

The impact of environmental change on the use of early pottery by East Asian hunter-gatherers

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The invention of pottery was a fundamental technological advancement with far-reaching economic and cultural consequences. Pottery containers first emerged in East Asia during the Late Pleistocene in a wide range of environmental settings but became particularly prominent and much more widely dispersed following climatic warming at the start of the Holocene. Some archaeologists argue that this increasing usage was driven by environmental factors, as warmer climates would have generated a wider range of terrestrial plant and animal resources that required processing in pottery. However, this hypothesis has never been directly tested. Here, in one of the largest studies of its kind, we conducted organic residue analysis of over 800 pottery vessels selected from 46 Late Pleistocene and Early Holocene sites located across the Japanese archipelago to identify their contents. Our results demonstrate that pottery had a strong association with the processing of aquatic resources, irrespective of the ecological setting. Contrary to expectations, this association remained stable even after the onset of Holocene warming, including in more southerly areas where expanding forests provided new opportunities for hunting and gathering. Nevertheless, the results indicate that a broader array of aquatic resources were processed in pottery after the start of the Holocene. We suggest this marks a significant change in the role of pottery of hunter-gatherers, corresponding to an increased volume of production, greater variation in forms and sizes, the rise of intensified fishing, the onset of shellfish exploitation and reduced residential mobility.

archaeology | early pottery | organic residue analysis | stable isotopes | Jōmon

The production and use of hard, fired earthen containers represents a key technological development in human history. From its prehistoric origins at the end of the last Ice Age, pottery became a fundamental tool for transforming, mixing, storing, and serving foodstuffs almost globally, and was only replaced relatively recently by metal containers. Understanding the motivations for the emergence and wider adoption of pottery is a key question in world prehistory. Ceramic vessels were first invented by hunter-gatherers in East Asia during the Late Pleistocene in Southern China, Japan and the Russian Far East (1–3) during glacial climatic conditions (*ca.* 18,000–16,000 cal BP). With climatic warming in the Early Holocene (*ca.* 11,500 cal BP), pottery was produced in much more substantial quantities and became more widely adopted (4). Organic residue analysis of East Asian early pottery (5–7) is beginning to elucidate the motivations that lay behind early pottery innovation and its more widespread adoption. However, so far there has been no systematic investigation of pottery use across the transition from the Pleistocene to the Holocene.

One of the best areas to investigate the development of ceramic technology is the Japanese archipelago due to the intensively studied sequence of hunter-gatherer pottery, known as Jōmon (meaning cord marked). The Jōmon ceramic sequences not only offer the chance to study potential continuity or change

in pottery function across the Pleistocene-Holocene transition (See SI Appendix, Figs. S1 and S2) but also offer scope to explore this process in a wide range of ecological settings (Fig. 1) because the main Japanese islands span a large latitudinal range (30°N–46°N), which ranged from steppe-tundra in the north to warm evergreen broadleaf forest in the south (Fig. 1). The transition from the Pleistocene to Holocene is clearly apparent in changes to the composition (see SI Appendix, Fig. S1) and extent of the pottery assemblages, although changes in volumes and sizes are more difficult to assess due to their highly fragmented nature. Firstly and most noticeably there is a substantial, 100-fold increase in the number of sherds recovered on early Initial Jōmon (Stage 4) sites compared to Final Incipient sites (Stage 3) across the archipelago (4). This cannot simply be explained by a greater intensity of occupation through time. Even large Incipient sites, such as Kuzuharazawa IV in Shizuoka, have less than a thousand sherds where similarly sized Initial Jōmon sites, such as Nakano B in Hokkaido or Jozuka in Kyushu have yielded tens to hundreds of thousands with the ratio of potsherd to other artefacts also dramatically increasing (8). Secondly, clearly defined regional styles and manufacturing techniques emerge in the Early Holocene that are thought to reflect a greater integration of production and use.

The emergence of regional pottery styles and greater scale of production corresponds to transformation of the local environment in many areas. These include the expansion of broadleaf forests, particularly in Southern Japan, (Fig. 1) with increased

Significance

The motivations for the widespread adoption of pottery is a key theme in world prehistory and is often linked with climate warming at the start of the Holocene. Through organic residue analysis, we investigated the contents of >800 ceramic samples from across the Japanese archipelago, a unique assemblage that transcends the Pleistocene-Holocene boundary. Against our expectations we found that pottery use did not fundamentally change in the Early Holocene. Instead aquatic resources dominated in both periods regardless of the environmental setting. Nevertheless, we found that a broader range of aquatic foods were processed in Early Holocene vessels corresponding to increased ceramic production, reduced mobility, intensified fishing and the start of significant shellfish gathering at this time.

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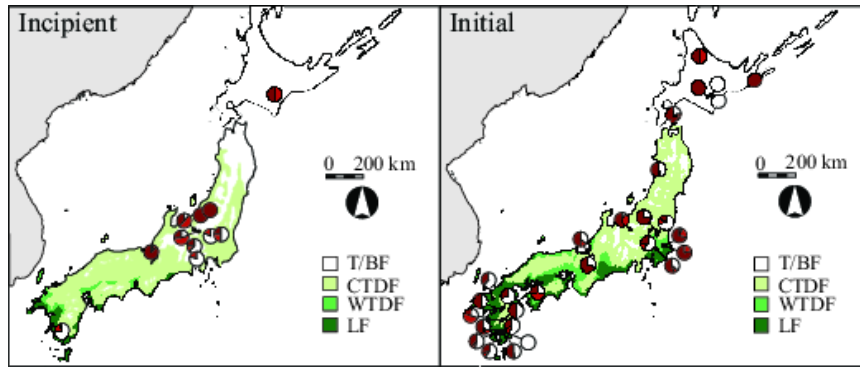


Fig. 1. Locations of the sampling sites, distributions of the aquatic biomarkers/phytanic acid SRR ratios (from Table 1) and change in vegetation cover (9, 10) across the Japanese archipelago from the Late Pleistocene/Incipient Jōmon (A) to Early Holocene/Initial Jōmon (B). The maps account for changes in sea level across these periods (44). Key: Dark red, complete suite of aquatic biomarkers and/or phytanic acid SRR ratio >75.5%; Red, partial suite of aquatic biomarkers and/or phytanic acid SRR ratio >75.5%; Open, absence of aquatic biomarkers and/or phytanic acid SRR ratio <75.5%; T/BF, tundra/boreal forest; CTDF, cool temperature deciduous forest; WTDF, warm temperature deciduous forest; LF, lucidophyllous forest.

Table 1. The frequency of aquatic derived residues associated with Incipient and Initial Jōmon pottery from Japan.

Period	# Samples (with lipid)	Full suite of aquatic biomarkers* % (n)	Partial suite of aquatic biomarkers** % (n)	Phytanic acid % (n)	>75.5% SSR-phytanic % (n)	Minimum number of aquatic vessels† % (n)
Incipient (ca. 14,460-11,310 cal BP)	179 (156)	30.8% (48)	7.1% (11)	93.6% (146)	43.6% (68)	46.8% (73)
Initial (ca. 11,500-8,000 cal BP)	622 (566)	10.8% (61)	6.9% (39)	77.0% (436)	42.0% (238)	45.2% (256)
Total	801 (722)	15.1% (109)	6.9% (50)	80.6% (582)	42.4% (306)	45.6% (329)

* Presence of C_{18} and C_{20} APAAs together with one of three isoprenoid fatty acids.

** Presence of C_{18} APAAs and TMTD.

† Having either phytanic acid SSR ratio >75.5% or containing aquatic biomarkers.

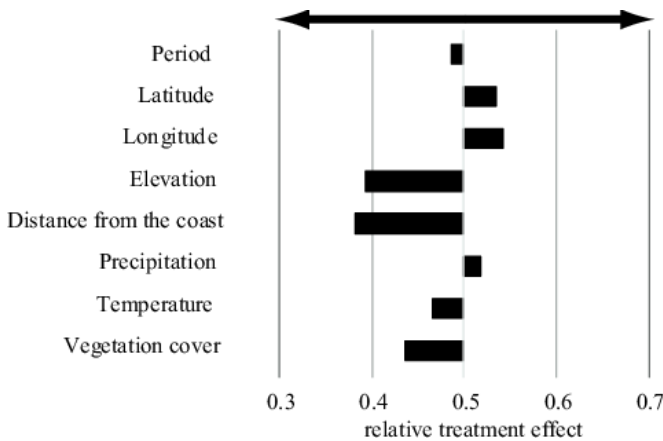


Fig. 2. Relative treatment effects (RTE) of different geographical and temporal variables on the presence of aquatic derived lipids in Incipient and Initial pottery using a non-parametric multivariate test. RTE of treatment "k" is defined as the probability that a randomly chosen subject from treatment "k" displays a higher response than a subject that is randomly chosen from any of the treatment groups, including treatment "k". The range of possible effect is 0.27 to 0.73.

opportunities for the exploitation of terrestrial resources, such as forest game, acorns and chestnuts, (9, 10) but also greater access to marine resources through expansion of the coastal shelf (11). Increased pottery production at this time is often seen as a response to the need for processing these newly available resources, as well as intensification and increased sedentism (12) in response to the ameliorated climate and changing coastline.

There is, however, little direct evidence to support this view. The analysis of animal and plant remains tentatively show a broadening of the available resources exploited in the Holocene (13) but the data are severely constrained due to generally poor organic preservation in Japan's prevailing acidic soils (14). Some of the best palaeoeconomic data derives from coastal and lacustrine shell middens that commence during the Initial Jōmon period and while these point to a broad economic base, with terrestrial plant and animal remains well represented in addition to fish remains and shell (e.g. (15, 16), it is unknown whether pottery use also broadened at this point.

Organic residue analysis provides the only approach for directly examining the contents of pottery vessels, and in the absence of quantifiable numbers of faunal and floral remains at the majority of sites (17), it is also a valuable tool for examining palaeoeconomic change through this critical period in East Asian prehistory. Previous studies have already shown that Incipient Jōmon vessels dating to the Late Pleistocene (ca. 15,000–11,500 cal BP) were predominantly used for processing aquatic species, particularly seasonally abundant marine and anadromous fish (5, 6). Produced in low numbers compared to other artefacts (4), it has been suggested that pottery did not have a major economic function at this time and may have been prestige items associated with the collective procurement of aquatic foods during periods of sedentism by otherwise largely mobile Pleistocene hunter-gatherer groups (5, 6, 18). In contrast, the only organic residue analysis of Initial Jōmon pottery is limited to a small number of sherds from the site of Torihama in Western Japan (5). It is therefore not known whether the function of pottery fundamentally changed in the Early Holocene, as a consequence of

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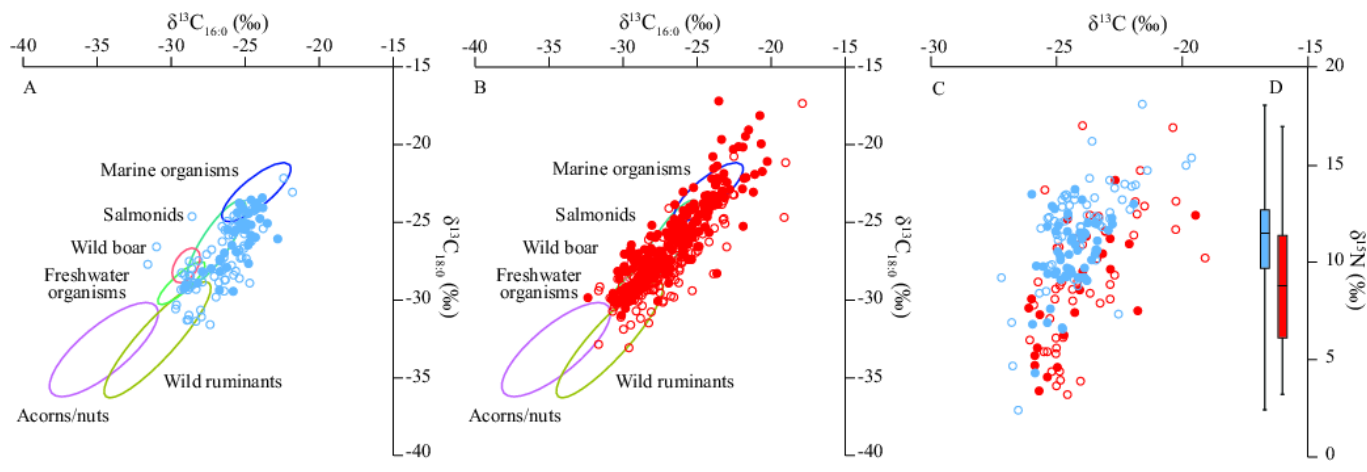


Fig. 3. Bulk and single compound stable isotope data from Late Pleistocene/Incipient Jōmon (blue) and Early Holocene/Initial Jōmon (red) ceramic vessels. $\delta^{13}\text{C}$ values of $\text{C}_{16:0}$ and $\text{C}_{18:0}$ *n*-alkanoic acids extracted from Late Pleistocene/Incipient (A) and Early Holocene/Initial (B) Jōmon pottery, which show a broadening of aquatic resources. The 95% confidence ellipses are based on modern Japanese authentic reference fats (5, 6, 21–23). Bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope data (C) obtained from carbonised residues adhering to Incipient and Initial Jōmon vessels (some data previously reported in (5, 6, 40, 41)). (D) Box plot of the $\delta^{15}\text{N}$ values, which also demonstrate a broadening of aquatic resources. Key: Filled circle, sample with aquatic biomarkers and/or phytanic acid SRR ratio >75.5%; Open circle, absence of aquatic biomarkers and/or phytanic acid SRR ratio <75.5%.

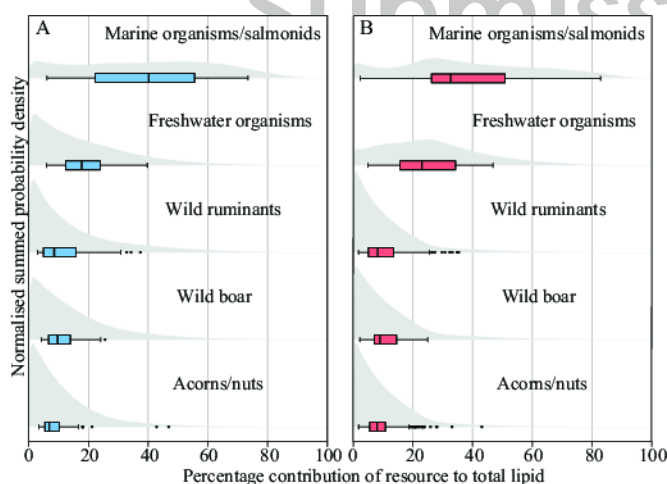


Fig. 4. Estimated percentage contributions of lipid from different food sources to (A) Late Pleistocene/Incipient and (B) Early Holocene/Initial Jōmon pottery using a concentration dependent mixing model. The model parameters are described in the SI Appendix. Box plots show the range of median % contributions estimated from each pot for each food source. The summed probability density distributions (grey) shows the relative likelihood of the contribution of each food resource summed across the two samples groups and normalised to account for differences in samples size.

the ameliorating climates, nor how responses varied across the archipelago.

To investigate further, here we present new chemical and isotopic analysis of 638 sherds and 77 charred deposits from 39 Incipient (*ca.* 14,460–11,310 cal BP) and Initial Jōmon sites (*ca.* 11,500–8,000 cal BP). The sites were chosen to examine variability over an ecological transect through Japan (see SI Appendix, Datasets S1 and S2), including inland and coastal localities (Fig. 1) at variable elevations (0–1,500 m). The majority of Incipient Jōmon sherds have cord-marked decoration corresponding to Phase 3a (*ca.* 14,460–12,000 cal BP) and 3b (*ca.* 12,030–11,310 cal BP) (see SI Appendix, Fig. S2) as defined by Taniguchi (12), with the majority corresponding to the Younger Dryas chronozone. When combined with previous data (5, 6), we have a comprehensive corpus of over 800 samples from 46 sites making this one of the largest studies of its kind. We hypothesised that en-

vironmental factors (e.g. site location, ecological zone, elevation) would largely determine the use of pottery with an increase in the processing of aquatic organisms in the cooler northern regions where terrestrial resources were less available. Further, we may expect to see a clear increase in oil rich plant products, such as nuts and seeds, and ruminant products, such as sika deer (*Cervus nippon*), and a shift away from aquatic resources in all but coastal sites at the start of the Holocene associated with climate amelioration.

Results and Discussion

Overall, interpretable amounts of lipids were readily extractable from fragments of Jōmon pottery and adhering charred deposits using an acid/methanol extraction procedure (see Methods Summary). In total, 94% (611/652) of the potsherds and 74% (111/149) of the carbonised deposits yielded appreciable quantities of lipids i.e. that were either above the minimum amount required for interpretation (>5 $\mu\text{g g}^{-1}$ for potsherds and >100 $\mu\text{g g}^{-1}$ for charred deposits) (6, 19) or contained distinctive lipids traceable to a specific source.

Evidence for the processing of aquatic foods

Although the procedure deployed is suitable for identifying fats, oils and waxes from a wide range of plant and animal products (20), a distinctive feature of many of the Jōmon sherds analysed was the presence of aquatic derived lipids. In total, 15.1% (109/722; Table 1) of the samples analysed satisfy the established criteria for the presence of ‘aquatic biomarkers’ in pottery (5, 20), which includes the presence of ω -(*o*-alkylphenyl) alkanolic acids (APAAs) with C_{18} and C_{20} carbon atoms and isoprenoid fatty acids (either phytanic, pristanic or 4,8,12-trimethyl tridecanoic acid (TMTD)). Notably the C_{20} APAAs are formed during the protracted heating of the $\text{C}_{20:\text{x}}$ mono- and polyunsaturated fatty acids which are only found in appreciable concentrations in freshwater and marine animals (21, 22). The presence of APAAs implies that the pottery vessels were subjected to prolonged heating (typically >270 $^{\circ}\text{C}$, >17h; (21, 22)), easily achieved through boiling or roasting of their contents, which is consistent with the presence of charred ‘foodcrusts’ on many vessels. Multi-branched isoprenoid fatty acids originate from the breakdown of phytol, a constituent of chlorophyll, but only accumulate at high concentrations in ruminant and aquatic animal tissues. In particular, TMTD is considered more of a characteristic of aquatic oils (23).

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409 These 'aquatic biomarker' estimates should be considered
410 as a minimum percentage, since APAAs are not always formed
411 during food preparation and both APAAs and isoprenoids may
412 be lost in the burial environment relative to other lipid molecules
413 with higher relative concentrations. A further 6.9% (50/722) have
414 C₁₈ APAAs and TMTD which are most likely aquatic in origin (i.e.
415 'partial aquatic biomarkers'; Table 1), while the majority of samples
416 (81%; 582/722) contained phytanic acid, the most frequent
417 isoprenoid acid. Among the resources available to Japanese Pleis-
418 tocene and Holocene hunter-gatherers, wild ruminants such as
419 sika deer offer the only other major source of phytanic acid other
420 than aquatic oils (7, 24). To distinguish these, we examined the
421 ratio of the two naturally occurring configurations, or diastere-
422 omers, of phytanic acid (3S,7R,11R,15-phytanic acid ~ SRR, and
423 3R,7R,11R,15-phytanic acid ~ RRR (see Methods Summary)).
424 Despite considerable overlap, the SRR isomer tends to dominate
425 in aquatic oils compared to ruminant fats (7, 24) and a SRR%
426 above 75.5% can be assigned to this source, using a conservative
427 limit (95% confidence). Over 52% (306/582) of the samples with
428 phytanic acid met this criteria, for the remainder the source of
429 phytanic acid is uncertain as it fell within both the aquatic and
430 ruminant range.

431 Using the SRR ratio and presence of aquatic biomarkers, we
432 conservatively assigned a minimum number of vessels analysed
433 that were used to process aquatic foods across the Pleistocene-
434 Holocene transition (Table 1). Overall, there was a striking
435 consistency in the use of pottery throughout the Japanese archipelago
436 regardless of period or environmental setting (Fig. 1). A non-
437 parametric multivariate inference test (25) showed significant
438 ($p < 0.001$) effects of period, latitude, longitude, elevation, distance
439 from the coast, precipitation, temperature and vegetation
440 cover on the frequency of aquatic resources in the vessels (Fig.
441 2; see SI Appendix). However, when the relative effects were
442 quantified (Fig. 2) the site's distance from the coast and its
443 elevation had the greatest effect but even this effect was not
444 strong (i.e. the relative effect value does not approach the min-
445 imum or maximum effect). The other environmental variables
446 and the period classification of the vessels had no or very weak
447 effects (0.43-0.54) on the presence/absence of aquatic derived
448 lipids. Pots were used to process aquatic resources at an equally
449 high frequency throughout the archipelago from Hokkaido and
450 Northern Honshu to Kyushu.

451 There was only a slight decrease in pottery used for process-
452 ing aquatic resources between the Incipient (47%, 73/156) and
453 Initial (45%, 256/566; Table 1) Jōmon. These results refute the
454 expectation of a dramatic change in the function of pottery at start
455 of the Holocene when terrestrial resources were more available,
456 even accounting for potential biases in site location between
457 periods (Fig. 2). These data corroborate what we have suggested
458 previously (5, 20) that pottery production for the exploitation of
459 aquatic resources was embedded as a cultural norm in the social
460 memories of these foragers.

461 Pottery from sites more distant from the palaeocoastline
462 tended to have fewer aquatic derived lipids but the effect was
463 marginal and co-varied with site elevation. Indeed, aquatic prod-
464 ucts were frequently identified in ceramics from inland riverine
465 and lacustrine sites (Fig. 1) most likely pointing to the exploita-
466 tion of freshwater resources and/or migratory species, such as
467 salmonids. To distinguish the source of these residues further we
468 examined the carbon isotope ($\delta^{13}\text{C}$) values of the major saturated
469 fatty acids (C_{16:0} and C_{18:0}) extracted from the sherds, and bulk
470 carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope values of any
471 adhering carbonised residues (see SI Appendix, Dataset S2).
472 In Fig. 3, the fatty acid data are compared with $\delta^{13}\text{C}$ values
473 obtained from modern authentic Japanese plants and animals
474 (5, 6, 26–28). These generally support the lipid biomarker data
475 with many vessels plotting in the reference ranges for aquatic

477 resources. Interestingly, there was only a weak negative corre-
478 lation between distance from the coast and the $\delta^{13}\text{C}_{16:0}$ value
479 (Spearman $\rho(560) = -0.25$ $p < 0.001$) and no correlation with the
480 bulk $\delta^{13}\text{C}$ value (Spearman $\rho(190) = 0.03$ $p = 0.6667$) as may have
481 been expected if marine resources were preferentially processed
482 at coastal sites compare to inland localities. This may be explained
483 by the exploitation of migratory fish, such as salmonids, which
484 have $\delta^{13}\text{C}$ values that approach the marine range (Fig. 3).

485 Fully marine species, beyond the isotopic range of reference
486 salmonids (Fig. 3; see SI Appendix, Dataset S3) were identified in
487 pottery from sites located >15 km from the prehistoric coastline,
488 the maximum logistical walking distance for a logistical day trip
489 (29), which suggests that aquatic resources were not only acquired
490 locally for direct consumption but could also have been preserved
491 (e.g. dried) and transported. These include an Incipient vessel
492 from Taisho 3 and 13 Initial vessels from Haizuka, Higashimyou,
493 Nishinojo, Nisshin 3 and Taisho 3. Although site elevation has
494 the greatest effect on the presence/absence of aquatic derived
495 lipids, even pottery from remote mountainous areas were also
496 used to process aquatic foods. At Yukura Cave (at elevation
497 of ca. 1534 m) almost half the vessels had residues typical of
498 salmonids with the nearest source, the Shinano river (30), located
499 ca. 15 km away. Conversely at these remote hunting sites and
500 more broadly in Japan's warmer forested areas, a surprisingly low
501 number of residues could be attributed to forest game species,
502 such as sika deer and wild boar (*Sus scrofa*) (Fig. 3), implying they
503 were processed in other ways.

504 There is also surprisingly limited data to suggest that plant
505 foods were processed in Incipient or Initial Jōmon pottery across
506 Japan. Low to trace amounts of leafy plant-derived lipids, includ-
507 ing phytosterol, long-chain even-numbered fatty acids or long-
508 chain odd-numbered alkanes, were present in some samples,
509 most notably at Kenshojo in Southern Kyushu (see SI Appendix,
510 Dataset S2). Isotopic analysis of the foodcrusts adhering to the
511 potsherds also generally had lower (<22) C:N atomic ratios
512 (mean = 12.0 ± 5.1) more typical of carbonised terrestrial animal
513 and marine tissues than plant remains (27) (See SI Appendix,
514 Dataset S2). Plant resources, particularly acorns and chestnuts,
515 and artefacts associated with plant processing are frequently
516 found on Incipient and Initial sites (9, 31–33) suggesting they were
517 an important feature of the Jōmon economy. While the organic
518 residue evidence cannot rule out the presence of plants in pottery
519 entirely, the data clearly show that Incipient and Initial Jōmon
520 vessels were not extensively used for this purpose. Rather we
521 contend that Incipient and Initial Jōmon hunter-gatherers had
522 a clear preference for preparing aquatic resources over terres-
523 trial animal and plant products in pottery. Moreover, we assert
524 that this cooking practice was pervasive over a wide range of
525 environmental settings and persistent through time and through
526 significant climate change.

527 *Holocene pottery used for processing of a wider array of aquatic* 528 *resources*

529 Although there is strong evidence that aquatic resources were
530 exploited in both periods we found evidence across the Japanese
531 archipelago of diversification in the types of aquatic foods pro-
532 cessed in the pottery at the start of the Holocene. A much
533 narrower range of $\delta^{13}\text{C}_{16:0}$ and $\delta^{13}\text{C}_{18:0}$ values were obtained from
534 Late Pleistocene (Incipient Jōmon) pottery when compared to
535 those from the Early Holocene (Initial Jōmon) (Figs. 2A and
536 2B). During the Incipient Jōmon, $\delta^{13}\text{C}_{16:0}$ and $\delta^{13}\text{C}_{18:0}$ values
537 are relatively homogenous i.e. have low variances ($\sigma^2 = 3.5$, $n =$
538 119, mean = -26.3%). Regardless of the geographic setting, the
539 majority of values fall within the ranges established from the
540 analysis of modern marine organisms and salmonids (Fig. 3A),
541 which was corroborated by the presence of aquatic biomarkers
542 in many of the samples. These data support the general model
543 proposed previously (6, 34, 35) that the earliest phases of pottery
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use are highly specialised and focused on seasonally available aquatic resources.

In contrast, the variance of $\delta^{13}\text{C}_{16:0}$ values significantly increased (Brown–Forsythe test $F(1,558)=10.42$ $p<0.005$) during the Initial Jōmon ($\sigma^2=6.9$, $n=441$, mean = -27.0‰ for $\text{C}_{16:0}$; Fig. 3B). This most likely reflects a broadening of the aquatic foods processed to encompass a greater range of both marine and freshwater species (Fig. 3B). The high frequency of the other aquatic derived lipids on Initial Jōmon sherds supports this contention but mixing with terrestrial animal and even plant resources, also relatively depleted in ^{13}C , cannot be ruled out entirely. In order to investigate the effects of mixing different resources in the vessels we applied a concentration dependent Bayesian mixing model (36) that used the $\delta^{13}\text{C}_{16:0}$, $\delta^{13}\text{C}_{18:0}$ and SRR% values as proxies, with priors based on the presence of isoprenoid and APAAs (see SI Appendix). This model was used to examine the likely probability of different proportions of lipids derived from plants (acorns and chestnuts), freshwater organisms (fish), wild boar, wild ruminants (sika deer) and marine organisms/salmonids to each pot. By summing the probabilities for each period and examining their densities (Fig. 4), only aquatic organisms can be reliably considered to have made a substantial contribution (i.e. $>25\%$ of total lipid) in either periods (Fig. 4) based on the assumptions used in the model. Noticeably, however, the percentage contribution of lipid from freshwater organisms is predicted to increase from the Incipient to Initial Jōmon (Fig. 4) consistent with a broadening of pottery use at this time.

Surprisingly few vessels contained substantial amounts of non-aquatic products. Ruminant, wild boar and acorn/chestnut were estimated by the model to have made a contribution of $>25\%$ in 21, 1 and 7 samples respectively. It should be noted that their contribution to the remaining vessels cannot be ruled out entirely; between 0 to 25% lipid contributions from non-aquatic sources were most likely, although depending on their lipid content, these could have had a greater relative contribution by total weight. Further distinction is not possible using the isotope approach and SRR% alone. Even where prior information from the biomarker evidence is deployed there is a high degree of equifinality regarding the source contributions.

A broadening of the range of aquatic resources processed in pottery during the Holocene and across the Japanese archipelago can also be seen from the bulk nitrogen ($\delta^{15}\text{N}$) stable isotope values of carbonised residues adhering to pottery (Fig. 3C and 3D). Nitrogen stable isotope values of charred deposits are often used to crudely distinguish between high trophic level aquatic resources and lower trophic level terrestrial organisms (37), although ^{15}N enrichment due to charring also needs to be accounted for (38, 39). In total, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were obtained on 157 samples from 21 sites (Fig. 3C), which were complemented with previously published data undertaken as part of AMS radiocarbon (^{14}C) dating programs (40, 41). As with $\delta^{13}\text{C}_{16:0}$, a broader range of nitrogen isotope values were obtained from the Initial Jōmon pottery (Incipient variance, $\sigma^2=5.6$, $n=119$; Initial variance, $\sigma^2=10.9$, $n=71$; Brown–Forsythe test $F(1,188)=13.49$ $p<0.005$). A decrease in $\delta^{15}\text{N}$ values (Fig. 3D) was also observed between the Incipient (median = 11.5‰) and Initial Jōmon (median = 8.8‰) and overall the distributions of the $\delta^{15}\text{N}$ values were significantly different (Mann–Whitney U test; $U=6024$; $p<0.005$). In contrast, the range of $\delta^{13}\text{C}$ values is similar ($U=4128$; $p=0.79$) between the Incipient (-27 to -20‰ , median = -24‰) and Initial Jōmon (-26 to -19‰ , median = -24‰).

Interestingly, aquatic biomarkers were frequently observed in charred deposits with lower $\delta^{15}\text{N}$ values (Fig. 3C) ruling out predominantly terrestrial input. Although outside the range of

marine finfish and marine mammals ($>12\text{‰}$, 17, 40), these $\delta^{15}\text{N}$ values are within the range of values obtained on lower trophic level freshwater fish and marine/freshwater shellfish (17, 40), accounting for a 1‰ increase with charring (38, 40). Therefore, a more likely explanation is that the observed broadening and decrease in $\delta^{15}\text{N}$ values of charred deposits observed in the Holocene (Fig. 3D) is due to a diversification of aquatic resource exploitation to encompass freshwater fishing and/or shellfish collection. This explanation is also consistent with the establishment of shell middens in Japan at this time (16) but currently we are unable to unequivocally distinguish shellfish derived residues with the methods at our disposal.

Conclusion

There is a dramatic increase in the scale of pottery use across Japan after the onset of Early Holocene warming. We have investigated the extent to which these environmental changes drove diversification in pottery function as a broader range of resources became readily available. The earliest pottery in Japan was used to process aquatic resources, but contrary to expectations, we found no evidence that its function expanded in the Early Holocene to include the processing of terrestrial animal and plant resources. Instead, our results show remarkable continuity and consistency in the function of pottery across the Pleistocene–Holocene transition, pointing towards a strong cultural association between pottery and the processing of aquatic resources. This pattern also holds throughout the different ecological zones of the Japanese archipelago. As a result, we suggest that after its first invention, pottery developed particular cultural associations linked to processing aquatic resources, and that these were robust enough to withstand the effects of major climatic and environmental transformations at the Pleistocene–Holocene transition. Moreover, these ‘culinary’ preferences persisted across Japan, even in warmer southern areas where abundant nut and plant resources were increasingly available. Our earlier study from the Torihama shell midden site (5–7) in Japan indicates that this cognitive association persisted until at least the Middle Holocene, and may only have been truncated by the arrival of rice and millet agriculture ca. 2,500 cal BP. A similar association between early pottery and aquatic resources has also been identified in adjacent regions of East Asia such as Sakhalin Island (6, 34, 35) and the Korean Peninsula (5–7). Here, pottery appears in the Early and Middle Holocene and from the outset demonstrates close association with processing of marine foods.

Our current research also identified an important new pattern, which is that pottery was used to process a broader spectrum of aquatic foods in the Early Holocene, including shellfish, freshwater fish and a greater range of marine taxa. This corresponds to significant climate warming ca. 11,500 years ago which may have reduced salmonid stocks in Northern Japan (42, 43) prompting a switch to other aquatic species, but also created greater opportunities for inshore fishing and shellfish gathering through the expansion of the marine shelf (11). Also at this time, pottery traditions began to flourish, with greater variation in forms and volumes reflecting intensified usage. We suggest that this represents an important change away from the small-scale and specialised use of pottery in the Late Pleistocene to a greater utilitarian function in the Early Holocene as fishing and shellfish gathering intensified. Whether this change served as a driving force for the wider-range dispersal of hunter-gatherer pottery from East Asia into surrounding areas along aquatic ecotones (2), needs to be tested through further organic residue analysis and greater AMS radiocarbon dating of early pottery sites.

Finally, we are unable to explain either the invention of pottery in the Late Pleistocene or its more varied and intensified use in the Holocene in purely functional terms. Indeed, aquatic foods were undoubtedly exploited by maritime East Asian hunter-gatherers well before pottery appeared (45). Social and demo-

681 graphic factors, indirectly linked to economic change, provide
682 a more compelling argument. We suggest that pottery was initially
683 developed as a novel, prestige technology during periods
684 of seasonal population aggregation focused on cooperative har-
685 vesting of migratory fish, such as salmonids. From the start of
686 the Holocene, however, it was produced in significantly larger
687 quantities, associated with intensification of aquatic resource
688 exploitation and increasing sedentism.

689 Methods summary

690 We obtained 652 ceramic sherds and 172 adhering carbonised
691 residues from 46 archaeological sites throughout the Japanese
692 archipelago. Assignment to the Incipient or Initial Jōmon was
693 based on pottery typology or independently through the AMS
694 radiocarbon (^{14}C) dating of associated organic materials.

695 **Organic residue analysis:** Lipids were directly extracted and
696 methylated with acidified methanol according to established
697 methods (6, 7). Briefly, methanol (1 or 4 mL) was added to
698 homogenised carbonised residues (10–20 mg) or ceramic powders
699 (0.5–1.0 g) drilled (2–5 mm depth) from the interior or exterior
700 surface of the sherd. The sample was sonicated in a water bath for

701 15 min, and acidified with concentrated sulphuric acid (200 or 800
702 μL). The acidified suspension was heated in a block for 4 h at 70
703 $^{\circ}\text{C}$. Lipids were extracted *n*-hexane (3 \times 2 ml), and subsequently
704 analysed by GC-MS and GC-c-IRMS (see SI Appendix). Interior
705 foodcrusts or exterior carbonised residues were also analysed
706 by Elemental Analysis-Isotope Ratio Mass Spectrometry (see SI
707 Appendix) using previously reported protocols (5, 6).

708 **Statistical and GIS:** All statistical tests were performed using
709 *R studio* (version 1.0.136) and *Past* (version 3.18). Mapping was
710 undertaken with QGIS (version 2.18.9).

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