Middle-Holocene sea-level fluctuations interrupted the developing Hemudu culture in the lower Yangtze River, China

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A B S T R A C T

The eastern coastal zone of China is densely populated and widely recognized as a center of rice domestication, which has undergone dramatic sea-level fluctuation during the Holocene epoch. Hemudu culture is distributed mainly in the eastern coastal area and was once presumed as a mature agricultural economy based on rice, making it an ideal case for examining the remarkable human-environment interaction in the Lower Yangtze River. Though numerous studies have been conducted on the cultural evolution, ecological environment, and rice domestication of Hemudu culture, the impact of sea-level fluctuation on human settlement and food production remains controversial. In this study, we report high-resolution pollen, phytolith, and diatom records, and accurately measured elevation from the Yushan site, which is the closest site of Hemudu culture to the modern coastline. Based on the data gathered, we suggest that the Hemudu culture and subsequent Liangzhu culture developed in the context of regression and were interrupted by two transgressions that occurred during 6300-5600 BP and 5000-4500 BP. The regional ecological environment of the Yushan site alternated between intertidal mudflat and freshwater wetlands induced by sea-level fluctuations in the mid-late Holocene. Though rice was cultivated in the wetland as early as 6700 BP, this cultivation was subsequently discontinued due to the transgression; thus, full domestication of rice did not occur until 5600 BP in this region. Comprehensive analysis of multiple proxies in this study promote the understanding of the relationship between environmental evolution, cultural interruption, and rice domestication.

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1. Introduction

Though low-elevation coastal zones (below 10 m in elevation) currently contain more than 10 percent of the world population (McGranahan et al., 2007; Small and Nicholls, 2003), these regions are highly vulnerable to risks resulting from sea-level rise and climate change (FitzGerald et al., 2008; Nicholls and Cazenave, 2010; Nicholls et al., 2007; PAGES, 2009). The Lower Yangtze River sits in the interface zone between marine and terrestrial areas that has experienced a dramatic evolution of sea level and climate during the Holocene (Chen and Stanley, 1998; Qin et al., 2011; Song et al., 2013; Yi et al., 2003). Accordingly, this area serves as an ideal place for studying human-environment interaction (Zong et al., 2011b, 2012).

The Lower Yangtze River is densely distributed with Neolithic sites and is widely regarded as a core area where rice agriculture originated (Fuller, 2011; Silva et al., 2015; Stanley and Chen, 1996; Wu et al., 2014b). These cultural sequences comprise the Shangshan (11,000-8500 BP), Kuhuqiao (8000-7400 BP), Majiabang (7000-6000 BP), and Hemudu Culture (7000-5000 BP) during the early to middle Holocene (Fig. 1a) (Liu and Chen, 2012; The Institute of Archaeology and China Academy of Social Sciences, 2010; Underhill, 2013). The Hemudu culture is the most significant
Neolithic culture and is identified by its distinct style of pile-dwellings and rice remains in southern China (Sun, 2013), which are distributed primarily in the eastern coastal area and divided into two main periods with a remarkable interruption and dispersal around 6000 BP (Wang and Liu, 2005).

The interruption and dispersal of Hemudu culture are closely related to the change in the hydrologic environment induced by sea-level fluctuation. The core dispute of sea-level curves proposed previously for the east coast of China lies in whether or not a mid-Holocene sea-level highstand exists (Chen and Stanley, 1998; Hori et al., 2001; Liu et al., 2004; Song et al., 2013; Zhao et al., 1994; Zong, 2004). Divergent views of sea-level change significantly affect the explanation of the palaeoenvironment and the subsistence of Hemudu culture in Hemudu and Tianluo sites (Li et al., 2012; Liu et al., 2016; Qin et al., 2006; Zhu et al., 2003). Nevertheless, whether the phenomenon of cultural interruption is a special case or universal experience, what environmental changes potentially caused the interruption and how the interruption affects the process of rice domestication remains controversial.

Cultural interruptions are identified by barren layers of soil (i.e., layers that lack relics) that are situated between two cultural layers common in the Lower Yangtze River (Wu et al., 2014a; Yu et al., 2000; Zhang et al., 2005). Results of pollen, phytolith, diatom, seed, and geochemistry from the Tianluoshan site reveal several cultural interruptions during and after Hemudu Culture that were induced by the two largest transgressions during 6400-6300 BP and 4600-2100 BP (Li et al., 2012; Patalano et al., 2015; Wang et al., 2010; Zheng et al., 2011). However, based on the analysis of pollen and foraminifera from the Hemudu site, some scholars argue that the sludge layers that lie within and above the Hemudu culture layer are both freshwater swamp sediments (Wang, 2006; Zhu et al., 2003), implying an expanded waterbody associated with the migration of the Yaojiang River (Liu et al., 2016; Wang and Liu, 2005; Wu, 1985). Whether the cultural interruptions were caused by marine transgression or land floods is still in dispute.

The discovery of the Hemudu site marks a milestone in Chinese agricultural archaeology with excellent preservation of organic materials in waterlogged conditions, especially abundant remains.
of rice (Zhao, 2010; Zhejiang Provincial Institute of Relics and Archaeology, 2003). Several intense debates on the characteristics of rice and subsistence of the Hemudu culture have been ongoing since the 1970s, and the core dispute lies in whether or not the rice is domesticated and rice farming is established (Fuller et al., 2007, 2009; Liu et al., 2007; Zheng et al., 2007). Though most scholars agree that rice domestication was a protracted evolutionary process that took at least 2000 years (Allaby et al., 2008; Fuller et al., 2014; Gross and Zhao, 2014), scholarly focus on how the cultural interruption affected the development of rice domestication is sparse.

In the present study, a high-resolution AMS$^{14}$C-dated profile is taken from the Yushan site, which is the closest site of Hemudu culture to the modern coastline. Through synchronized analyses of sporopollen, phytolith, and diatoms integrated with sedimentological information from the Yushan profile, we attempted to: 1) explain the possible cause of cultural interruption, 2) reconstruct the evolution of the local environment, and 3) trace the process of rice domestication.

2. Geographical background and site description

The study area is located in the subtropical region of southeast China under the influence of the East Asian Monsoon. The mean temperature is $-4^\circ C$ in January and $-28^\circ C$ in July, and the average annual precipitation is ca. 1100 mm (Ningbo Chorography Codification Committee, 1995). Regional vegetation is characterized by subtropical mixed forests of evergreen and deciduous trees. The region's most common evergreen trees are Lithocarpus, Cyclobalanopsis, Quercus, while its most common deciduous trees are Liquidambar, Castanea, Celtis, and Ulmus.

The Yushan site (30° 02'N, 121° 33'E) is located on the southeastern slope of Yushan hill, Ningshao coastal plain of the south Hangzhou Bay in eastern China (Fig. 1a). The site is about 2 m above local mean sea level (the Yellow Sea datum) and 7.3 km west to the present-day coastline. The Yushan site was excavated by Ningbo Municipal Institution of Cultural Relics and Archaeology and divided into four cultural periods of Hemudu Culture, Liangzhu-Qianshanyang Culture, Shangzhou Dynasty, and Tangsong Dynasty. Sediment cores indicated that the occupied site was approximately 16,500 m$^2$ in area, and 1500 m$^2$ were excavated during stage I in 2013 (Ningbo Municipal Institution of Cultural Relics and Archaeology and Zhenhai Administration, 2016).

3. Material and method

3.1. Sediment and sampling

The Yushan profile analyzed in this study was in the south section of trench T0213 (Fig. 1b and c), and the surface elevation of the section ranged from 1.98 m to 2.03 m, as measured by the Zhenhai Urban Planning and Survey Research Institute of Ningbo. The thickness of the Yushan profile was approximately 275 cm and had been divided into 10 layers according to the sediment and inclusion (Fig. 2) (Ningbo Municipal Institution of Cultural Relics and Archaeology and Zhenhai Administration, 2016). The upper 60 cm of the profile encompassed historic and modern sediment, which included layers 1 to 3, and was not sampled. The lower 215 cm encompassed prehistoric and natural layers, which included layers 4 to 10, and was subsampled at 5 cm intervals for the microfossil analyses. A total of 43 samples were collected, and 2 g of each sample was used for pollen, phytolith, and diatom analysis.

The lower 215 cm of the Yushan profile was divided into seven units from the bottom to the top (Fig. 2). Unit 10 (275-250 cm) was composed of pure dark green clay, which was widely distributed in the Ningshao Plain. Unit 9 (250-215 cm) consisted of dark gray clayey silt and belonged to the early Hemudu Culture Period. Numerous excavated pottery sherds were tempered with charred plants and sand. Unit 8 (215-180 cm) was mainly composed of yellow gray clay with no artificial remains excavated. Unit 7 (180-150 cm) consisted of dark gray silt with fine sand that belonged to the late Hemudu Culture Period. Artificial remains were composed primarily of sand pottery and red clay pottery. Unit 6 (150-120 cm) was dark black peat and contained rich humus and plant debris. A few sand pottery sherds belonging to Liangzhu Culture were excavated in this layer. Unit 5 (120-100 cm) consisted of gray-green clay and in it, no artificial remains were found. Unit 4 (100-60 cm) was composed of yellowish silt; numerous streaks of brown rust were distributed in this layer.

3.2. Radiocarbon dating

Nine soil samples were collected in the boundaries of each layer (Fig. 2) and were screened to retrieve dating materials. Most of the dating materials were charred seeds, except for one plant fragment. These materials were submitted to the Radiocarbon Dating Laboratory of Peking University. These ages were calibrated using the IntCal13 dataset (Reimer et al., 2013) by OxCal v4.2.4 program (Ramsey, 2009). Full details of the nine ages in the present study are displayed in Table 1.

A total of nine AMS radiocarbon ages were obtained, and most of the ages calibrated followed a consistent stratigraphic order with depth ranges, except for the YS21 sample. The dating age corresponded well to the three cultural periods determined by the pottery sherds excavated from the site. An age-depth model was constructed using the Bacon model (Blaauw, 2010) and applied to the diagram of pollen. This chronology indicated that the Yushan profile spanned the last 7300 years.

3.3. Pollen analysis

Samples were treated according to the following standard procedure developed by Moore et al. (1991). First, a tablet of exotic Lycopodium spores (27,637 N/tablet) was added to each sample to calculate the palynological concentrations. Second, 10% HCl and 40% HF were added to remove carbonates and silicates, respectively. Third, the samples were heated with 10% KOH to dissolve humic matters. Fourth, an acetolysis solution, made by mixing 10 ml of H$_2$SO$_4$ with 90 ml of acetic anhydride, was added to remove cellulose. Fifth, the materials remaining after the acid-alkaline reactions were sieved through a 7 $\mu$m mesh in an ultrasonic instrument in order to concentrate the pollen. Finally, the residue was suspended in glycerine and mounted on slides for microscopic examination at 400 $\times$ magnifications.

Each sample was counted for pollen and spores over 500 grains (average 608 grains). A total of 26,169 grains of pollen and spores had been obtained from the 43 samples. Identification of pollen and spores were made with reference to modern and Quaternary atlas (Institute of Botany and South China Institute of Botany, 1982; Tang et al., 2016; Wang et al., 1995). Poaceae pollen was divided into three size categories (<35 $\mu$m, 35–40 $\mu$m, >40 $\mu$m), and the Poaceae grains (>40 $\mu$m) from the sediment of eastern China had been identified as domesticated rice pollen (Chaturvedi et al., 1998; Wang et al., 1995). Quercus pollen was separated into two categories, Quercus (deciduous) and Quercus (evergreen), based on the surface, tricolpoderitate, and size that were thought to have ecological significance (Cao and Zhou, 2002; Wang and Pu, 2004).

3.4. Phytolith analysis

Phytoliths were extracted using the conventional wet digestion
Fig. 2. The sampled profile in the south section of the trench T0213. Stratigraphically, it is divided into ten sediment units and representative potteries were shown in the cultural layer. Samples from units ④ to ⑩ were analyzed. Locations of the dating samples are shown in the scale of depth on the left side by a red rectangle. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
AMS 14C dates for Yushan site.

<table>
<thead>
<tr>
<th>Sample no.</th>
<th>Depth (cm)</th>
<th>Material</th>
<th>Conventional $^{14}$C age ($^{14}$C yr BP)</th>
<th>Calibrated $^{14}$C age ($^{14}$C yr BP)</th>
<th>Dating ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>YS14</td>
<td>65–70</td>
<td>plant fragment</td>
<td>$4040 \pm 30$</td>
<td>$4782-4771$ (2.0%)</td>
<td>BA151803</td>
</tr>
<tr>
<td>YS21</td>
<td>100–105</td>
<td>seed</td>
<td>$4365 \pm 25$</td>
<td>$5032-5018$ (3.8%)</td>
<td>BA151804</td>
</tr>
<tr>
<td>YS26</td>
<td>125–130</td>
<td>seed</td>
<td>$4300 \pm 25$</td>
<td>$4976-4859$ (91.6%)</td>
<td>BA151805</td>
</tr>
<tr>
<td>YS31</td>
<td>150–155</td>
<td>seed</td>
<td>$4525 \pm 25$</td>
<td>$5307-5214$ (29.8%)</td>
<td>BA151806</td>
</tr>
<tr>
<td>YS37</td>
<td>180–185</td>
<td>seed</td>
<td>$4785 \pm 25$</td>
<td>$5991-5751$ (14.8%)</td>
<td>BA151807</td>
</tr>
<tr>
<td>YS44</td>
<td>215–220</td>
<td>seed</td>
<td>$5495 \pm 25$</td>
<td>$6394-6372$ (3.6%)</td>
<td>BA151808</td>
</tr>
<tr>
<td>YS47</td>
<td>230–235</td>
<td>seed</td>
<td>$5665 \pm 25$</td>
<td>$6529-6521$ (0.6%)</td>
<td>BA151809</td>
</tr>
<tr>
<td>YS50</td>
<td>245–250</td>
<td>seed</td>
<td>$5860 \pm 25$</td>
<td>$6744-6637$ (95.4%)</td>
<td>BA1518010</td>
</tr>
<tr>
<td>YS53</td>
<td>260–265</td>
<td>seed</td>
<td>$6225 \pm 25$</td>
<td>$7253-7146$ (49.3%)</td>
<td>BA1518011</td>
</tr>
</tbody>
</table>
method as follows (Piperno, 1988; Runge, 1999). First, the organic matter was oxidized by H₂O₂ (30%). Second, a tablet of exotic Lycopodium spores (27,637 N/tablet) was added. Third, carbonates were removed by HCl (10%). Fourth, the phytoliths were recovered by heavy liquid (ZnBr₂, 2.35 g/cm³). Finally, the recovered phytoliths were permanently mounted on glass microscopic slides with Canada balsam. Identification and counting of phytoliths were carried out using a Leica DM 750 microscope at 400 × magnification. At least 400 phytoliths (average 468 grains) were counted for each sample.

Phytoliths were classified according to the system proposed by Lu et al. (2006) and described according to the International Code for Phytolith Nomenclature (ICPN1.0) (Madella et al., 2005). Rice was the only cereal identified in this study that included three distinctive phytolith types: (1) Rice bulliform produced in the leaf bulliform cells; (2) Paralleled bilobates produced in leaf cells; (3) Double-peaked glume phytoliths produced in the epidermis of the rice husk (Gu et al., 2013). The morphological characteristics of rice bulliforms and double-peaked phytoliths were measured for further discrimination of wild and domesticated rice (Lu et al., 2002; Zhao et al., 1998; Zheng et al., 2003).

3.5. Diatom analysis

Diatoms were extracted and identified simultaneously with phytoliths. Twenty-two samples at 10 cm intervals were selected for analysis, and no additional extraction processes were required. Diatoms were identified with reference to modern and archaeological studies in this region (Liu et al., 2011; Wang et al., 1987, 2010; Zheng et al., 2011). Diatoms were classified into three types of freshwater species, brackish species, and marine species. At least 300 diatoms (average 290 grains) were counted for each sample, except for three samples in which diatoms were rare, counting was less than 50 grains.

4. Results

4.1. Pollen assemblages

A total of 78 pollen types were identified including 43 arboreal taxa, 18 herbaceous taxa, 7 aquatic taxa, 7 fern taxa, and 3 algae taxa, of which the major pollens are shown in Appendix Fig.A1. The stratigraphic diagrams of pollen percentages of the Yushan profile were constructed by C2 version 1.7.4 software (Juggins, 2007) and divided into five pollen assemblage zones according to the sediment facies (Fig. 4).

4.1.1. Zone I (275-250 cm, 7300-6700 BP)

This zone was characterized primarily by a high proportion (approximately 64%) of trees and shrubs, which was dominated by evergreen and deciduous Quercus (28% and 8%, respectively), Pinus (12%), and Liquidambar (5%). The proportion of upland herbs was approximately 35% and composed mostly of Poaceae (<35 µm) (13%) and Chenopodiaceae (19%). Pinus and Chenopodiaceae exhibited a declining trend from 21% to 5% and 30% to 6%, respectively. In contrast, Poaceae (<35 µm) increased rapidly from 3% to 33%.

4.1.2. Zone II (250-215 cm, 6700-6300 BP): Hemudu Culture Period II

Pollen zone II showed a gradual increase in trees and shrubs from 58% to 64%. The content of evergreen Quercus increased slightly from 32% to 36%. Poaceae (<35 µm) reached the peak and decreased from 29% to 14%. The percentage of Pinus and Chenopodiaceae remained low at 3% and 3%, respectively. Cyperaceae increased gradually from 4% to 18%. Typha rose to 2%, and Myriophyllum reached the peak of 4%.

4.1.3. Zone III (215-180 cm, 6300-5600 BP)

There was a slight decrease in the percentage of trees and shrubs, from 73% to 65%. Evergreen Quercus declined to a low of 24%, whereas Pinus rose to a high average of 8%. Poaceae (<35 µm) declined rapidly and then remained at a low value of 12%. Poaceae (>35 µm) rose from 0.8% to 8%. Typha increased from 3% to 9%, while Myriophyllum nearly disappeared.

4.1.4. Zone IV (180-120 cm, 5600-5000 BP): Hemudu Culture Period III and Liangzhu Culture

The percentage of Cyperaceae and Typha all exhibited a remarkable increase, reaching peaks of 28% and 31%, respectively. Pinus and Chenopodiaceae decreased and remained at a low content of 2% and 0.9%, respectively. Poaceae (<35 µm) showed a declining trend from 21% to 9%, whereas Poaceae (35–40 µm) and Poaceae (>40 µm) retained relatively high values of 4% and 7%, respectively.

4.1.5. Zone V (120-60 cm, 5000-4500 BP)

There was a remarkable recovery in the percentages of Pinus, Pterocarya, and Chenopodiaceae that reached 4%, 2%, and 2%, respectively. Both evergreen and deciduous Quercus increased rapidly, reaching peaks of 37% and 18%, respectively. Cyperaceae decreased from 14% to 0.2%, and Typha kept a stable level of 10%. Poaceae (35–40 µm) and Poaceae (>40 µm) reached peaks of 8% and 14%, respectively, and then decreased afterward.

4.2. Phytolith assemblages

Thirty-three phytolith morphotypes were identified from the Yushan profile, and the major phytoliths are shown in Appendix Fig.A1. The stratigraphic diagrams of phytolith percentages of the Yushan profile were constructed by C2 version 1.7.4 software (Juggins, 2007) and divided into five phytolith assemblage zones according to the sediment facies (Fig. 4).

4.2.1. Zone I (275-250 cm, 7300-6700 BP)

The phytolith assemblage zone I was characterized by high proportions of smooth elongate (27%) and bilobate (19%). The percentage of short saddle (6%) and tower (10%) exhibited an increasing trend, while that of point (9%) decreased gradually. No phytoliths of rice were recovered from this zone.

4.2.2. Zone II (250-215 cm, 6700-6300 BP): Hemudu Culture Period II

The proportions of reed phytoliths (plateau saddle and reed bulliform) appeared and reached peaks of 9% and 2%, respectively. The percentage of short saddle (6%) and tower (10%) exhibited an increasing trend, while that of point (9%) decreased gradually. No phytoliths of rice were recovered from this zone.

4.2.3. Zone III (215-180 cm, 6300-5600 BP)

Phytolith zone III was characterized by a high proportion of smooth elongate (27%), square (14%), and point (9%), while the percentage of short saddle (4%), plateau saddle (0.5%), hat (1%), and tower (9%) decreased to lower levels. Rice bulliform nearly disappeared and was only found in a few samples.
4.2.4. Zone IV (180-120 cm, 5600-5000 BP): Hemudu Culture Period III and Liangzhu Culture

The percentage of bilobate (24%) and cross (6%) increased to high levels, while that of smooth elongate (16%), square (5%), and point (2%) decreased to low levels. Cyperaceae phytoliths of polygonal cones were widely recovered and increased to the peak of 3%. Rice bulliform reached the peak of 1% and decreased afterward. Double-peaked glume cells appeared for the first time, accounting for 0.2%.

4.2.5. Zone V (120-60 cm, 5000-4500 BP)

The percentage of smooth elongate (21%), long saddle (7%), and point (6%) increased to high levels, while that of bilobate (19%), cross (1%), and sinuate elongate (2%) decreased. Rice phytoliths were still recovered from a few samples. Bilobates parallel was widely recovered in this zone and increased to the peak of 0.9%.

4.3. Diatom assemblages

Diatoms were recovered in abundance in nearly all samples studied; 24 major morphotypes were identified, as shown in Appendix Fig.A1, including marine, brackish, and freshwater species. The stratigraphic diagrams of diatom percentages of the Yushan profile were constructed by C2 version 1.7.4 software (Juggins, 2007) and divided into five zones according to the sediment facies and diatom assemblage (Fig. 5).

4.3.1. Zone I (275-250 cm, 7300-6700 BP)

Diatom assemblages in zone I were dominated by marine species of Campylodiscus spp (26%), Conscinodiscus spp (46%), Triceratium favus (1%), Cyclotella stylonur (5%), and Diploneis smithii (4%). No freshwater diatom was recovered from this zone.
4.3.2. Zone II (250-215 cm, 6700-6300 BP): Hemudu Culture Period II
Marine diatoms decreased sharply and nearly disappeared in Zone II. In contrast, this zone was dominated by brackish diatoms of Nitzschia scalaris (39%) and Pinnularia yarrensis (21%), and freshwater diatoms of Amphora ovalis (20%), as well as Navicula cuspidata & radiosa (8%).

4.3.3. Zone III (215-180 cm, 6300-5600 BP)
Marine diatoms of Campylodiscus spp (18%), Conscinodiscus spp (40%), T. favus (0.8%), C. stylum (7%), and D. smithii (4%) increased again and played leading roles. In addition, brackish diatoms of P. yarrensis (22%) also accounted for a high proportion.

4.3.4. Zone IV (180-120 cm, 5600-5000 BP): Hemudu Culture Period III and Liangzhu Culture
This zone was dominated by brackish diatoms of N. scalaris (43%), and freshwater diatoms of Pinnularia major (28%), N. cuspidata & radiosa (11%), Cymbella minutu & asper (4%), and Eunotia praerupta & pectinaria (6%). Several samples revealed only a few marine diatoms.

4.3.5. Zone V (120-60 cm, 5000-4500 BP)
Marine diatoms of Campylodiscus spp (62%) and Conscinodiscus spp (17%) increased and played a leading role. Freshwater diatoms of P. major (14%) decreased sharply and only accounted for a minor proportion.

4.4. Identification of rice pollen and phytolith

Rice bulliform phytoliths were recovered from 20 samples with concentrations ranging from 1151 to 27,637 grains/g; concentrations of 11 of these samples exceeded 5000 grains/g. Two samples for each cultural period were selected for a detailed check of rice bulliform (Fig. 4). In total, 389 rice bulliform phytoliths were identified. Fish scale decorations of most rice bulliforms were weathered and unable to be counted (Lu et al., 2002). Morphological characteristics of each individual bulliform were also measured (Zheng et al., 2003). The average vertical length (VL) and horizontal length (HL) of rice bulliform were 42.9 ± 7 μm and 34.7 ± 5.1 μm, 45.3 ± 7.9 μm and 37.2 ± 6.1 μm, 42.3 ± 7.9 μm and 36 ± 6.4 μm from the bottom up, respectively. Only one sample of double-peaked glume cells was suitable for discriminant analysis (Zhao et al., 1998) and classified as domestic rice.

The percentage of Poaceae fluctuated significantly between different zones with several peak values of approximate 34.5%. However, the composition of the Poaceae pollen changed radically. The first peak, which occurred in zone II, was composed almost entirely of Poaceae (<35 μm), whereas the peaks in zone IV were mainly promoted by the rise of Poaceae pollen (>40 μm). The percentage of rice pollen (>40 μm) to Poaceae pollen was as low as 1.1% in zones I and II, rose rapidly to a high value of 28% in zone III, and remained at that percentage until it peaked again to 37% in zone V.

5. Discussion

5.1. Reconstruction of the ecological environment

According to the analysis of sediment, pollen, phytoliths, and diatoms, the Yushan site experienced environmental alternations between intertidal mudflats and freshwater wetlands controlled by the fluctuation of relative sea level (RSL) (Fig. 6) (Zheng et al., 2011). Diatom assemblages of zones I, III, and V were composed primarily of marine diatoms Campylodiscus spp and Conscinodiscus spp, which are common in offshore, coastal, and intertidal zones in the Lower Yangtze River (Liu et al., 2011; Wang et al., 1987; Zhuang et al., 2014), indicating seawater environments and marine transgression. In contrast, diatom assemblages of zones II and IV were
dominated by freshwater diatoms *A. ovalis* and *P. major* and brackish diatoms *N. scalaris* and *P. yarrensis*, which are commonly recovered from shallow lakes, freshwater marshes/swamps, and coastal lagoons (Yang et al., 2008; Zong and Horton, 1998; Zong et al., 2011a), indicating freshwater wetland environments and regressive events (Fig. 6a).

Based on the survey of modern plants along southeastern China, coastal mudflats can be divided into several plant communities according to elevation and inundation time. From the low tide line to the high tide line are bare flat, *Scirpus maritimus* & *Scirpus triqueter* community, *Suaeda* spp community, *Typha* spp community, and *Phragmites australis* community (Gao and Zhang, 2006; Tang and Lu, 2003; Wu et al., 2008). The zones I, III, and V were characterized by a high proportion of Chenopodiaceae, which indicated *Suaeda* spp widespread on the supratidal zone of the marine layer (Fig. 6a) (Xiao et al., 2014). Zones II and IV were characterized by a high proportion of aquatic sporopollen of *Typha* and *Myriophyllum* that indicated the existence of a freshwater wetland (Fig. 6a) (Ma et al., 2010).

In addition, the pollen and phytolith results corresponded well.
in zones II and V with reference to reeds and sedges (Fig. 6a). In zone II, the percentage of Poaceae (<35 μm) pollen reached its peak, possibly due to the expansion of wild rice, weed, or reed. Meanwhile, reed phytolith (reed bulliform and plateu saddle) also reached its peak. In zones IV and V, the percentage of Cyperaceae pollen reached its peak, while that of sedge phytolith (polygonal cones) emerged, accounting for the highest proportion in the profile. The remarkable coincidence between the pollen and phytolith indicated two events of regression and formation of wetland that occurred during 6700–6300 BP and 5600–5000 BP, which provided a rich habitat for the development of Neolithic culture and the cultivation of rice (Zheng, 2012; Zong et al., 2007).

Previous studies suggested that settlements in the Yangtze coastal plain gradually moved seawards over the course of the Neolithic period (Stanley and Chen, 1996; Zong et al., 2012). Newly emerged marshes and mudflats in the process of regression provided rich wild food resources (Yuan et al., 2008; Zheng, 2012) and were suitable for rice cultivation, hence may attract people migrate following the receding sea. The sedimentary strata in the Yushan site were similar to that of the Tianluoshan site while the beginning of Hemudu culture at the Yushan site was approximately 300 and 700 years later than that at Tianluoshan site, respectively (Zheng et al., 2011). Compared to the Tianluoshan site, the Yushan site was located closer to the coastline, which resulted in the regression occurring later than at the Tianluoshan site. In other words, some ancient people of Hemudu culture may have migrated with the regression to search for new wetlands suitable for inhabitation.

5.2. Cultural interruption and sea-level fluctuation

Evidence of pollen and diatoms in the Yushan profile discussed above indicates that the three natural layers of zones I, III, and V were all formed by marine transgressions. As for zone I, abundant data from cores revealed that the marine layers were widely distributed before human settlement in Zhejiang province (Fig. 7b) and varied from several meters to approximately 45 m in thickness (Feng and Wang, 1986). Many foraminifers including the species Ammonia beccarii were recovered from the layer beneath the cultural layer at the Hemudu site, illustrating an inner-shelf shallow sea environment (Zhu et al., 2003). Recent studies on the spatio-temporal distribution of Neolithic sites indicate that the East China coastal plain experienced widespread transgression and turned into a shallow marine environment during 9000–7000 BP (Li et al., 2018; Zheng et al., 2018), and forming the marine layer of zone I in the Yushan profile.

As for zones III and V that interrupted and overlay Hemudu and the subsequent Liangzhu cultural layers, some scholars argued that these layers were freshwater swamps, with no genera of foraminifera found in the Hemudu site (Zhu et al., 2003). Nevertheless, evidence of diatoms and seeds from the Tianluoshan site indicated that these layers of cultural interruption were likely to be the result of transgression induced by sea-level fluctuation in the mid-late Holocene (Wang et al., 2010; Zheng et al., 2011). This dispute may derive from different sea-level indicators (Wang, 1989) or varied local environment. Diatoms in zones III and V, as discussed above, indicated the existence of two large-scale marine transgressions. In fact, the Hemudu culture developed above the intertidal mudflat formed by the regression beginning around 7500–7000 BP (Zheng et al., 2018; Zhu et al., 2003); nevertheless, several transgressive events induced by sea-level fluctuation still occurred in the process of regression (Zheng et al., 2011).

In addition, the interruption layer between the Hemudu periods II and III was also found in several sites distributed along the coast of the Ningshao Plain, such as at Loujiagiao (Zhejiang Provincial Institute of Cultural Relics and Archaeology et al., 2010), Fujiashan (Ningbo Municipal Institute of Cultural Relics and Archaeology, 2013), and Tianluoshan (Zheng et al., 2011) (Fig. 7a). The estimated date of the interruption layer ranged from 6400 to 5600 BP and the depth ranged from 2.9 to 1.1 m to the surface (Fig. 7b, Table 2). In the present study, accurate elevation and age were measured at the Yushan site and the effects of local subsidence and sediment consolidation were also considered (Appendix Table A1) (Zhan and Wang, 2014; Zhang and Liu, 1996; Zong, 2004). Accordingly, we suggest that the RSL was at least 0.4 m above the present during 5600 BP. When it comes to the other transgression that ended in 4500 BP, the RSL was up to 1.8 m above the present at this site.

5.3. Process of rice domestication

The concentration of rice bulliform exceeded 5000 grains/g in a few samples from zone II and reached the peak of approximately 27,000 grains/g in samples from zones IV and V, indicating that rice cultivation (Fujiwara, 1976) had already started during the Hemudu Culture Period II in this region. Measurements on rice bulliform phytoliths from zones II and IV fell into the area close to that after the Majiabang culture and did not shift towards larger sizes (Fig. 8a) (Fuller et al., 2007; Qin et al., 2006). Though morphological features of bulliform from modern Oryza sativa display wide overlaps with that of wild species (Fig. 8b) (Gu et al., 2013), previous studies of rice bulliform from archaeological sites show an increasing trend through the Neolithic Age (Zheng et al., 2000, 2003). Thus, we suggest these rice had already been cultivated and was in the process of domestication since 6700 BP.

Although the use of a size threshold to identify rice pollen is still disputed (Mao and Yang, 2015), two main criterions of 35 μm (Li et al., 2015; Shu et al., 2007; Yang et al., 2012) and 40 μm (Chaturvedi et al., 1998; Wang et al., 1995; Zong et al., 2007) (Fig. 8d) are widely applied to modern field and ancient sediment. A great change occurred in the composition of Poaceae in zone IV as the percentage of rice pollen (~40 μm) rose sharply from 1.1% to 28% and continued its upward trend (Fig. 8c). In contrast, the peak of Poaceae pollen percentage in zone II was nearly all comprised of Poaceae (<35 μm). The remarkable contrast between these two zones indicated that rice cultivated in the Hemudu Culture Period II was more similar to the wild type, whereas the rice in Hemudu Culture Period III was more likely to be fully domesticated. In sum, we suggest that rice farming have already established in this region at least since 5600 BP.

Though modern genetic dataset suggests rice may have originated from the Pearl River basin (Huang et al., 2012), numerous evidences of genetics, archaeobotany and computational modelling are consistent with the domestication of O. sativa japonica in the Yangtze River valley (Fuller et al., 2010b; Gross and Zhao, 2014; Silva et al., 2015). The process of domestication has been recognized a protracted and dynamic transition taking thousands of plant generations (Allaby et al., 2008; Fuller et al., 2010a). The rate of domestication is not a constant, instead it varies along the process in response to different human behaviors (Fuller et al., 2010a). The long process of pre-domestication in the Lower Yangtze River (Fuller, 2007; Fuller et al., 2010b) may be the result of the unstable environment induced by sea-level fluctuations. The accelerated accomplishment of rice domestication during the Hemudu Culture Period III may attribute to the formation of the paddy field systems, which efficiently separates cultivated rice from other wild plants and significantly reduces cross-pollination with free-growing wild rice (Fuller and Qin, 2009; Fuller et al., 2010b).

6. Conclusion

Evidence of pollen, phytoliths, and diatoms integrated with
Fig. 7. The phenomenon of cultural interruption along the coast of Ningshao Plain. (a) Distribution of archaeological sites of Hemudu culture and location of the sites with cultural interruptions (Appendix B. Supplement dataset S2). (b) Schematic diagram of sediment stratigraphy from these archaeological sites. Natural layers that underlie and interrupt the Hemudu cultural layers are displayed in gray.
sedimentological information from the Yushan site indicates the existence of a dynamic interaction between human activity and the sea-level fluctuation beginning in 6700 BP. Hemudu culture and the subsequent Liangzhu culture developed in the context of regression and were interrupted by two transgressions that occurred during 6300-5600 BP and 5000-4500 BP. The regional ecological environment of the Yushan site alternated between intertidal mudflats and freshwater wetlands induced by sea-level fluctuation in the mid-late Holocene. Though rice was first cultivated on wetlands beginning in 6700 BP, its cultivation was halted by the subsequent transgression; thus, the full domestication of rice in this region was protracted until 5600 BP.

Declaration of interest

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

This research has not been submitted for publication nor has it been published in whole or in part elsewhere. We attest to the fact that all authors listed on the title page have contributed significantly to the work, have read the manuscript, attest to the validity and legitimacy of the data and its interpretation, and agree to its submission to the Quaternary Science Reviews.

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

We understand that the Corresponding Author is the sole contact for the Editorial process. He is responsible for communicating with the other authors about progress, submissions of revisions and
final approval of proofs. We confirm that we have provided a current, correct email address which is accessible by the Corresponding Author.

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Appendix B. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quascirev.2018.03.034.

Appendix A

Table A1

Correction for sediment compaction settlement for Yushan profile.

<table>
<thead>
<tr>
<th>Unit</th>
<th>Depth Measured (cm)</th>
<th>Lithology</th>
<th>Porosity (n)</th>
<th>Porosity (n0)</th>
<th>Thickness (h/cm)</th>
<th>Compaction capacity (Δh)</th>
<th>Depth Corrected (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1−3</td>
<td>0−60</td>
<td>silt</td>
<td>0.5</td>
<td>0.48</td>
<td>60</td>
<td>2.4</td>
<td>−41.4−21</td>
</tr>
<tr>
<td>4′</td>
<td>60−100</td>
<td>clayey silt</td>
<td>0.68</td>
<td>0.63</td>
<td>40</td>
<td>6.3</td>
<td>21−67.3</td>
</tr>
<tr>
<td>5</td>
<td>100−120</td>
<td>clay</td>
<td>0.7</td>
<td>0.62</td>
<td>20</td>
<td>5.3</td>
<td>67.3−92.6</td>
</tr>
<tr>
<td>6</td>
<td>120−150</td>
<td>clayey silt</td>
<td>0.68</td>
<td>0.63</td>
<td>30</td>
<td>4.7</td>
<td>92.6−127.3</td>
</tr>
<tr>
<td>7</td>
<td>150−180</td>
<td>silt</td>
<td>0.5</td>
<td>0.48</td>
<td>30</td>
<td>1.2</td>
<td>127.3−158.5</td>
</tr>
<tr>
<td>8′</td>
<td>180−215</td>
<td>clay</td>
<td>0.7</td>
<td>0.62</td>
<td>35</td>
<td>9.3</td>
<td>158.5−202.8</td>
</tr>
<tr>
<td>9</td>
<td>215−250</td>
<td>clayey silt</td>
<td>0.68</td>
<td>0.63</td>
<td>35</td>
<td>5.5</td>
<td>202.8−243.3</td>
</tr>
<tr>
<td>10</td>
<td>250−275</td>
<td>clay</td>
<td>0.7</td>
<td>0.62</td>
<td>25</td>
<td>6.7</td>
<td>243.3−275</td>
</tr>
</tbody>
</table>

* The Yangtze Delta has experienced a weak subsidence in the Holocene and the small amount of subsidence was not calculated in this study.

References


Stockholm.

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