources with increased hunting and less plant food. Population re-increased during the Satsumon/Okhotsk culture periods (1500–700 cal. yr BP), which may be the result of Okhotsk immigration because of climate cooling in the regions north of Hokkaido and enhanced inner-Hokkaido trade (between Satsumon and Okhotsk) and trade with communities outside Hokkaido. During the Ainu period (*c.* 700–100 cal. yr BP), site, and possibly population numbers, re-decreased significantly and concentrated in eastern Hokkaido. Whether social and/or climatic factors brought about the Satsumon–Ainu cultural transition and the observed change in population pattern remains unresolved.

Keywords
archaeological site distribution patterns, Hokkaido, Holocene climate change, human–environment interactions, hunter–gatherer cultures, Neolithic, Palaeolithic, quantitative archaeology

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Introduction

Hokkaido, the northernmost region of today's Japan, is one of the areas where foraging as dominant subsistence strategy persisted well into historic times. While agricultural societies started to develop during the first millennium BC in most of Central and Southern Japan, a hunter–gatherer life style was carried on by different cultures in Hokkaido until the immigration of Japanese farmers from Honshu in the second half of the 19th century (Hudson, 2013). In archaeological research, post-glacial hunter–gatherers are still often regarded as relatively static and marginal. However, recent work has revised this view suggesting that many hunter–gatherer populations had a rich and dynamic history (Bettinger, 2001). This also holds for the hunter–gatherer prehistory of Central Japan (Habu, 2004) and Hokkaido (Weber et al., 2013), which is marked by several cultural and behavioural transitions. Despite an abundant collection of archaeological material, the factors and mechanisms which triggered the shifts in the northern Japan hunter–gatherer populations remain insufficiently understood (Weber et al., 2013).

As one of the first scholars, VG Childe (1928) accounted for the central importance of climate forcing on prehistoric societies which was from the 1960s to the late 1970s further emphasised by the tradition of processual archaeologists (e.g. Binford, 1968; White, 1959). During the following three decades, archaeological

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research, on the other hand, assigned a rather subordinate role to climate and mostly acknowledged human agency as fundamental means by which cultural change was accomplished (Van de Noort, 2013). However, a growing number of studies has underlined the significance of past climate and environmental changes on different time scales as a factor driving cultural dynamics of both prehistoric foraging (e.g. Miyazuka, 2015; Müller et al., 2011; Tallavaara and Seppä, 2012; Williams et al., 2010) and agricultural (e.g. Haug et al., 2003; Leipe et al., 2014a, 2014b; Tarasov et al., 2006; Weiss, 1997; Zhang et al., 2007) communities.

To better understand the structure and dynamics of past cultures and to gain insights into the role of past climate and environmental changes, it is crucial to reconstruct demographic properties including, for example, spatio-temporal population distribution (i.e. migration patterns), population size and density (Renfrew, 2009; Riede, 2009). In addition to genetic information of human remains, archaeological site and non-genetic artefact data are frequently used as proxies in palaeodemography (Bocquet-Appel, 2008; Chamberlain, 2009). Numerous authors have performed time-series analyses of summed radiocarbon date frequencies to estimate changes in prehistoric population dynamics in different parts of the world (see Brown, 2015; Dolukhanov et al., 2002; Müller et al., 2014 and references therein). This approach requires a sufficiently large dataset of reliable ^{14}C dates. Although great progress has been made in expanding radiocarbon datasets since the 1960s (Riede, 2009), extensive sample sizes covering large time scales are not available for many study regions including Hokkaido. Alternatively, numerous authors have used archaeological site numbers, density and distribution to determine correlations between past changes in climate/environmental conditions and cultures (e.g. An et al., 2004; Li et al., 2009; Tarasov et al., 2006; Wagner et al., 2013; Yu et al., 2012; Zheng et al., 2008). Such approach appears to be particularly suitable for Japan, where a large amount of archaeological data, mostly obtained by extensive and well-organised rescue excavation work conducted during the last *c.* 50 years, is available (Habu and Fawcett, 2008). However, as far as we are aware, the only estimations and simulations of population density over different cultural periods (Initial Jomon–Haji) are confined to regions in Central Japan (Koyama, 1978, 1984; Koyama and Sugito, 1984).

Here, we use information on location and chronological classification of archaeological sites from Hokkaido published on a website operated by the Hokkaido Prefectural Board of Education in order to analyse the spatio-temporal patterns of site distribution from the Palaeolithic to the historic Ainu period. The results are compared with published palaeoenvironmental records from the study area and adjacent regions in order to check whether large-scale climate and environmental change could be potentially regarded as one of the driving forces affecting the prehistoric hunter–gatherer population of Hokkaido. This attempt has little to do with environmental determinism, though recent climate change clearly demonstrates a danger of underestimating its impact on humans in various landscapes and environmental zones. Other factors (e.g. demography, social conflicts, epidemics and migrations) should be tested against the archaeological site distribution data presented in this study. However, these tests are beyond the scope of the recent paper and the authors' expertise.

Environmental setting of the study region

The archaeological data analysed in this study are confined to the territory of Hokkaido Prefecture, which is bounded by the Sea of Japan, Sea of Okhotsk and Pacific Ocean (Figure 1a and b). The prefecture comprises the main island of Hokkaido and several smaller islands including Okushiri, Teuri, Yagishiri, Rishiri and Rebun and stretches between *c.* 45.5–41.4°N and 139.4–145.8°E. The climate is mainly influenced by ocean currents and the East Asian Monsoon system. The Tsushima Warm Current and the Oyashio Cold Current (Figure 1b) create a sea surface temperature gradient between the Sea of Japan to the west and the Pacific Ocean to the east. According to the Japan Oceanographical Data Center (Koizumi, 2008), along 42°N latitude modern surface water temperatures west of Hokkaido range from 19 to 20°C in summer to 6–7°C in winter, while sea surface temperatures east of Hokkaido reach 15–16°C in summer and about 1°C in winter. This ocean current influence also results in higher mean annual temperatures in the western (*c.* 6–10°C) in contrast to the eastern (*c.* 2–6°C) lowlands of Hokkaido (Figure 2).

During winter, Hokkaido is mainly influenced by cold continental air flow from northern to north-western directions controlled by the East Asian Winter Monsoon (EAWM) circulation. The Tsushima Warm Current promotes enhanced moisture uptake over the Sea of Japan, which results in heavy snow-falls especially in western Hokkaido (Kuroyanagi et al., 2006). The East Asian Summer Monsoon (EASM) circulation, which is driven by the air pressure gradient between the Asiatic Low over Siberia and the Hawaiian High over the northern Pacific Ocean, transports warm and moist air from southern to south-eastern directions.

Data and methods

Source and structure of archaeological data

The archaeological data utilised in this study are derived from a database ('Guide to the archaeological sites of the north') accessible via a website (http://www2.wagamachi-guide.com/hokkai_bunka) and operated by the Hokkaido Prefectural Board of Education (http://www.dokyoi.pref.hokkaido.lg.jp). The continuously updated database stores information on archaeological excavation sites of Hokkaido Prefecture. The website, which is available in Japanese language only, has implemented a dynamic topographic map to visualise the position of each archaeological site. It also allows users to query data by address, administrative level (e.g. city or village), name and type of excavation and/or archaeological period(s). In addition to this queryable data, geographic coordinates and elevation (in m a.s.l.), a description of the site surrounding and a list of recovered archaeological artefacts are assigned to each excavation site entry. The sites are chronologically classified into nine cultural periods comprising the Palaeolithic, Jomon (divided into Incipient, Initial, Early, Middle, Late and Final Jomon subperiods), Epi (i.e. Zoku) Jomon, (divided into first and second half), Satsumon (divided into first and second half and the Tobinitai subperiod), Okhotsk, historic Ainu, the Middle Ages (subdivided into first and second half), the early modern period and modern history. Some archaeological sites were classified by archaeologists as 'Undefined' because they could not be assigned confidently to one of the cultural/historical periods. Sites which belong to this category were not considered for further analysis.

Data processing, analysis and mapping

We organised all archaeological sites by cultural periodisation presented above. The database contains only two sites associated with the Incipient Jomon, which spans a relatively long time range (*c.* 14,000–10,000 cal. yr BP according to Weber et al., 2013). We therefore combined the Incipient and Initial Jomon into one subperiod. The subperiods of the Epi Jomon (including first and second half and undefined) and the Satsumon (including first and second half, Tobinitai and undefined) were respectively combined into one period. The cultural periods comprising the Middle Ages, early modern period and modern history are not discussed in this study. Accordingly, a total of 10 archaeological/cultural

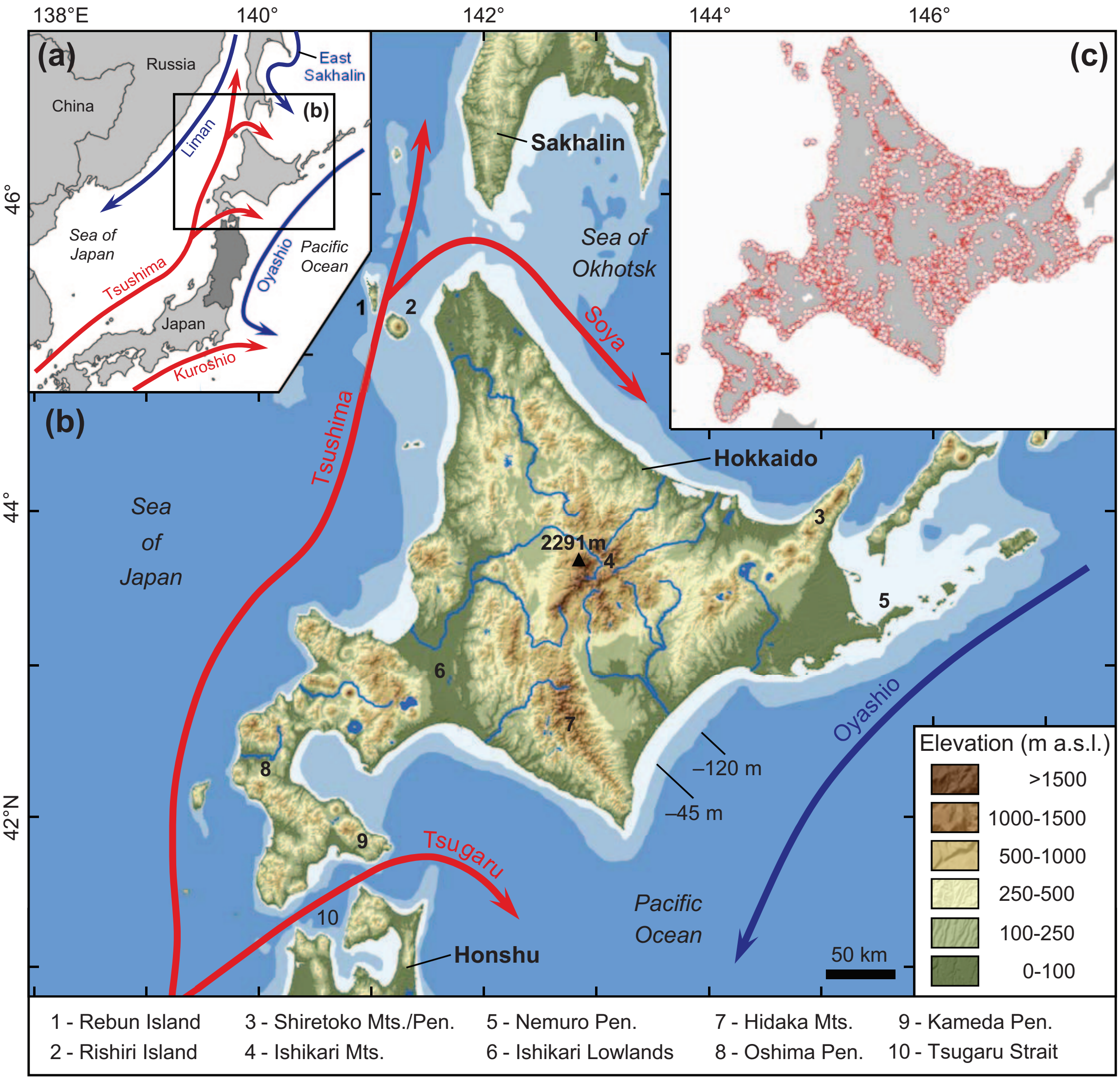


Figure 1. Map compilation illustrating (a) the location of Hokkaido Prefecture and the Tohoku region (dark grey area); (b) the study region's topography derived from Shuttle Radar Topography Mission (SRTM) v4.1 data (Jarvis et al., 2008), cold (blue) and warm (red) ocean currents of surrounding seas; and (c) the distribution of 12,056 archaeological sites extracted from the Hokkaido Prefectural Board of Education database (http://www2.wagamachi-guide.com/hokkai_bunka) and analysed in this study. Bathymetric isolines −120 and −45 m below modern sea level are representative of the sea levels at *c.* 20,000 cal. yr BP (according to Oba and Irino, 2012) and *c.* 11,000 cal. yr BP (according to Tanigawa et al., 2013), respectively, and drawn based on gridded General Bathymetry Chart of the Ocean (GEBCO_2014 Grid, http://www.gebco.net) data at 30 arc seconds resolution.

units, including the Palaeolithic, Incipient–Initial, Early, Middle, Late, Final and Epi Jomon, the Satsumon, Okhotsk and historic Ainu, were distinguished for our analyses.

The database does not provide absolute ages for the cultural periods because there is no commonly accepted absolute chronology for Hokkaido at present. Instead there are several chronologies proposed which partly differ significantly from each other in terms of the calendar age of the boundaries between archaeological cultures. The onset of permanent human presence (i.e. the Palaeolithic period) is not yet finally clarified. Especially the published chronology for the Neolithic (ceramic period) is largely based on pottery typologies. The establishment of an absolute chronology based on reliable radiocarbon dates is still in progress (Habu, 2014). To allow discussion of the spatio-temporal changes in site distribution in relation to palaeoenvironmental reconstructions, we have summarised a chronological framework of Hokkaido's prehistory (Figure 3) based on Hanihara et al. (2008), Habu (2014) and a review in Weber et al. (2013) using the BP (Before Present, with 'present' referring to 1950) time scale in cal. yr (calendar years). We decided to discuss changes observed at the transitions of successive archaeological cultures instead of using time-slices defined in calendar years. Therefore, absolute chronology is used only as a general frame for comparison with other archives and for discussion of environmental feedbacks. To strengthen the discussion of changes in the spatio-temporal development of archaeological sites, additional information about subsistence strategies and life style for each analysed cultural periods is provided (Figure 3).

For visual inspection of the spatio-temporal patterns of site distribution, we plotted the archaeological sites assigned to each of the 10 defined cultural periods on a simple base map using site geographic coordinates and ArcGIS Desktop v10.2 (Environmental Systems Research Institute (ESRI), 2013). To better identify the trends in spatial distribution of sites between two successive periods, we further determined the sites which were abandoned/newly established at each of the eight cultural transitions (from Palaeolithic/Incipient–Initial Jomon to Satsumon/Ainu).

For calculating the shortest linear distance between each archaeological site and the coastline we used the Proximity toolset in ArcGIS Desktop v10.2 (ESRI, 2013). The employed function considers the curvature of the earth spheroid, thus allowed accurate distance determination. The coastline (i.e. terrestrial

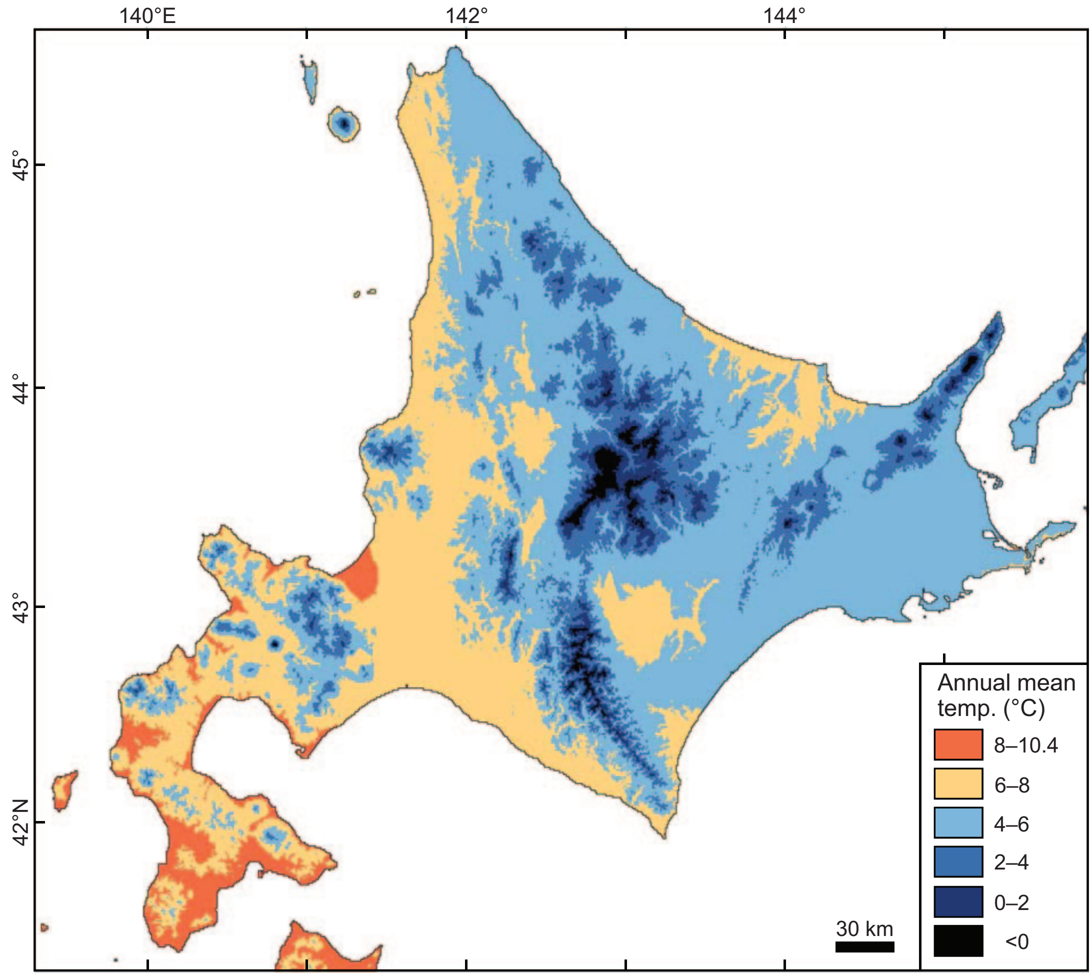


Figure 2. Mean annual temperature for Hokkaido based on a global high-resolution (30 arc seconds) surface climate dataset averaged over a 50-year (1950–2000) interval (Hijmans et al., 2005).

boundary) of Hokkaido Prefecture is spatially defined according to administrative zone data provided by the Japanese National Land Information Office (2014) in ESRI shapefile format. For better comparability, the distances are arranged in 14 categories for each defined period.

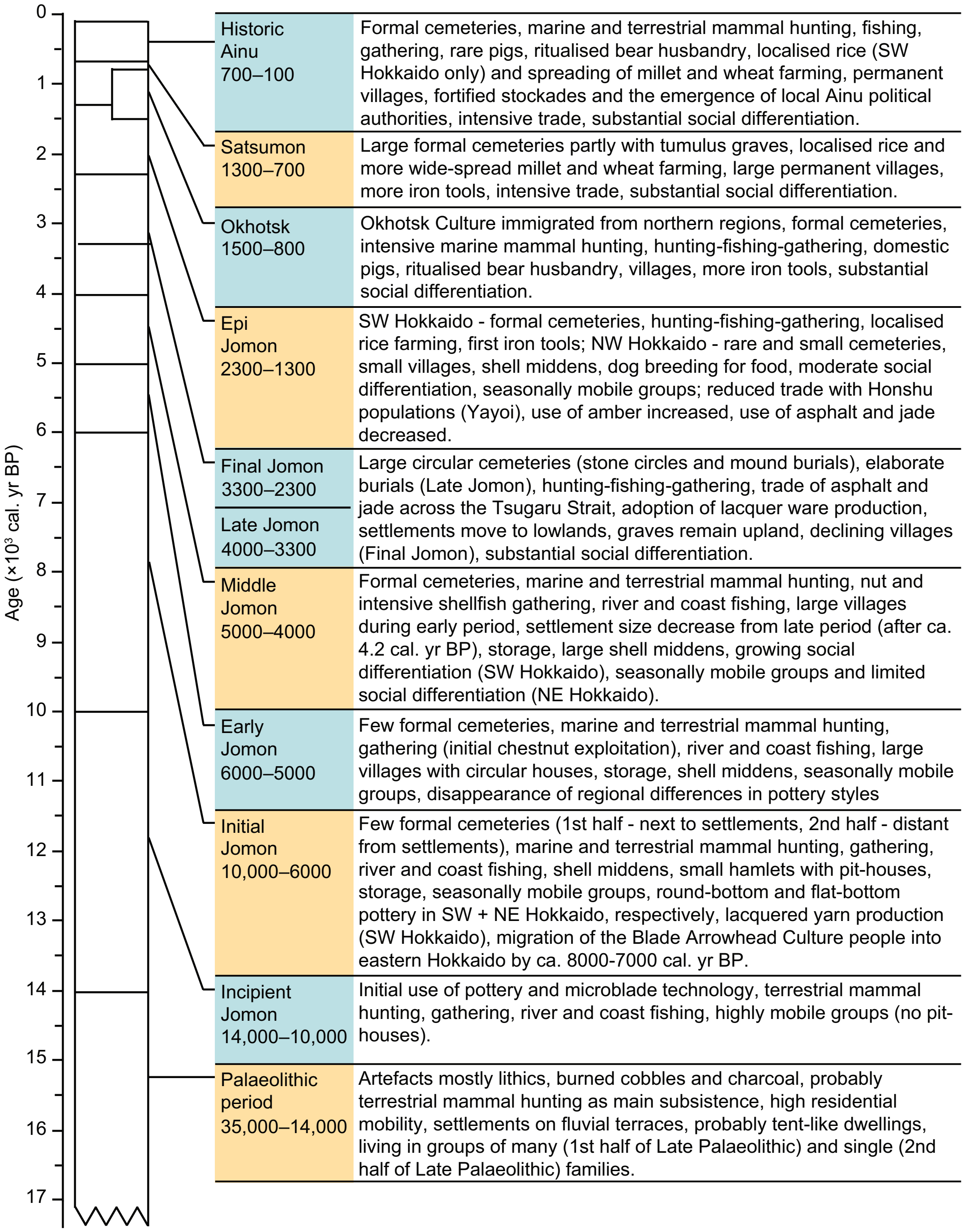
Results

We have extracted a total number of 12,056 archaeological sites (Figure 1c) from the online database (total content as per 20 November 2014) of which 7177 sites are assigned to the interval between the Palaeolithic and historic Ainu and are the subject of the current study (Figures 4 and 5). The archaeological sites are distributed over an altitudinal gradient between 1 and 2030 m a.s.l. However, with only 18 sites located above 500 m a.s.l., high-elevated sites are seldom. The site-specific linear distances to the sea organised in 14 categories vary from <1 to >90 km (Figures 4 and 5). Together with the number and distribution of sites during each cultural period (Figure 4) and at each cultural transition (Figure 5), the distances to the sea also show significant changes over the examined time interval. With 88.7% of all sites situated within 2 km from the modern coastline, the Okhotsk culture exhibits by far the highest affinity to the sea, and, in accordance to its relatively small area of occupation, the lowest number of sites ($n = 194$). Disregarding the Okhotsk culture, proximity to the sea is highest in the Epi Jomon and lowest in the Palaeolithic with 44.5% and 2.1% of sites located within 2 km from the modern coastline, respectively. The total number of sites ranges from 671 (Palaeolithic) to 2757 (Middle Jomon) falls again to *c.* 1500 during Epi Jomon and rises again to a maximum number during the Satsumon and Okhotsk culture period (Figure 6a). A more detailed account and discussion of the results presented in Figures 4–6 and the detected spatio-temporal patterns in site distribution is outlined in the following section.

Discussion

Hokkaido experienced a long hunter–gatherer prehistory which ranged from the Palaeolithic to the mid-19th century. We propose that the spatio-temporal analysis of archaeological sites may help to verify the postulated variability of hunter–gatherers in Hokkaido. Since the prehistoric cultures of Hokkaido did not go through major economic transformations (i.e. introduction of intensive crop cultivation, animal husbandry and metallurgy), we further assume that the identified dynamics in the cultural sequence (Figures 4, 5a and b) might be linked to changes in environmental conditions. However, plant cultivation in Hokkaido (at least in the southern and central parts) has been reported since the Epi Jomon and particularly during the following Satsumon culture (Crawford, 2011; Habu, 2004), suggesting an increased role of plant food during the last two millennia and likely influencing the archaeological site number and distribution. In the following discussion we try to address these two hypotheses.

The archaeological sites registered to date in the Board of Education database show a dense distribution throughout Hokkaido Prefecture (Figure 1c). Only in the high-elevated areas such as the Ishikari, Hidaka and Shiretoko Mountains, where environmental conditions are unfavourable and excavation activities have been rare, sites are largely absent. However, our results indicate substantial changes in the spatial distribution of sites over the



Historic Ainu 700–100	Formal cemeteries, marine and terrestrial mammal hunting, fishing, gathering, rare pigs, ritualised bear husbandry, localised rice (SW Hokkaido only) and spreading of millet and wheat farming, permanent villages, fortified stockades and the emergence of local Ainu political authorities, intensive trade, substantial social differentiation.
Satsumon 1300–700	Large formal cemeteries partly with tumulus graves, localised rice and more wide-spread millet and wheat farming, large permanent villages, more iron tools, intensive trade, substantial social differentiation.
Okhotsk 1500–800	Okhotsk Culture immigrated from northern regions, formal cemeteries, intensive marine mammal hunting, hunting-fishing-gathering, domestic pigs, ritualised bear husbandry, villages, more iron tools, substantial social differentiation.
Epi Jomon 2300–1300	SW Hokkaido - formal cemeteries, hunting-fishing-gathering, localised rice farming, first iron tools; NW Hokkaido - rare and small cemeteries, small villages, shell middens, dog breeding for food, moderate social differentiation, seasonally mobile groups; reduced trade with Honshu populations (Yayoi), use of amber increased, use of asphalt and jade decreased.
Final Jomon 3300–2300	Large circular cemeteries (stone circles and mound burials), elaborate burials (Late Jomon), hunting-fishing-gathering, trade of asphalt and jade across the Tsugaru Strait, adoption of lacquer ware production, settlements move to lowlands, graves remain upland, declining villages (Final Jomon), substantial social differentiation.
Late Jomon 4000–3300	
Middle Jomon 5000–4000	Formal cemeteries, marine and terrestrial mammal hunting, nut and intensive shellfish gathering, river and coast fishing, large villages during early period, settlement size decrease from late period (after ca. 4.2 cal. yr BP), storage, large shell middens, growing social differentiation (SW Hokkaido), seasonally mobile groups and limited social differentiation (NE Hokkaido).
Early Jomon 6000–5000	Few formal cemeteries, marine and terrestrial mammal hunting, gathering (initial chestnut exploitation), river and coast fishing, large villages with circular houses, storage, shell middens, seasonally mobile groups, disappearance of regional differences in pottery styles
Initial Jomon 10,000–6000	Few formal cemeteries (1st half - next to settlements, 2nd half - distant from settlements), marine and terrestrial mammal hunting, gathering, river and coast fishing, shell middens, small hamlets with pit-houses, storage, seasonally mobile groups, round-bottom and flat-bottom pottery in SW + NE Hokkaido, respectively, lacquered yarn production (SW Hokkaido), migration of the Blade Arrowhead Culture people into eastern Hokkaido by ca. 8000-7000 cal. yr BP.
Incipient Jomon 14,000–10,000	Initial use of pottery and microblade technology, terrestrial mammal hunting, gathering, river and coast fishing, highly mobile groups (no pit-houses).
Palaeolithic period 35,000–14,000	Artefacts mostly lithics, burned cobbles and charcoal, probably terrestrial mammal hunting as main subsistence, high residential mobility, settlements on fluvial terraces, probably tent-like dwellings, living in groups of many (1st half of Late Palaeolithic) and single (2nd half of Late Palaeolithic) families.

Figure 3. Archaeological culture sequence of the Hokkaido region (according to Habu, 2014; Hanihara et al., 2008; Weber et al., 2013) including information on settlement structure and subsistence for the Incipient Jomon–historic Ainu period of Hokkaido (according to a review in Weber et al., 2013) and the Palaeolithic period of the whole of Japan (according to Inada, 2001, 2004).

represented time period. In the following, we discuss the major trends in archaeological site distribution patterns with reference to published environmental and climate reconstructions.

Palaeolithic/incipient–Initial Jomon transition

A total of 671 sites are associated with the Palaeolithic (Figure 6a). With regard to the relatively long time interval of the Palaeolithic (Figure 3), site numbers are low. The spatial distribution of the sites (Figure 4a) implies that human presence was mainly confined to inland areas. About 90% of all sites are located in a distance of >10 km from the modern coastline. Although solid archaeological evidence is very limited and inconclusive (e.g. Lake Nojiri Excavation Research Group, 2014), it is generally assumed that the megafauna, which inhabited the Japanese islands and represented a valuable energy-rich food source, was hunted by Palaeolithic people (Inada, 2004). On Hokkaido, fossil remains confirm the existence of a large land mammal fauna including *Mammuthus primigenius* (woolly mammoth), *Bison priscus* (steppe bison), *Palaeoloxodon naumanni* (Naumann's elephant) and *Sinomegaceros yabei* (Yabe's giant deer) (Iwase et al., 2012; Kawamura, 2007). Our findings corroborate the hypothesis that the subsistence of Palaeolithic populations was mainly based on terrestrial foods with a likely focus on (large) terrestrial mammals, and suggest that marine food resources did not play an important role. Although Palaeolithic coastal sites would be currently submerged because of the global sea level rise following the Last Glacial Maximum (Figures 1b and 6f), the distinctly low site frequencies between the modern coastline and the 10-km distance isoline suggests otherwise (Figure 4a). A possible reason for the

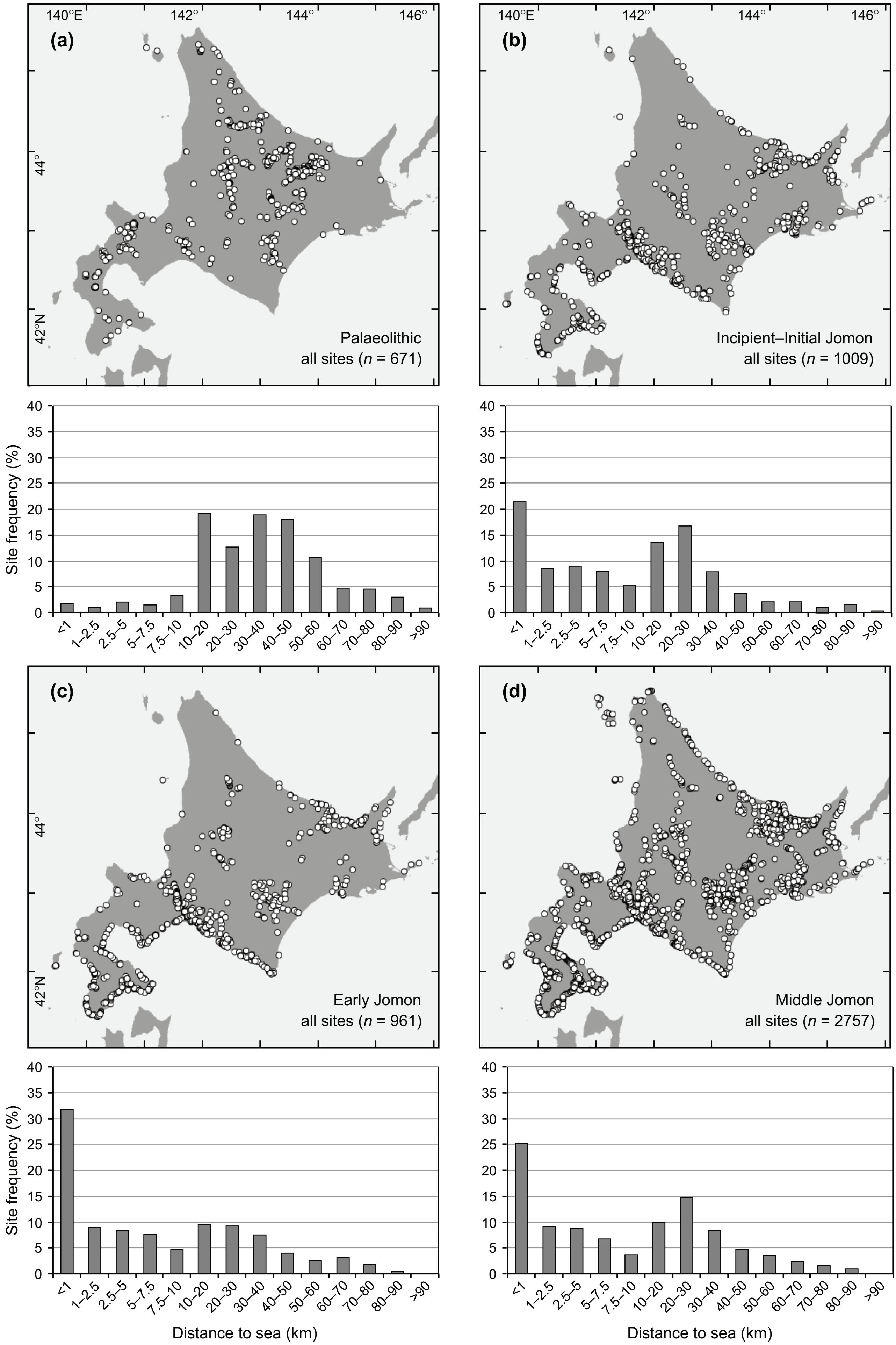
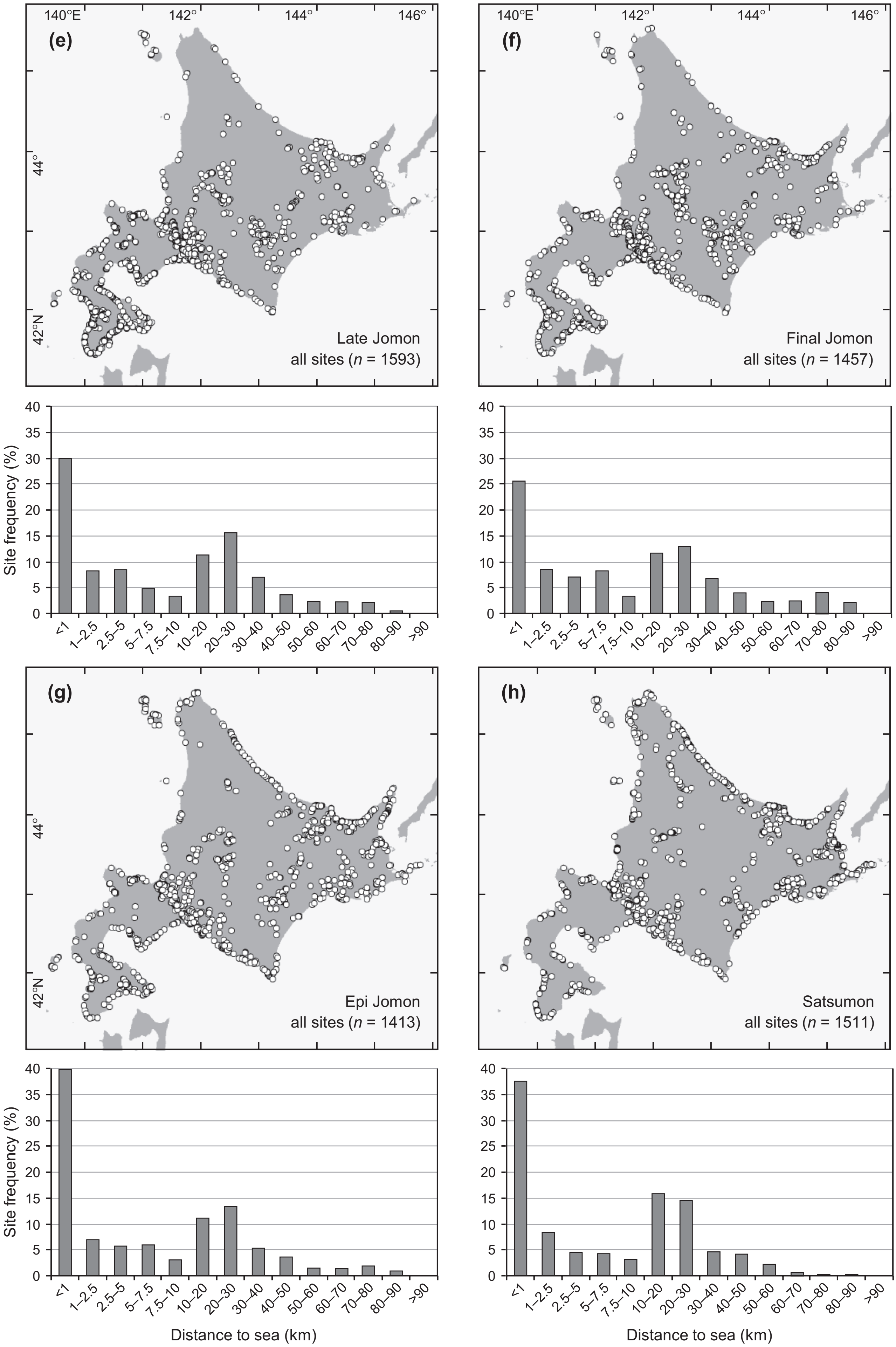


Figure 4. (Continued)



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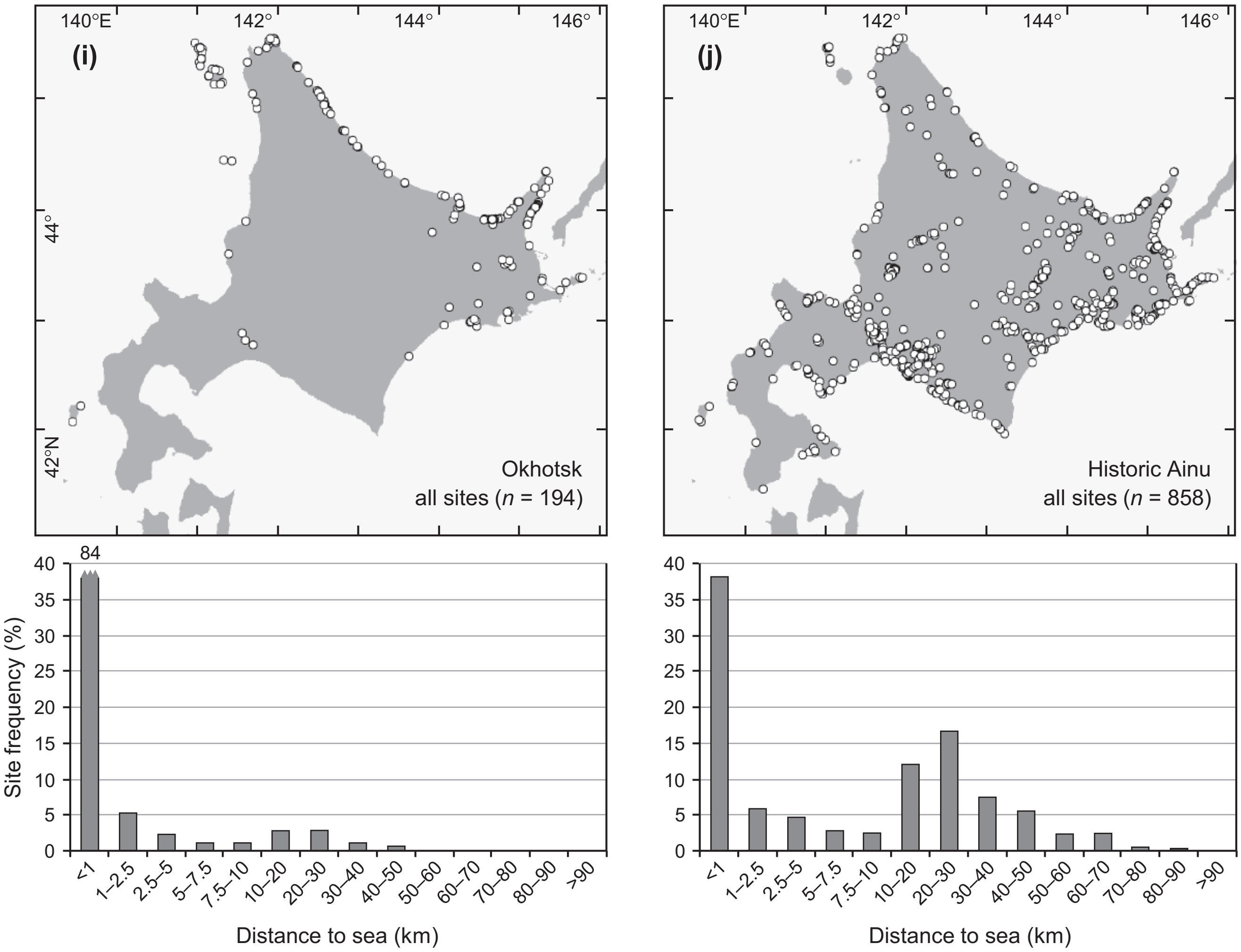
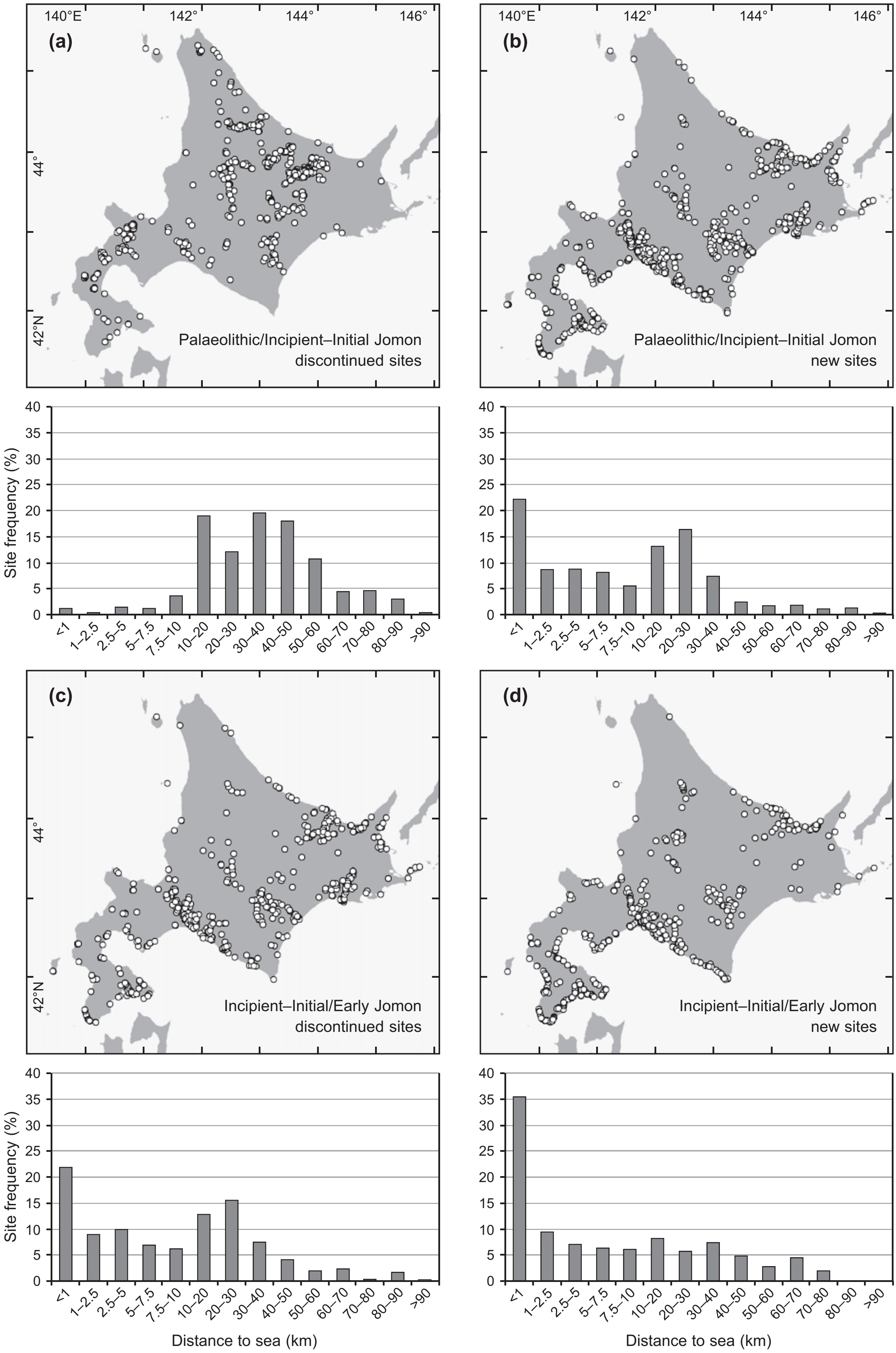


Figure 4. (a–j) Spatial distribution of archaeological sites and their linear distance to the modern coastline for each of the 10 analysed Hokkaido region cultural (sub)periods.

non-exploitation of marine resources of the rich grounds along the Japanese coastlines, which needs to be verified elsewhere, may be fluctuating (unstable) climate and environmental conditions in the more exposed coastal lowlands during the late Pleistocene glacial interval prior to *c*. 14,000 cal. yr BP. On the other hand, the extensively studied archaeological record of Europe also shows that the diet of Middle and Upper Palaeolithic hominids was mainly based on terrestrial gathering and hunting with only little evidence for marine resource exploitation (D'Errico, 2003).

The transition to the Incipient–Initial Jomon phase is marked by a slight increase in total site number (Figure 6a) and a substantial increase in sites which are located in direct vicinity (<1-km distance) to the modern coastline (Figure 5a and b). Contemporaneously, sites distant to the sea (>10 km) decreased significantly. It is remarkable that in this phase the site mean linear distance to the sea noticeably decreased reaching a level, which, with minor fluctuations, persists through the entire Neolithic period (Figure 6b). Altogether, these changes confirm the suggested shift in subsistence strategy including marine adaptation along with the emergence of the Jomon pottery period. Given the proposed onset of the Incipient Jomon period in Hokkaido (*c*. 14,000 cal. yr BP), the associated subsistence–settlement changes were likely related to a period of climate amelioration associated with the lateglacial Bølling/Allerød interstadial (Figure 6g) as reflected by the appearance of *Quercus* (Figure 6c), a temperate deciduous taxon on Rebun Island (Figure 1b), reconstructed higher winter temperature in northern Sakhalin (Figure 6d) and increased precipitation in south-eastern China (Figure 6e). Moreover, it appears that the maritime adaptation is not connected to the so-called Jomon transgression – the marine transgression in the region of Japan after the last glaciation – as suggested in earlier publications (e.g. Okada, 1998). Around 14 cal. yr BP sea level was still lower (*c*. –80 m) compared with modern conditions (Figure 6f). Another factor which should be considered is the need for Palaeolithic communities to diversify their food sources (e.g. shift in hunting targets to smaller sized terrestrial mammals) as a result of the disappearance of large terrestrial mammals. However, the timing and reason (climate change and/or human predation and overkill) of this late Pleistocene extinction/disappearance is still an issue of ongoing research (Iwase et al., 2012; Norton et al., 2010).

There is also a clear shift in site concentration from the northern to the southern part of Hokkaido (Figure 4b). This spatial change in human activities may indicate more favourable living conditions in the southern parts of Hokkaido during the lateglacial and early Holocene. One factor may be the climate which was probably milder in this region. Another explanation for the shift in subsistence strategy is that the waters off the southern coast are marked by an abundant marine fauna providing rich hunting and fishing grounds. This is indicated by a reconstructed pattern of marine currents which fundamentally differs from that of today (Figure 1a and b). As suggested by marine diatom records, the Oyashio Cold Current flowed through the Tsugaru Strait from *c*. 20,000–9000 cal. yr BP, when the Tsushima Warm Current was not yet fully established (Koizumi et al., 2006). This would have created nutrient-rich waters and a higher abundance of fish and sea mammals along the southern and south-eastern margin of



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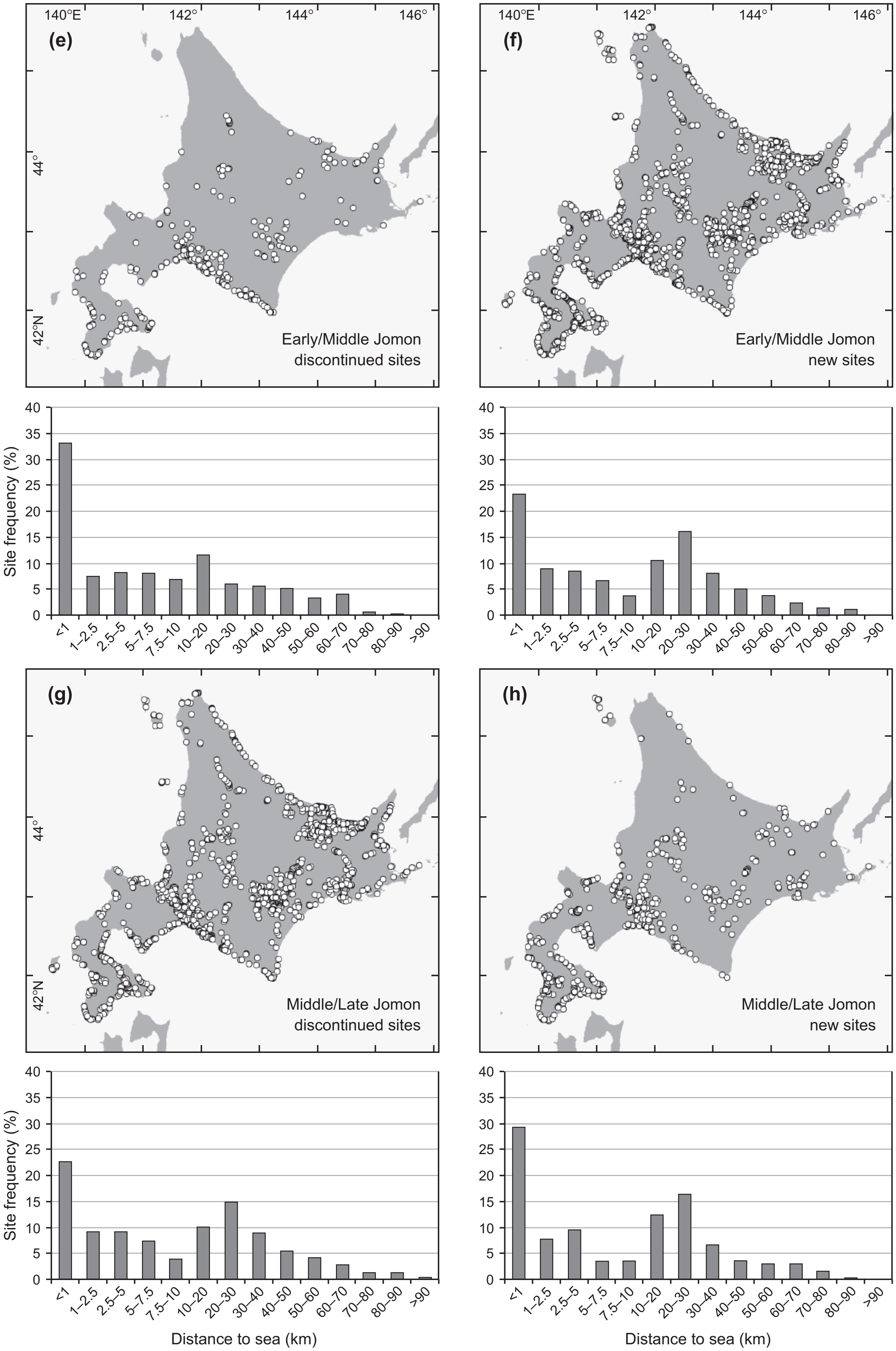

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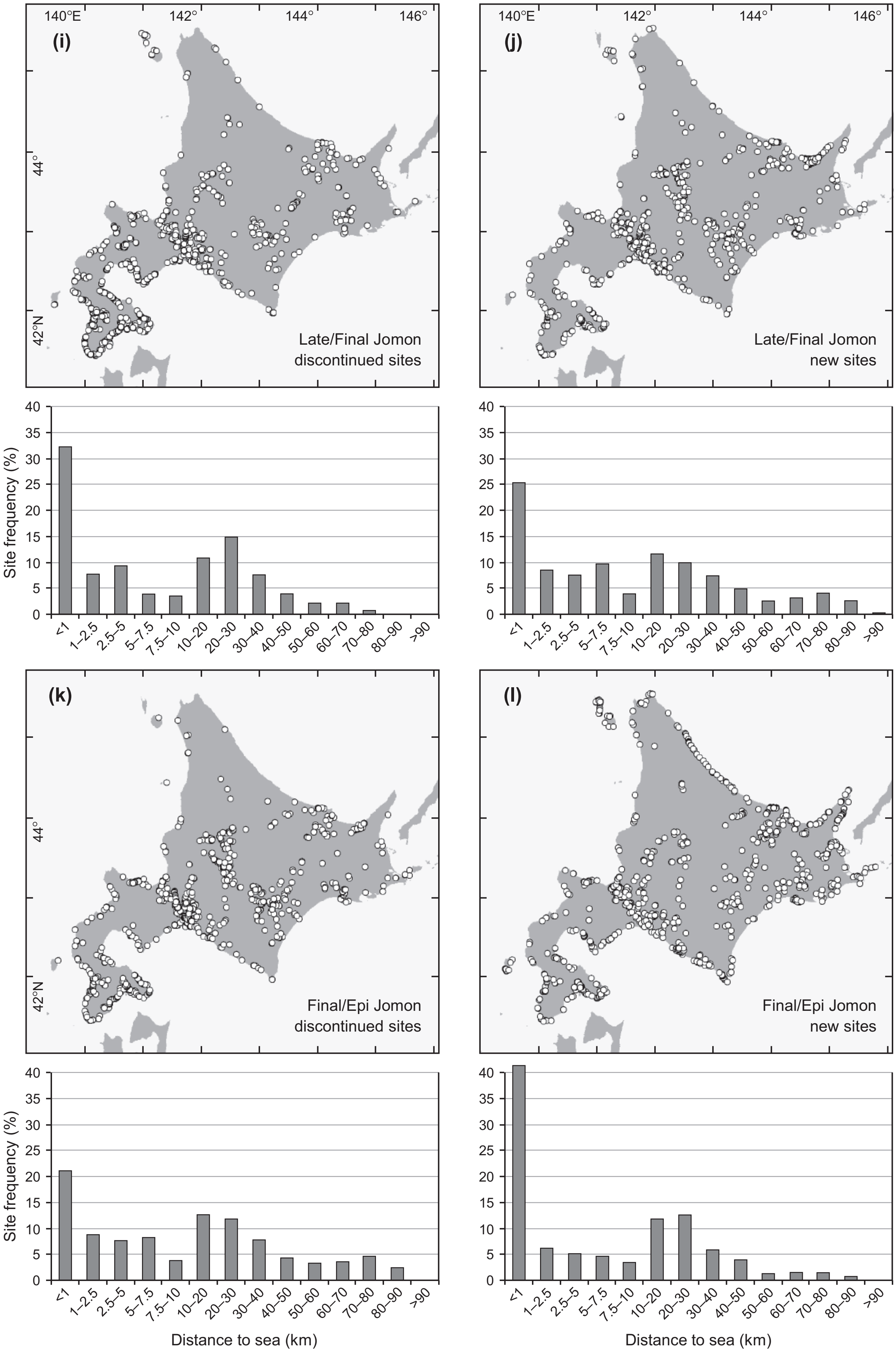

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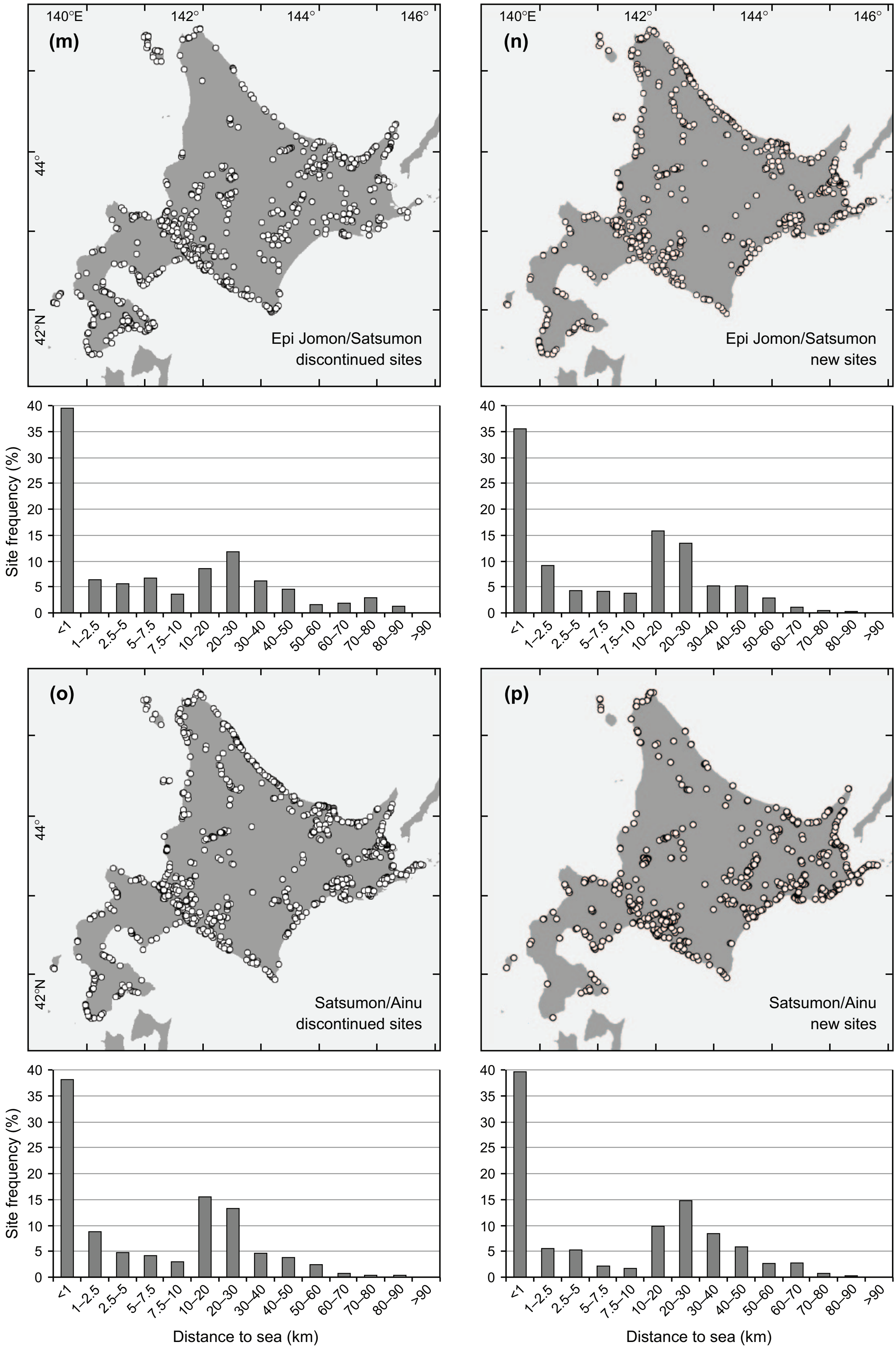

Figure 5. (a–p) Spatial distribution of abandoned and newly established archaeological sites for each of the eight analysed cultural transitions (Palaeolithic/Incipient–Initial Jomon to Satsumon/historic Ainu) of the Hokkaido region including site linear distance to the modern coastline.

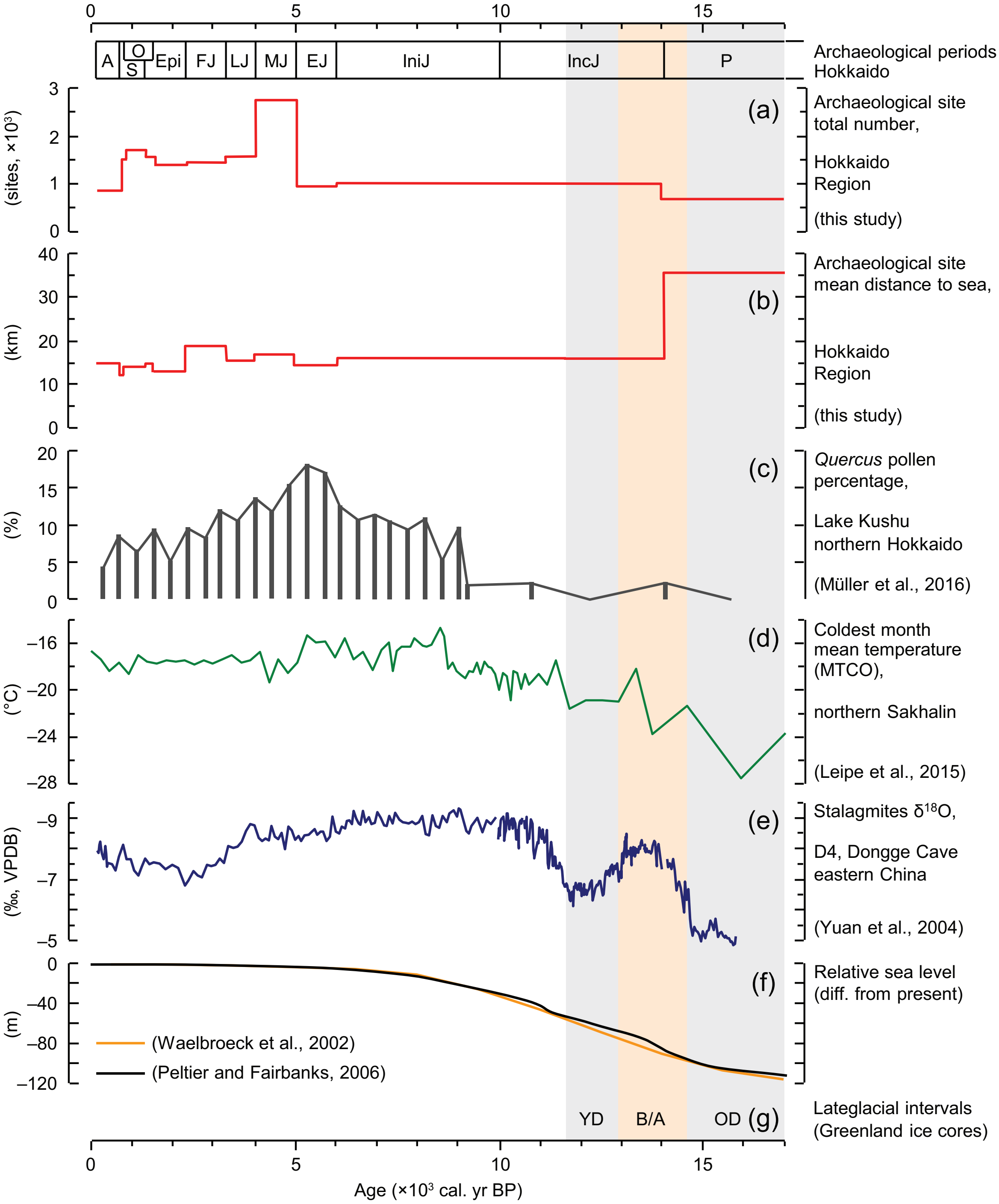

Figure 6. Chart compilation showing (a) the absolute number of archaeological sites (Hokkaido Prefecture) per period (this study); (b) the mean distance between archaeological sites (Hokkaido Prefecture) and the sea (this study); (c) the *Quercus* fossil pollen percentages of the RK12 sediment core from Lake Kushu, Rebun Island, northern Hokkaido (45.43°N, 141.03°E, 3 m a.s.l., according to Müller et al., 2016); (d) the modern analogue technique (MAT) reconstruction of the coldest month mean temperature based on the fossil pollen record from Khoe, northern Sakhalin (51.34°N, 142.14°E, 15 m a.s.l., according to Leipe et al., 2015); (e) the stalagmite δ^{18}O record D4 from Dongge cave (25.28°N, 108.08°E, 680 m a.s.l., according to Yuan et al., 2004) in China; (f) the reconstructed (Waelbroeck et al., 2002) and ICE-5G(VM2) model simulated (Peltier and Fairbanks, 2006) changes in relative global sea level; and (g) lateglacial intervals (OD: Oldest Dryas; B/A: Bølling/Allerød; YD: Younger Dryas) based on Greenland ice core isotope analyses (according to Lowe et al., 2008). Archaeological culture sequences of the Hokkaido region are illustrated according to Habu (2014), Hanihara et al. (2008) and Weber et al. (2013).

Hokkaido. Analyses of botanical macro remains from Initial Jomon sites on the Kameda Peninsula (Figure 1b) suggest that they also incorporated perennial shrubs, nuts and, to a lower degree, annual herbaceous plants into their diet (Crawford, 1983, 2011). A higher abundance of these plants because of more favourable climate (i.e. growing) conditions may be a supplementary reason for the concentration of sites in southern Hokkaido.

Early and Middle Jomon

Compared with the previous cultural sequence, the total site number of the Early Jomon subperiod appears to decrease (Figure 6a), but increases when taking into account its (relatively short) duration. The number of sites located in the vicinity of the sea further increases (Figures 4c, 5c and d). While a low site concentration persists in the northern part of the island, there is indication that human activity obviously also declined along the south-eastern coast (Figure 5c and d). The increase in sites continues into the Middle Jomon when the highest frequency is registered (Figure 6a). In this phase, all parts of Hokkaido, including the north, appear to be inhabited (Figure 4d). For the first time, the frequency of sites located within 1-km distance to the sea decreases in favour of more inland located sites (Figure 5e and f).

The described changes in site numbers and distribution well reflect the process of sedentarisation postulated by Habu (2014) for entire insular East Asia, which involves a diversification in the richness of food resources during the early stage followed by a phase of subsistence specialisation, where few food sources were intensively exploited and stored. The incorporation of new food sources (marine food) is seen in the 'coastal trend' in site distribution during the Incipient–Initial and Early Jomon phases. The broad abundance of sites along the coastlines as well as in the interior of Hokkaido during the subsequent Middle Jomon well illustrates a location-dependent subsistence specialisation (e.g. marine/inland fishing and hunting and exploitation of plants). Hokkaido's vegetation reacted on the Holocene climate amelioration by an increase in the population and growing area of acorn, chestnut, horse chestnut, walnut and hazelnut along with other temperate plants producing edible fruits, roots and berries, which are known as important food resource of Jomon people on Hokkaido and northern Honshu (Crawford, 2011; Habu, 2004; Yamada and Shibauchi, 1997). There is vague evidence of cultigens like *Fagopyrum esculentum* (buckwheat) during the Early Jomon and *Setaria italica* subsp. *italica* (foxtail millet) during the Middle Jomon from sites on the Kameda Peninsula (Crawford, 2008). Evidence for cultivation of *Echinochloa crus-galli* (barnyard grass) is more robust. This wild plant was widely used as a food source in Hokkaido (Crawford, 2011). The oldest remnants were found in sites which date to *c*. 9000–8700 cal. yr BP (Crawford, 1983). However, based on size measurements of seeds from the Kameda Peninsula, Crawford (2011) argues that it went through a selection (domestication-like) process during the Early and Middle Jomon phases. *Echinochloa esculenta/Echinochloautilis* (Japanese barnyard millet) – a species that is cultivated on a small scale in the cold climates of Japan, China and Korea – is believed to have been domesticated from *E. crus-galli* as early as 4000 years ago in Japan (Hilu, 1994). The development of site numbers and distribution from the Incipient–Initial to Middle Jomon well agrees with the contemporaneous trend from weak local ecological disturbance with few exploited plants to a greater degree of disturbance marked by a higher number of used annual and perennial weedy and biennial plants as put forward by Crawford (1997) and supported by archaeological excavations.

The development from Initial to Middle Jomon is accompanied by progressive climate amelioration indicated by the rising amount of *Quercus* pollen in the Lake Kushu (Rebun Island, northern Hokkaido region) sediments (Figure 6c). This well-dated sedimentary record (age model relies upon 57 AMS radiocarbon dates: Müller et al., 2016) shows that *Quercus* pollen percentages in the study area began to continuously increase from *c*. 9000 cal. yr BP, culminated around the Early/Middle Jomon transition (5000 cal. yr BP), and then gradually decreased. Correspondingly, Igarashi's (2013) review on Holocene pollen records from Hokkaido reveals a steady rise in *Quercus* pollen between 9000 and 8000 cal. yr BP in almost all regions of the island. This is broadly in line with the pollen-based quantitative reconstruction from northern Sakhalin (Leipe et al., 2015), which suggests Holocene winter temperature optimum conditions for the interval *c*. 8500–5000 cal. yr BP (Figure 6d) and justifies a major spread of temperate broadleaved woody plants on Sakhalin (Igarashi and Zharov, 2011).

The results of environmental reconstructions likely indicate that the trend towards more favourable climate conditions could have had a direct influence on socioeconomic changes registered in regional archaeological records. Among other advantages, the warmer climate promoted the enrichment of existing boreal flora with temperate and cool mixed forest communities, which in turn allowed a diversification of plant food resources and supported a rise in population as indicated by the increase in site numbers.

However, the millennium of 'highest flourishing' (Middle Jomon phase: *c*. 5000–4000 cal. yr BP) appears to be synchronous with the climate deterioration seen in the environmental proxies (Figure 6c and d). We propose that this possibly explains the combination of diversification and intensification in the use of natural plant resources especially recognised during the Middle Jomon phase. A similar development is seen in the cultural succession of the Bronze Age Harappan Civilisation (5200–3000 cal. yr BP; Possehl, 2002) of the Indian subcontinent. Recent palaeoenvironmental studies (Giosan et al., 2012; Leipe et al., 2014a) suggest that the Harappan culture emerged along a long-term trend of Indian Summer Monsoon (precipitation) weakening, which improved environmental stability on the Indus River alluvial plains favourable for agricultural activities. The Mature Harappan phase (4500–3900 cal. yr BP) was characterised by continuously decreasing summer monsoon precipitation superimposed by a centennial-scale pulse of North Atlantic controlled winter and spring aridity (Leipe et al., 2014a). The recognised establishment of urban centres (Possehl, 2002) and diversification of cultivated crops (Fuller and Madella, 2001; Weber, 2003) may be a response to this aridification (see Leipe et al., 2014a). It seems plausible that the recorded changes in subsistence in both cultures represent successful adaptation strategies to population growth and deteriorating climate conditions, which allowed persistence of cultural flourishing beyond the period of optimum climatic conditions. A comparable phenomenon was also discussed for northern and central China (Wagner et al., 2013), where the spatial and temporal distribution of archaeological sites during the Neolithic and Bronze Age reveals major increase in site numbers and social complexity about 4000 to 3000 cal. yr BP, that is, when temperature and precipitation curves show a decrease.

Late to Epi Jomon

The subsequent Late, Final and Epi Jomon stages are characterised by a continuous decline in total amount of sites. From the Middle Jomon with 2757 sites and the Epi Jomon with 1413 sites, the amount of sites halved (Figure 6a). For several regions in Central Japan, a shift in settlement size from relatively large sites with high numbers of pit-dwelling during the Middle Jomon to smaller sites during the Late and Final Jomon has been reported (Imamura, 1996; Muto, 2004). If we consider a similar change in settlement size for the Hokkaido region, the indicated population decline in Hokkaido was probably even more intensive. The site distribution maps (Figure 4e and f) show a habitation trend towards southern Hokkaido during the Late and Final Jomon with only few sites in the northern regions. Especially during the Late Jomon, sites concentrated in the southern and south-western part (Figures 4e and 5h). Assuming that the general modern pattern in ocean currents had been established before the Late Jomon, these areas were probably, like today (Figure 2), marked by higher mean temperatures than the northern and eastern regions. These features verify the common view (e.g. Okada, 2003) that changes in settlement patterns and numbers are a result of adaptation to reduced food resources caused by climate deterioration, which is documented by the decline in *Quercus* pollen percentages in northern Hokkaido (Figure 6c and Igarashi, 2013) and the onset of a pronounced Asian Summer Monsoon (ASM) weakening around 4000 cal. yr BP (Figure 6e). The transition from the Middle to Late Jomon probably marks a tipping point at which diversification and intensification of environmental exploitation could no longer outbalance the decline in food resources caused by climate deterioration. This long-term climate change may have been further enhanced by a hemispheric-scale phase of climate deterioration known as the 4.2 kyr BP event (Redman et al., 2007), which was identified to be linked to the decline of the Middle Jomon culture by Yasuda et al. (2004). This centennial-scale phase of North Atlantic cooling is also regarded as the main driver of the demise of different ancient civilisations including the Akkadian empire (e.g. DeMenocal, 2001), Egypt's Old Kingdom (e.g. Weiss, 1997) and Harappan Civilisation (e.g. Leipe et al., 2014a).

Further evidence for climate deterioration in northern Japan comes from the appearance of different types of stone circles (burial and/or ceremonial sites) on hill tops especially in south-western Hokkaido and the Tohoku region of northern Honshu (Figure 1a) during the Late Jomon stage. In addition, there was an increase in grave-goods (Nakamura, 1999) and ceramic and stone figurines (Bailey, 2009). These practices are interpreted as evidence for shifts in social organisation as a result of climate deterioration (Imamura, 1996; Kodama, 2003). When the decrease in food source abundance let to a higher mobility and smaller dispersed settlements, stone circles were probably multi-functional facilities serving as markers for burials, as monuments to consolidate group identity and/or as places for ritual practices (Kodama, 2003).

Compared with the Final Jomon, the frequency of sites located nearby (<1-km distance) the sea are significantly higher during the Epi Jomon (Figures 4g and 5l). Additionally, there is a clear shift in sites to northern Hokkaido, with particular focus on the northern Sea of Okhotsk coast. The Epi Jomon people, largely restricted to Hokkaido, are believed to represent the continuation of the Jomon culture sustaining a hunter–gatherer life style (Aikens and Higuchi, 1982). However, different from the preceding Late and Final Jomon, Epi Jomon communities are characterised by a higher mobility and a lower degree of plant exploitation. Plant food is mainly represented by nuts as well as shrub and vine fruits with no clear evidence for plant cultivation (Crawford, 1987, 2011; D'Andrea, 1995). The primary subsistence strategy was based on river fishing, with *Oncorhynchus* (salmon) spp. as the major prey, and maritime hunting (Fujimoto, 2004; Okada, 1998). The large amount of sites (*c*. 40%) situated in direct neighbourhood to the sea and probably to river estuaries well reflect these interpretations. Once more, there is evidence that climate conditions possibly played an important role on the revealed changes in human activities in Hokkaido. During the Epi Jomon, cool conditions in northern Hokkaido (Figure 6c) and a weak summer monsoon circulation in eastern Asia (Figure 6e) prevailed. The biome reconstruction method (Prentice et al., 1992, 1996) applied to fossil pollen data from Oshima Peninsula (SW Hokkaido) also indicates cooler conditions by lowered biome scores for temperate deciduous forest during the Epi Jomon phase (Leipe et al., 2013).

A possible analogue to the human–environment interactions during the Epi Jomon has been reported in the Lake Baikal region, which also represents a long sequence of hunter–gatherer cultures occupying coastal and forest-dominated environments. In the Cis-Baikal region, a cultural hiatus (*c*. 6850–6150 cal. yr BP), separating late Mesolithic and early Neolithic cultures from late Neolithic and Bronze Age cultures (Weber et al., 2002), coincided with an interval of major changes in regional vegetation (Bezrukova et al., 2010), climate (Tarasov et al., 2007) and atmospheric circulation (Kostrova et al., 2013). Hunter–gatherer groups who subsequently re-inhabited the region are characterised by a higher mobility, smaller groups and a broad subsistence strategy (Weber et al., 2002). These findings suggest that successful adaptation of hunter–gatherer cultures to increasing food shortage may be more generally characterised by changes in subsistence, mobility and social organisation as documented in both study regions.

Satsumon, Okhotsk and Ainu cultures

Regarding the sites' distances to the sea, there is overall continuity in relatively high frequencies of coastal sites from the Epi Jomon through to the Ainu culture (Figures 4g and j). A particularly high affinity to sea environments is suggested for the northern Hokkaido-affiliated Okhotsk culture with *c*. 84% of sites located within a distance of <1 km to the modern coastline (Figure 4i). Especially prominent is the rise in archaeological sites ($n = 1511$) during the Satsumon period. If we add the sites ($n = 194$) associated with the Okhotsk culture, which, during most of the time, coexisted with the Satsumon, the site frequency (1705 sites) is even higher. Many of the newly established Satsumon sites are located along the northern and north-eastern coastlines of Hokkaido, while more sites were abandoned than newly established on Oshima Peninsula (Figure 5m and n). Considering the increase in settlement size (Weber et al., 2013) in comparison to the Epi Jomon subperiod, the rise in site frequency may be satisfactorily interpreted as a rise in population.

Based on a fossil pollen record from Central Honshu, Sakaguchi (1983) inferred a phase of increased temperatures between *c*. 1200 and 650 cal. yr BP, which might be related to the 'Medieval Warm Period'. His findings are reflected in historical records from Central Japan pointing out hot summers between *c*. 1250 and 650 cal. yr BP and mild winters between 1050 and 650 cal. yr BP (Maejima and Tagami, 1986). However, such warmer phase is not yet recognised in the so far published pollen records from Hokkaido. A contrary climate development in the wider study region with decreased summer precipitation and cooler climate conditions is suggested by the $\delta^{18}O$ record from Dongge Cave (Yuan et al., 2004; Figure 6e) and the quantitative temperature reconstruction from Sakhalin (Leipe et al., 2015; Figure 6d), respectively. A possible explanation for the recorded increase in archaeological sites may be a population rise because of immigration from northern Honshu. As suggested by different cultural traits (e.g. pit-dwellings and pottery types) in the Hokkaido archaeological record, there was a strong influence on the Satsumon culture by the 'final Kofun' of the Tohoku region (Imamura, 1996; Muto, 2004). The latter culture is believed to have been forced to migrate towards the north by territorial claims of the first state in south-western Japan (Crawford, 2011; Yokoyama, 1990). This could also explain the abundant remains of a variety of crops – including *Hordeum vulgare* (barley), *Triticum* (wheat), *Setaria italica* (foxtail millet), *Panicum miliaceum* (broomcorn millet), *Fagopyrum esculentum* (buckwheat), *Cucumis melo* (melon), *Linum usitatissimum* (flax) and *Glycine max* (soybean) – found in Satsumon sites (Crawford, 2011; Yamada, 1993). Although agricultural activities were largely limited to south-western Hokkaido (Imamura, 1996), recent finds of charred barley seeds in Okhotsk cultural layers on Rebun Island (Müller et al., 2016) suggest that the exchange of agricultural goods against products gained by hunter–gatherers in the north should not be excluded and possibly contributed to the wealth of the Hokkaido population in general. In the north-eastern regions, the main subsistence strategies remained the same as those of the preceding Epi Jomon (i.e. fishing, hunting and gathering). If these findings are correct, it appears that the Tohoku immigrants pushed the local Epi Jomon population to northern and north-eastern Hokkaido (Figures 4g, h, 5m and n) and settled the climatically more favourable south-western regions (Figure 2).

About two centuries prior to the emergence of the Satsumon, the Okhotsk culture started to spread from Rebun and Rishiri islands along the north-eastern Hokkaido coastline towards Nemuro Peninsula and the southern Kuril Islands. Artefacts like pottery, iron and bone tools (Muto, 2004) as well as phylogenetic studies (Sato et al., 2007) suggest that this culture has its origins in the region of the lower Amur River (Russian Far East). Although domesticated pigs, dogs and crops (e.g. *Hordeum* *vulgare* and *Setaria italica*) and different wild plants were also used as a food source (Amano, 2003; Crawford, 2011), their major subsistence activities (marine fishing and especially sea mammal hunting) are well reflected in the coastal distribution of sites (Figure 4i). A reason for this southward migration via Sakhalin into the northern and eastern coastal region of Hokkaido may have been an increase in sea ice extent in the Sea of Okhotsk on a temporal (longer sea ice season) and/or spatial scale. Indeed, a general reduction in surface temperature of the Sea of Okhotsk during the late Holocene is suggested by a marine alkenone record from the south-eastern Sea of Okhotsk reflecting influx of cold water masses from the North Pacific (Max et al., 2012). Additionally, based on marine diatom assemblages from the south-central Sea of Okhotsk, Koizumi et al. (2003) inferred a cold stage characterised by sea ice development *c*. 1800–1300 cal. yr BP. An opposite (i.e. warming) trend for the late Holocene based on another alkenone sea surface temperature record from off the northern tip of Shiretoko Peninsula (Harada et al., 2006) was proposed for the south-western end of the Sea of Okhotsk indicating a stronger influence of the generally warmer Sea of Japan via the Soya Warm Current (Max et al., 2012; Figure 1b). Even if such seasonally extended sea ice cover may have led to increased pinniped productivity and enhanced hunting conditions as proposed by Yamaura (1998), it would have greatly hampered winter fishing, which is also regarded important for pig feeding (Hudson, 2004), and whale hunting.

The relatively high total number of archaeological sites which likely reflect increased population numbers in Hokkaido during the Satsumon and Okhotsk periods might be the result of trade activities which likely led to the development of a certain wealth among Hokkaido's hunter–gatherers. Since the Epi Jomon, there is indication by the presence of rice, iron tools, glass and stone beads for trade activities with Honshu (Hudson, 2004). During the Satsumon, who had much cultural traits in common with contemporary Honshu people, it seems that salmon was an important good in the trade with Honshu (Segawa, 1989). The Okhotsk culture is known for its trade relation towards the north and south. Goods like iron, bronze, coins and jasper were obtained from outside the Okhotsk domain (Amano et al., 2013; Kikuchi, 1986) in exchange with sea mammal furs and walrus ivory (Kato, 1975; Yamaura, 1998). However, that trade played an important role in the Okhotsk culture is still not universally accepted (see discussion in Hudson, 2004).

The last stage of Hokkaido's hunter–gatherer sequence is represented by the (historic) Ainu. Today, it is widely accepted that the Ainu emerged from the amalgamation of the Okhotsk and Satsumon cultures (Utagawa, 2002). The transition to the Ainu culture period is marked by a substantial reduction in sites ($n=858$; Figure 6a), which is also clearly traceable in the site distribution maps (Figure 4h and j). An interesting feature is that a large amount of sites have been left abandoned in both northern and south-western Hokkaido (Figure 5o and p). The main concentration centres of archaeological sites are now found in the eastern part, the Ishikari Lowlands and along the coast southwest of the Hidaka Mountains (Figure 4j). The onset of the Ainu culture coincides with the onset of the 'Little Ice Age' (LIA) (Lamb, 1965). This cool climate period is believed to have been of global scale (Broeker, 2001) with lowest temperatures between *c*. 550 and 250 cal. yr BP (Mann et al., 2009). LIA climate deterioration reflected by a weaker summer monsoon is also evident from north-eastern China (Chen et al., 2015). However, whether the LIA had a significant impact on Hokkaido's latest hunter–gatherer populations remains an open question. For a better understanding especially of the late Holocene cultural transitions, regional high-resolution and well-dated palaeoenvironmental records are essentially required.

Conclusion

The spatio-temporal analysis of a comprehensive set of archaeological sites (Palaeolithic to historic Ainu) from Hokkaido Prefecture stored in a web-published database reveals substantial changes in distribution patterns, which supports the prehistoric cultural classification established for this region. Comparison of the results with available palaeoclimate reconstructions suggests that the foraging societies were largely susceptible to natural climate and environmental changes.

There is evidence that the Jomon era was brought about by lateglacial climate amelioration. The separation of Hokkaido from the Asian landmass and the disappearance of large terrestrial mammals after the Last Glacial Maximum might have also played a role on the fundamental change in subsistence strategy. However, when and why the fauna vanished remains an open question. The commonly described expansion and decline of the Jomon culture and associated subsistence transformations are well reflected in the archaeological site data from Hokkaido.

Our results confirm a close relation between early–middle Holocene climate amelioration and the population increase during the Incipient–Middle Jomon and between late Holocene climate deterioration and the population decrease during the Late–Final Jomon. Temporal changes in site numbers and distribution patterns also underpin the assumption that the period of highest prosperity (Middle Jomon) coincides with the culmination of plant use and most diversified subsistence strategy, which subsequently declined towards the end of the Jomon era. The recorded diversification and intensification in subsistence during the Middle Jomon may reflect a successful adaptation strategy to population growth and climate cooling which allowed cultural persistence beyond the period of optimum climatic conditions (i.e. after *c*. 5000 cal. yr BP). Comparison of archaeological findings and palaeoclimate reconstructions in the environmentally similar Cis-Baikal and Hokkaido regions suggest that a shift to higher mobility, smaller groups and a broad subsistence is a universal adaptation strategy to increasing shortage in food resources.

While there is evidence that the southward migration of the Okhotsk culture was coincident with changing environmental conditions (i.e. enhanced sea ice extent in the Sea of Okhotsk), the emergence of the Satsumon culture may have been driven by human impact (i.e. immigration from northern Honshu). The re-increase in total site numbers and thus likely population during the Satsumon/Okhotsk cultures may indicate a period of prosperity derived from enhanced trade activities within the Hokkaido region and beyond. Although the spatio-temporal site distribution changes related to the Ainu culture are broadly coeval with the cold phase known as LIA, there is so far no clear indication how and to what extent it affected northern Japan. To further enhance our understanding of past human–environment interactions, there is a vital need for both establishing robust archaeological chronologies for northern Japan based on absolute dating techniques and regional well-dated high-resolution palaeo-climate and -environmental records.

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