

# Feeding prehistoric coastal community: A study of marine faunal remains at the Jingtoushan site

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**Abstract** This article examines the abundant marine mollusc, and fish remains at the Jingtoushan shell midden (8,300 to 7,800 cal a BP) in Zhejiang Province, China, to investigate the fishing economy, community development, the palaeoenvironment, and their interactions among the prehistoric populations in the lower Yangtze River Basin and southeastern coastal China. It also attempts to explore the prosperity and decline of coastal settlements in China during the Neolithic Age and the potential reasons for their rise and fall, respectively. Based on the ecological and biological principles of marine animals, standard zooarchaeological methods and radiocarbon dating analysis are used for sampling, identification, measurement, and quantification. Results show that at least 11 mollusc taxa and 14 fish taxa can be identified from the Jingtoushan faunal assemblage. The ancient Jingtoushan residents possibly lived in a settlement close to the coast and engaged in inshore and offshore fishing, hunting, and gathering as their primary subsistence strategies, with low-level rice cultivation as a supplementary means of sustenance. Eventually, the changes in the coastal environment could be one of the reasons why the Jingtoushan residents abandoned their settlement. The research contributes to Chinese Neolithic archaeology with new evidence of the exploitation of marine resources around 8000 a BP in the eastern coastal areas and the relationship between Neolithic community development and environmental changes.

**Keywords** Neolithic Age, Marine faunal remains, Fishing economy, Palaeoenvironment, Community development

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## 1. Introduction

The blue oceans cover approximately 71% of the earth's surface, making up almost 99% of the living area on the planet, which contributes to vital economic, ecological, and societal significance for humanity (Costanza, 1999; Fagan, 2017). Maritime culture embodies the interactive relationships between humans and the ocean, which they endeavour to understand, govern, develop, and exploit. It also represents a complex of sentiments and materials that contain

human perceptions, concepts, thoughts, consciousness, and mentalities, resulting in subsistence patterns such as economic structures, legal systems, customs, languages and art forms (Qu, 1997). Humans began to use marine animal resources approximately two million years ago, when molluscs were exploited in the Asia-Pacific tropical islands. The earliest record of humans using molluscan resources and the occupation of the shell middens can be traced to between 130,000 and 30,000 years ago on the coast of South Africa (Volman, 1978; Brink et al., 1982; Shackleton, 1982; Balbo et al., 2011). The exploitation of fish resources occurred somewhat later. The abundant pelagic fish remains and the world's oldest fishhook found at the Jerimalai shelter in East

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Timo suggest that coastal populations had developed pelagic fishing skills and sophisticated maritime technology at least 42,000 years ago (O'Connor et al., 2011).

Maritime culture is an integral component of Chinese culture. Coastal shell midden, a common type of archaeological site in the coastal regions, can provide critical evidence to explore Chinese maritime culture and how ancient populations utilised marine resources. Different from natural shell deposits, shell middens contain large quantities of artefacts, animal and shell remains with traces of consumption, shell tools and worked shells (Lv, 2014). China's coastline extends for thousands of kilometres, with a wide coastal zone that preserves over 200 coastal shell middens, which can be addressed as three groups: the Liaodong Peninsula shell middens, the Jiaodong Peninsula shell middens, and southeastern coastal China shell middens, based on their geographical location, environmental context, and archaeological culture (Yao, 2007; Zhao, 2014; Zhang and Hung, 2016). Most of these shell middens belong to the Neolithic Age, while some are dated to the Qin and Han Dynasties (221 BP–220 AD) and some even later.

The subsistence economy is an essential part of archaeological culture. The taxonomic abundance of mollusc and fish remains in shell middens reflects not only the coastal palaeoenvironment but also the capability of coastal populations to exploit and utilise marine resources (Thomas, 2015a, 2015b; Lambrides and Weisler, 2016). The Xiaozhushan site is a representative example among the coastal shell middens of the Liaodong Peninsula, spanning 7,000–4,000 a BP. The marine animals unearthed from Xiaozhushan include 11 species of gastropods, 18 species of bivalves, one species of crustacean, four species of fish, and three species of marine mammals. Several species of birds and numerous terrestrial mammals are also unearthed. The exploitation of marine animals did not change significantly from the early to the late phase at Xiaozhushan, but the terrestrial mammal remains displayed an increase in the introduced domesticated animals and a decrease in wild animals (Jin and Jia, 2009; Lv et al., 2017). Since the 1990s, shell middens on the Jiaodong Peninsula have been systematically surveyed, excavated, and studied, yielding significant results on environmental archaeology and subsistence economy research (Cheng, 1992; Yuan, 1998; The Institute of Archaeology, Chinese Academy of Social Sciences, 1999; Song, 2011; Wang et al., 2012, 2014; Li, 2014; Song and Wang, 2016). The coastal shell middens on the Jiaodong Peninsula can be traced back to the Beixin and Dawenkou cultures of approximately 7,000–6,500 a BP (Zhang and Hung, 2016). Marine mollusc and fish remains, as well as terrestrial floral and faunal remains, are commonly found at these sites (Song, 2022). Research on the stable isotopes of human bones from the Beiqian site indicates that the human diet consists of 44.1% marine molluscs and fish,

34.1% C<sub>4</sub> plants, and 21.8% terrestrial animals (Wang et al., 2012, 2014). Coastal shell middens are commonly distributed in southeastern China. The earliest Neolithic shell midden was found on the eastern coast of Fujian Province, with radiocarbon dates of approximately 7,800 cal a BP (Chen, 2004). Owing to their proximity to subtropical seas, these sites usually contain a rich diversity of marine animals but occasionally terrestrial animals, significantly different from those on the Jiaodong and Liaodong Peninsulas (Lin, 1973; Yan, 2009; Li, 2013; Zhuang, 2021).

A comprehensive understanding of marine resource exploitation along Neolithic China's coast has been established after decades of research. Geographically, the coastal shell middens are distributed more evenly in southeastern China, whereas those in northern China are distributed in clusters. There is quite a large gap between the Jiaodong Peninsula and the eastern coast of Fujian Province. Chronologically, few coastal sites earlier than 7,000 years survived due to the rise of sea-levels and coastline changes during the early Holocene (Zhang and Hung, 2016). To sum up, the earliest shell middens in the Liaodong and Jiaodong Peninsulas can be dated to approximately 7,000 a BP, and in southeastern China, it can be dated to approximately 7,800 a BP; earlier sites are still missing.

Zhejiang Province is located in southeastern coastal China, which is an essential geographic area leading to Taiwan Island, Southeast Asia and the Pacific islands, that helps explore cultural and population interactions between the lower Yangtze River Basin, Taiwan Island, and Southeast Asia. The discovery of the Jingtoushan site in Yuyao City in Zhejiang Province provides an excellent opportunity to discuss the marine culture in China and the use of marine resources by ancient peoples. The Jingtoushan site is the first coastal shell midden found in Zhejiang Province. The cultural deposits at the Jingtoushan site are more than 2 m thick in total, and a large number of mollusc, fish and other faunal remains have been uncovered. As the earliest coastal shell midden found in China, the Jingtoushan site (~8,000 cal a BP) offers essential information on the utilisation of marine resources by the ancient population 8,000 years ago. Additionally, its geographic location contributes to understanding the interactions between ancient peoples living on China's southeastern coast and in Island Southeast Asia. We used zooarchaeological methods, including identification, morphometrics, and quantification, combined with radiocarbon dating to investigate how the ancient population exploited and used marine animal resources, to interpret the prosperity and decline of coastal communities, and to discuss the fishing economy, community development, palaeoenvironment, and their interactions in coastal southeastern China.

## 2. Site background and archaeological contexts

The Jingtoushan site is located in the town of Sanqi in Yuyao

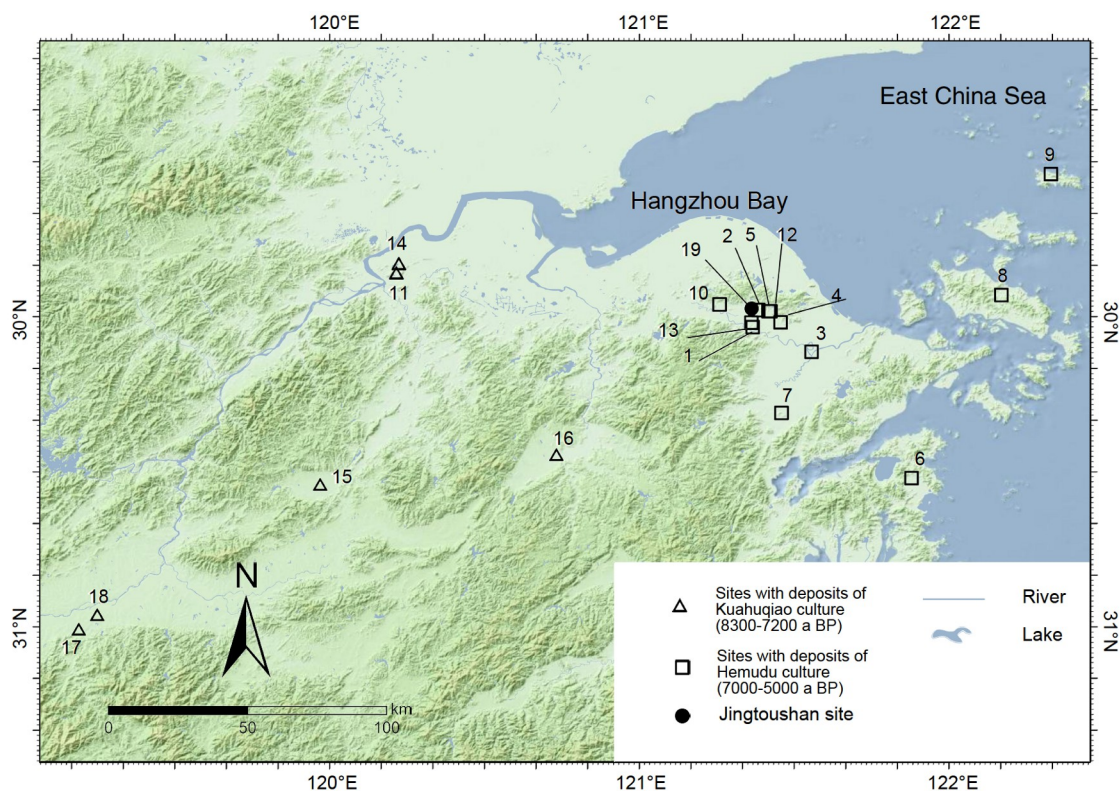
City, Zhejiang Province, with geographic coordinates of 121.3635°E and 30.0265°N (Figure 1). Currently, its elevation is 2 m above sea level (Zhejiang Provincial Institute of Cultural Relics and Archaeology et al., 2021). This site is situated in the southern area of Hangzhou Bay and at the junction of the Siming Mountain Range and the Yao River Valley in the eastern part of the Ningbo-Shaoxing Plain. This region is under a subtropical monsoon climate control, with an average daily temperature of 28.2°C in July and 4.1°C in January. The average annual precipitation is 1547.1 mm (Committee for Yuyao City Water Conservancy, 1993).

The Jingtoushan site was first discovered in 2013. In September 2019, the Zhejiang Provincial Institute of Cultural Relics and Archaeology, the Ningbo Institute of Cultural Heritage Management Research, and the Hemudu Site Museum together conducted the first season of excavation and unearthed an area of 750 m<sup>2</sup>. Radiocarbon dates showed that the site was occupied at about 8,300 to 7,800 cal a BP, spanning 500 years (Table 1). The total depth of cultural deposits is about 2.2 m, consisting of 13 cultural layers (cultural layers 9 to 20). These cultural layers can be divided into 3 phases: the early phase (cultural layers 16 to 20), the

middle phase (cultural layers 13 to 15), and the late phase (cultural layers 9 to 12) (Zhejiang Provincial Institute of Cultural Relics and Archaeology et al., 2021).

Various artefacts have been uncovered at the Jingtoushan site. Pottery typology shows possible connections with the Kuahuqiao and Hemudu cultures in the lower Yangtze River region, and further research is in progress (The Institute of Archaeology, Chinese Academy of Social Sciences, 2010; Zhejiang Provincial Institute of Cultural Relics and Archaeology et al., 2021). Organic remains are well-preserved due to the waterlogged environment. Jingtoushan yielded the oldest wooden bowls and lacquerware in China (Zhai et al., 2022). Wooden paddles and fishing nets, which could be used to acquire marine resources, were also the oldest ever recorded in China.

Both terrestrial and marine animals, including pigs (*Sus* sp.), dogs (*Canis lupus familiaris*), water buffaloes (*Bubalus* sp.), deer (Cervidae), marine molluscs, fish (Pisces), and birds (Aves), were unearthed. The plant remains include sawtooth oak (*Quercus acutissima*), peach (*Prunus persica*), Sichuan pepper (*Zanthoxylum* sp.), and Chinese pistache (*Pistacia chinensis*) (Zhejiang Provincial Institute of Cul-



**Figure 1** The location of Jingtoushan shell midden, and main sites of Hemudu and Kuahuqiao cultures (Based on Arc GIS 10.2 Software; Coordinate database: Jiang, 2014; Wang et al., 2014; Liu et al., 2021;). 1. Hemudu site (7,000–5,300 a BP); 2. Tianluoshan site (7,000–5,500 a BP); 3. Cihu site (5,900–5,300 a BP); 4. Xiaodongmen site (5,600–5,000 a BP); 5. Fujiashan site (6,800–6,300 a BP); 6. Tashan site (6,000–5,000 a BP); 7. Mingshanhou site (6,000–5,000 a BP); 8. Baiquan site (6,000–5,000 a BP); 9. Sunjiashan site (5,500–5,000 a BP); 10. Zishan site (7,000–5,000 a BP); 11. Xiasun site (7,800–7,600 a BP); 12. Baziqiao site (6,000–5,500 a BP); 13. Xiangjiashan site (6,000–5,300 a BP); 14. Kuahuqiao site (8,300–7,200 a BP); 15. Shangshan site (10,000–8,500 a BP); 16. Xiaohuangshan site (9,000–7,500 a BP); 17. Qingdui site (9,000–8,000 a BP); 18. Hehuashan site (10,400–8,000 a BP); 19. Jingtoushan site (8,300–7,800 a BP).

**Table 1** Radiocarbon dating results at the Jingtoushan site (Zhejiang Provincial Institute of Cultural Relics and Archaeology et al., 2021)

Lab. #	Sampling stratigraphy	Material	Measured age (a BP)	Calibrated age (cal a BP)	
				1 $\sigma$ (68.3%)	2 $\sigma$ (95.4%)
Beta-570111	12A	Charcoal	7180±30	7969–8013	7939–8025
Beta-570112	12B	Charcoal	7250±30	8012–8165	7980–8170
Beta-570113	13	Charcoal	7170±30	7965–8012	7937–8022
Beta-570114	14	Sawtooth oak acorn	7160±30	7959–8010	7933–8022
Beta-570115	14	Bone collagen	7210±30	7975–8024	7943–8165
Beta-570116	14	Charcoal	7100±30	7872–7963	7847–8007
Beta-570117	15	Bone collagen	7190±30	7973–8016	7939–8031
Beta-570118	16	Blood cockle	7730±30	7953–8121	7863–8195
Beta-570119	16	Charcoal	7130±30	7879–8002	7871–8013
Beta-570120	17	Bone collagen	7130±30	7879–8002	7871–8013
Beta-570121	17	Charcoal	7200±30	7975–8019	7939–8158
Beta-570122	18	Sawtooth oak acorn	7110±30	7875–7967	7863–8010
Beta-570123	19	Bone collagen	7300±30	8037–8169	8028–8174
Beta-570124	20	Sawtooth oak acorn	7240±30	7989–8163	7973–8169
Beta-570125	20	Charcoal	7230±30	7974–8158	7966–8168
Beta-570126	20	Blood cockle	7800±30	8013–8182	7945–8286

tural Relics and Archaeology et al., 2021). Charred rice grains and husks have also been found at this site.

### 3. Materials and methods

#### 3.1 Sampling

The mollusc remains were collected using column sampling (Claassen, 1998; The Institute of Archaeology, Chinese Academy of Social Sciences, 1999). A 50 cm by 50 cm column was chosen in the south of trench T409 where thick mollusc deposits were located, measuring 2.2 m in depth with 12 cultural layers (cultural layer 12 was further divided into 12A and 12B) (Figure 2a). Artificial layers, a typical shell midden sampling strategy, were set up as sampling units during excavation: measuring from the bottom of each cultural layer, every 5 cm was marked as an artificial layer; if the top artificial layer of the cultural layer was thinner than 5 cm, it was marked as an artificial layer as well (Yuan, 1998; The Institute of Archaeology, Chinese Academy of Social Sciences, 1999). A total number of 44 artificial layers were set up in the column (Figure 2b), and were excavated one by one (Figure 2c). The deposit of each artificial layer was removed, collected, and wet sieved through 2 layers of meshes (5 mm and 1 mm). The remaining residues were dried, collected, and marked with their corresponding artificial layer numbers. Animal remains were collected from the dried residues, and categorised into molluscs, fish, reptiles, birds, and mammals. A subsample was taken in each artificial layer

for identification and quantification. Each subsample contains 1 kg molluscs which are randomly collected from the molluscan remains. If the molluscs from a single artificial layer weighed less than 1 kg, they were entirely taken for analysis. A series of dating samples were taken during excavation and taken to the Radiocarbon Laboratory of the Australian National University for testing.

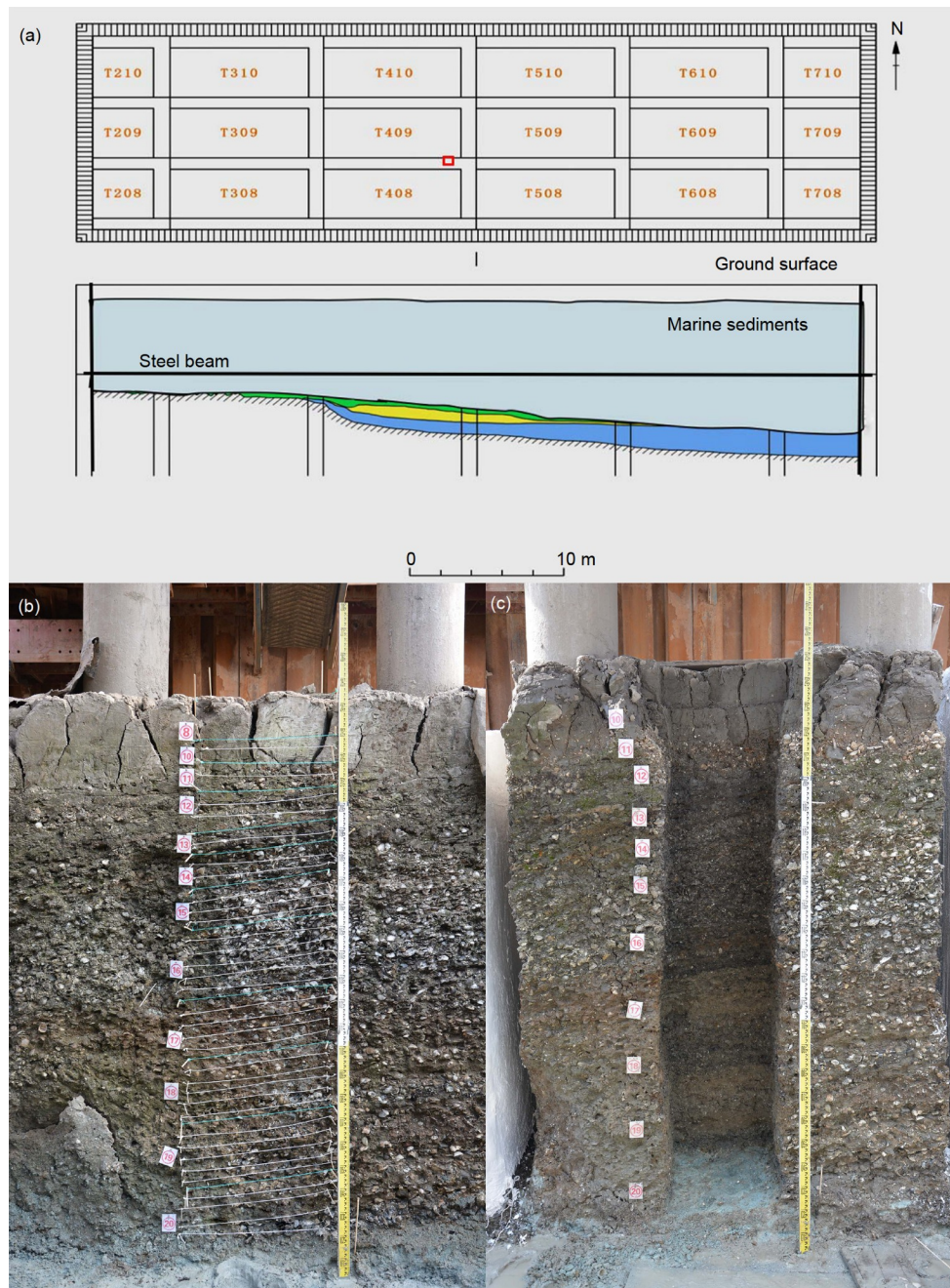
All fish remains excavated from the cultural layers 11–18 of trench T509 were selected for research. During excavation, we also used two sieves with mesh sizes of 5 mm and 1 mm to wet sieve the deposit of each cultural layer and collect artefacts and animal remains. Animal remains were further sorted into mammals, birds, reptiles and fish, and the fish remains were taken for research in this study.

#### 3.2 Identification and morphometrics

##### 3.2.1 Identification and morphometrics of mollusc remains

The identification of mollusc taxa was made based on published atlases and research papers; the geographic distribution of molluscs in China was referred to during identification (Editorial Committee of Fauna of Zhejiang, 1991; Xu and Zhang, 2008; Zhang, 2008; Wang et al., 2010; Zheng et al., 2013). Among the molluscs, the shape of oyster shells may change markedly according to their habitats, therefore, the Jingtoushan oysters were temporally identified to the genus level based on mollusc morphology and geographic distribution (Li et al., 2013). Molecular biology studies have shown that the oysters in this area mainly be-





**Figure 2** Location of the sampling column and sampling process at the Jingtoushan site (a) the red square refers to the column sampling area; (b) artificial layers in column sampling: labels refer to cultural layers; green lines mark the cultural layers; white lines mark the artificial layers (c) profile of cultural layers after column sampling.

long to the genus *Crassostrea* (Wang et al., 2010). Subsequently, measurements of shell length (SL) and shell height (SH) of blood cockles (*Tegillarca granosa*) were taken following the protocols for morphometric analysis (Claassen, 1998; Xu and Zhang, 2008), in order to evaluate size changes through time and determine whether shellfish harvesting caused survival pressure for the local mollusc populations.

### 3.2.2 Identification of fish remains

Fish remains were identified based on a reference collection

containing 120 fish individuals from 58 families, 80 genera, and 97 species, which are commonly distributed in the East China Sea and the Yangtze River system (Appendix 1, <https://link.springer.com>). Fish were collected from the fishery markets in the cities of Ningbo and Zhoushan from September 2021 to January 2022 and were made into reference specimens of skeletal parts following the ichthyoarchaeological procedures (Wheeler and Jones, 1989).

As there are different perspectives on taxonomic classification in current ichthyological studies, determining the

identification level of fish remains at the Jingtoushan site was a prerequisite for this study. The taxonomy of *Lateolabrax* remains controversial: for example, the *Lateolabrax* along China's coast was considered to be the Japanese seabass (*Lateolabrax japonicus*) (Feng and Jiang, 1998), but the latest taxonomy research shows that they are mainly the Chinese seabass (*L. maculatus*), which belongs to the genus *Lateolabrax* together with *L. japonicus* and the blackfin seabass (*L. latus*) (Wu and Zhong, 2021). Similarly, Japanese scholars have distinguished Chinese seabass from Japanese seabass from the morphological, genetic and ecological perspectives (Yokogawa and Seki, 1995). As for biogeographic distribution, *L. maculatus* are widely distributed along China's coast, especially in the East China Sea and the Yangtze River estuary, whereas *L. japonicus* are distributed on the Japanese archipelago south of Hokkaido and along the eastern coast of the Korean Peninsula (Feng and Jiang, 1998; Wu and Zhong, 2021). *L. latus* is endemic to Japan and lives mainly offshore (Feng and Jiang, 1998). Assuming that there are little ecological and biological differences between these three species between ancient times and the current period, the seabass remains excavated from China's coastal sites are more likely to be *L. maculatus*.

At least four genera of Sparidae live near the Zhejiang coast: *Acanthopagrus*, *Argyrops*, *Pagrus*, and *Evynnis* (Zhao et al., 2016). Based on the morphological characteristics of the dentition and premaxilla of seabream at the Jingtoushan site, we preliminarily identified the sparid remains to the genus *Acanthopagrus*. There are two species of *Acanthopagrus* in the Zhejiang seas: yellowfin seabream (*Acanthopagrus latus*) and blackhead seabream (*A. schlegelii*). By comparing the skeletal reference specimens of *A. latus* and *A. schlegelii*, we were able to distinguish both species from their dentary, premaxilla, maxilla, and so on. The yellowfin and blackhead seabreams were identified from Jingtoushan, and quantified separately.

Drum fish (Sciaenidae) remains could only be identified at the family level, as the taxonomy of drum fish is still controversial academically (Zhu et al., 1963). At least four species of drum fish could be identified based on the morphology of sagittal otoliths excavated from the Jingtoushan site, namely the large yellow croaker (*Larimichthys crocea*), the small yellow croaker (*Larimichthys polyactis*), the brown croaker (*Miichthys miuy*), and the dusky roncador (*Megalonibea fusca*). After comparing the skeletal systems of these four species, we found that they are morphologically similar (Ye et al. 2007; Wang et al. 2016; Zhao et al. 2016). Therefore, the term Sciaenidae was used during identification and quantification. There are three species of mullet (Mugilidae) in the Zhejiang waters: grey mullet (*Mugil cephalus*), redeye mullet (*Liza haematocheila*) and carinate mullet (*Liza carinataus*) (Zhao et al., 2016). Despite the morphological differences in the oper-

cles and vertebral columns of these fish, their remains cannot be determined at the species level morphologically; therefore, the mullet remains were also identified at the family level. In addition, pufferfish (*Takifugu* sp.) carry toxins in their bodies, which limits the collection and process of modern specimens; hence, their skeletons were identified only to the genus level as well (Zhao et al., 2016; Kimura, 2021).

As for the Chondrostei fish, Yangtze sturgeon (*Acipenser dabryanus*) and Chinese sturgeon (*Acipenser sinensis*) live in the Zhejiang waters (Zhao et al., 2016). Since they are Grade I protected animals in China, wild sturgeons are illegal to get (Department of Policies, Regulations and Planning, State Oceanic Administration, 2012). We identified the sturgeon remains referring to the skeletal specimens of cultured hybrid sturgeon, only to the genus level.

Although there is a lack of reference specimens of Elasmobranchii, a preliminary identification and quantification was carried out based on the anatomical literature of Elasmobranchii in the Zhejiang waters. The remains of stingrays (*Dasyatis* sp.) and eagle rays (*Aetobatus* sp.) could be identified by specific skeletal parts, such as the dorsal fin spines and teeth (Zhu and Meng, 2001; Zhao et al., 2016). Ground sharks (Carcharhiniformes) and mackerel sharks (Lamniformes) vertebrae could be distinguished by the articular foramina and radial calcareous lamellae (Kozuch and Fitzgerald, 1989; Burris, 2004; Tong, personal communication).

### 3.3 Quantitative analysis

Quantitative analysis is used to understand the composition and relative importance of the molluscan and fish remains. Two standard quantification methods in zooarchaeology were used: the number of identified specimens (NISP) and the minimum number of individuals (MNI) (Reitz and Wing, 2008). During the quantification of bivalves, MNI, which is the essential quantification method in archaeomalacology, was applied, by calculating the frequency of the non-repetitive elements (NREs) of shells (Claassen, 1998; Mason et al., 1998). Quantification of molluscs was carried out by artificial layers. The quantification of fish remains was done by cultural layer. The number of remains (NR) was used to show the total number of fish remains, and NISP and MNI were used to evaluate the abundance and relative proportions of the fish remains of species (Roselló and Morales, 1994; Reitz and Wing, 2008). The MNI was determined based on the number of well-preserved skeletal parts with typical identification characteristics of different taxa such as the maxilla, premaxilla, dentary, and sagittal otoliths. Skeletal parts without diagnostic features such as the vertebrae and fin spines were not used for MNI counts.

## 4. Results

### 4.1 Chronology

The radiocarbon dating samples were mainly blood cockles and charcoal. We calculated the carbon reservoir ages of the blood cockle samples based on the calibrated parameters of the Marine 20 database from molluscs in Keelung, Taiwan Island, which is the zone closest to the study area (Yoneda et al., 2007; Reimer and Reimer, 2017). OxCal v4.4.3 and IntCal20 calibration curves allowed us to calibrate the radiocarbon dates to calendar years. Among the ten collected samples, we received only nine pieces of valid data, except for the sample from the cultural layer 10 due to contamination (Table 2). We calibrated the radiocarbon dating data based on relevant information (Stuiver and Polach, 1977). The calibrated dates (about 9,000 to 8,000 cal a BP) were much earlier than the 8,300 to 7,800 years indicated by archaeological reports (Zhejiang Provincial Institute of Cultural Relics and Archaeology et al., 2021). On the one hand, the lack of the latest cultural layers (9 and 10) in the sampling area could have shortened the chronological sequence; on the other hand, shells could generate earlier dates due to the marine reservoir effect, compared with bones and seeds (Thomas, 2015a). The radiocarbon dates of charcoal from layers 12A and 20, however, are similar to those in Table 1, so we still use the dates of (8,300–7,800 cal a BP) in this article for discussion.

### 4.2 Taxa and relative proportions of mollusc remains

A total number of 7,537 mollusc specimens from 44 subsamples in the sampling column have been analysed; all could be identified at the genus or species level. Four species and one genus of bivalves (Lamellibranchia) have been identified, including the blood cockle (*Tegillarca granosa*), the Chinese razor clam (*Sinonovacula constricta*), the black clam (*Cyclina sinensis*), the oblique ark shell (*Barbatia ob-*

*liquata*), and the oyster (*Crassostrea* sp.). Four species and two genera of gastropods have been identified, including the girdled horn shell (*Cerithidea cingulate*), the granulated dogwhelk (*Thais luteostoma*), the burned nassa (*Nassarius siquijorensis*), the Chinese ear snail (*Ellobium chinense*), the nerite snail (*Nerita* sp), and the rapana snail (*Rapana* sp.) (Figure 3). These molluscs are still commonly distributed in Zhejiang Province.

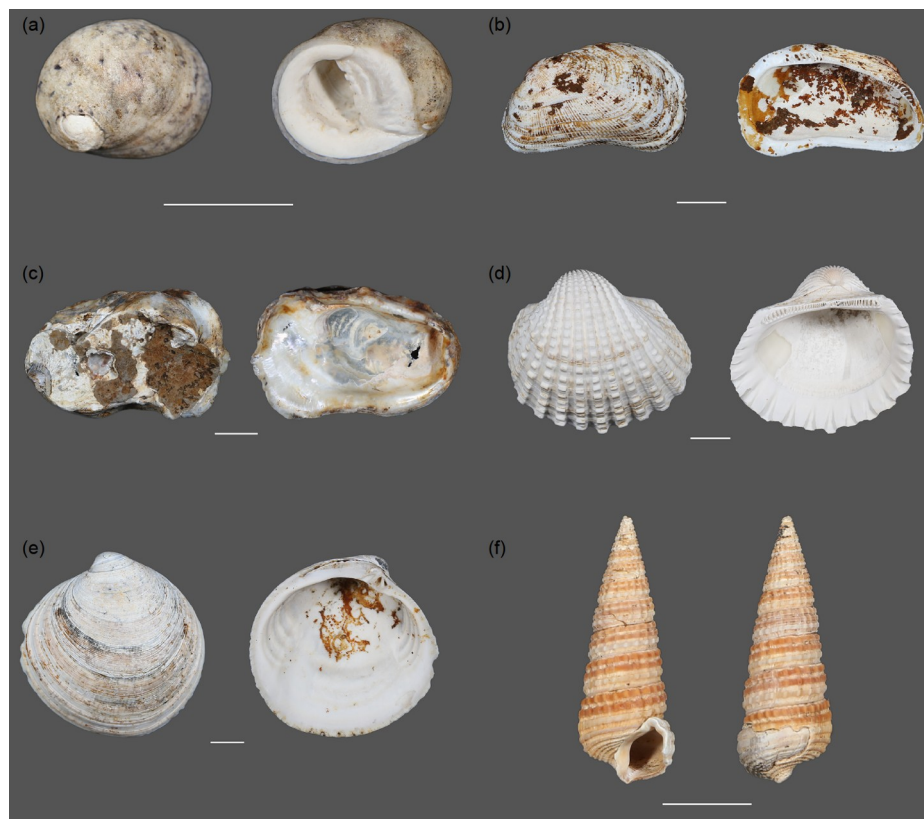
Bivalves dominate all molluscs, with the average proportions of the NISP and MNI exceeding 90%. Oysters are the most abundant species. Although the NISP and MNI and relative proportions of oysters fluctuate considerably among different artificial layers, the average ratios of the NISP and MNI are 63.94% and 64.72%, respectively. Blood cockles have an average NISP and MNI ratio of above 20%; the proportion is 7% for Chinese razor clams and 3% for oblique ark shells (Appendix 2). In contrast, gastropods account for less than 5%. Among them, girdled horn shells are the most common, with NISP and MNI values of 2.82% and 3.19%, respectively. The other five gastropod taxa have NISP and MNI values of less than 1% (Appendix 2, Figures 4, 5).

As mentioned above, oysters are challenging to identify at the species level simply based on morphology. However, blood cockles can be identified precisely, and they were relatively abundant in all artificial layers. The size variations in their shells are representative of the molluscs' exploitation efficiency by the Jingtoushan people. Hence, 864 complete shells of blood cockles from 44 artificial layers were selected for measurement, and their shell length and height were taken. The statistical data reveal that the maximum, minimum, and mean values of shell length and shell height of the blood cockles fluctuate but in general decrease through time (Figure 6). The maximum values of the mean shell length and shell height of the blood cockles appear in the earliest artificial layer (20-5, SL=53 mm, SH=45 mm, respectively). It fluctuates repeatedly in the middle layers and occasionally reaches a large size, such as in the layer 16. In the later layers

**Table 2** Radiocarbon dating results from the sampling column at the Jingtoushan site

Lab. #	Sampling stratigraphy	Material	Measured age (a BP)	Calibrated age (cal a BP)	
				1 $\sigma$ (68.3%)	2 $\sigma$ (95.4%)
ANU-69933	11	Charcoal	7169±25	7943–8005	7935–8016
ANU-69935	12A	Charcoal	7150±24	7934–7976	7875–8011
ANU-69924	13	Blood cockle	7797±25	8543–8592	8458–8600
ANU-69925	15	Blood cockle	7849±25	8558–8637	8544–8686
ANU-69918	17	Blood cockle	7795±25	8541–8593	8457–8600
ANU-69919	18	Blood cockle	7795±26	8540–8594	8456–8601
ANU-69920	19	Blood cockle	7937±25	8641–8851	8602–8980
ANU-69921	20	Blood cockle	7866±24	8594–8639	8549–8717
ANU-69936	20	Charcoal	7293±27	8025–8164	8020–8170





**Figure 3** The dominating mollusc taxa at the Jingtoushan site (scale bar: 1 cm). (a) *Nerita* sp.; (b) right shell of *Barbatia obliquata*; (c) right shell of *Crassostrea* sp.; (d) left shell of *Tegillarca granosa*; (e) left shell of *Cyclina sinensis*; (f) *Cerithidea cingulate*.

(10 and 11), the mean values of shell length and height decrease to around 32 mm and 26 mm, respectively, significantly smaller than those in the stage exhibiting larger shells.

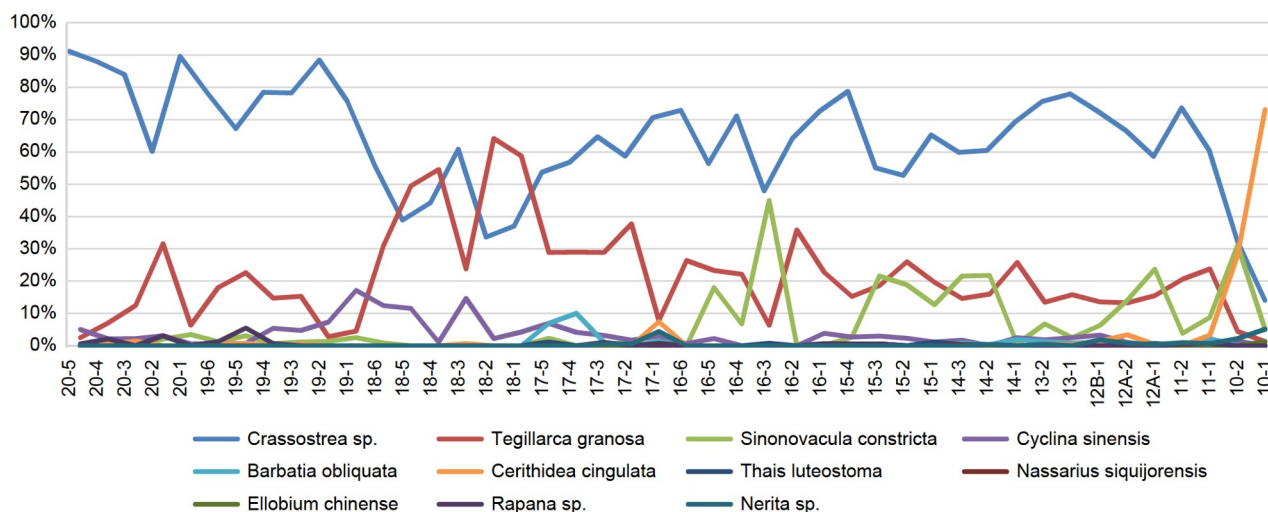
#### 4.3 Taxa and relative proportions of fish remains

An abundance of fish remains were unearthed at the Jingtoushan site, with an NR of 18,347 in trench T509. The NISP is 12,827, with an NISP/NR rate of 69.91%. There are at least 14 fish taxa, including the pufferfish (*Takifugu* sp.), drum fish (Sciaenidae), mullet (Mugilidae), yellowfin seabream (*Acanthopagrus latus*), blackhead bream (*Acanthopagrus schlegelii*), Chinese seabass (*Lateolabrax maculatus*), conger eel (Congridae), silver eel (*Muraenesox cinereus*), eagle ray (*Aetobatus* sp.), stingray (*Dasyatis* sp.), ground shark (Carcharhiniformes), mackerel shark (Lamniformes), Elasmobranchia fish (Elasmobranchii), and sturgeon (*Acipenser* sp.) (Figure 7). Appendixes 3, 4 and 5 show the NISP and MNI statistics, proportions of fish, and skeletal distributions.

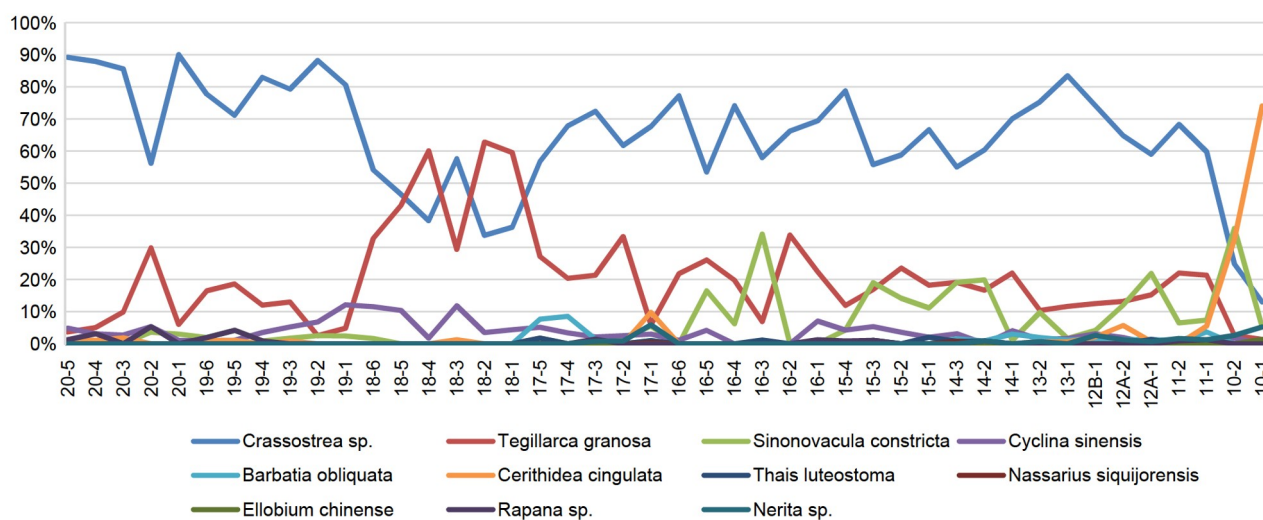
Overall, Chinese seabass, blackhead seabream, and drum fish dominate the NISP of fish remains at the Jingtoushan site, but the number of fish taxa varies in different cultural layers (Appendixes 3, 4). Chinese seabass is the most abundant, with an average of 29.50% and 17.44% for the NISP and

MNI, respectively. The proportion of NISP fluctuates between 17.57% and 37.83% in different cultural layers, and is the most abundant fish in most of the cultural layers. Chinese seabass is only surpassed by the drum fish and blackhead seabream in a few cultural layers (e.g. cultural layer 16), and is the third most abundant fish in this layer (Appendix 3). Blackhead seabream is the second most abundant fish at the Jingtoushan site, with a mean NISP of 20.34% and a mean MNI of 13.89%, respectively. Yellowfin seabream has an average NISP of 10.69% and an average MNI of 8.24%. Drum fish has mean NISP and MNI proportions of 14.46% and 12.05%, respectively, whereas mullet has mean NISP and MNI ratios of 7.76% and 12.14%, respectively. The mean proportions of the NISP and MNI in pufferfish are 4.47% and 8.62%, respectively. The conger eel has average NISP and MNI ratios of 4.99% and 3.94%, respectively, and has average NISP and MNI ratios of 2.65% and 2.37%, respectively. Owing to the skeletal structure of the conger and the silver eels, only the vertebrae are preserved, whereas the cranium bone and the girdle bones are rare. Similarly, the mean proportions of the NISP and MNI (less than 2%) of sturgeons, eagle rays, stingrays, and sharks are relatively small, this is, less than 2%, due to their cartilaginous skeletal structure; sturgeon scutes, a few vertebrae and teeth of Elasmobranchii fish could be preserved (Appendix 5).





**Figure 4** Mollusc NISP proportions of artificial layers in the sampling column at the Jingtoushan site.



**Figure 5** Mollusc MNI proportions of artificial layers in the sampling column at the Jingtoushan site.

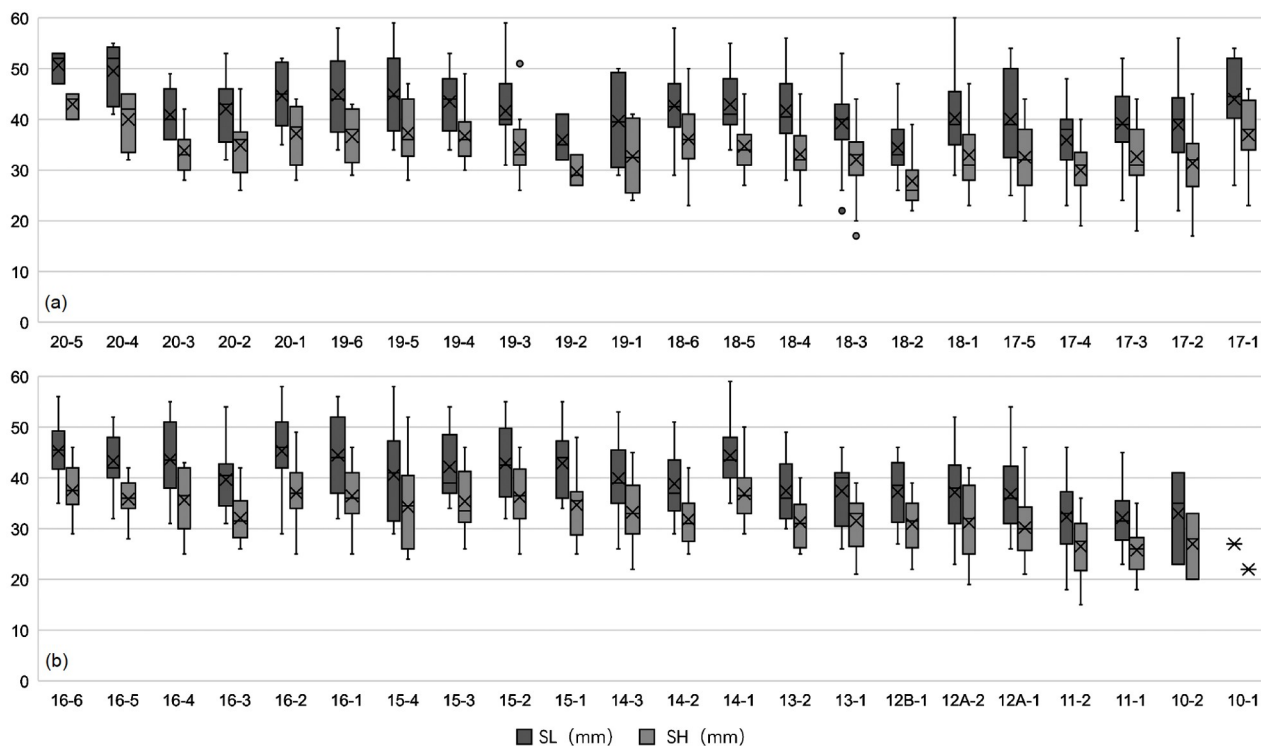
#### 4.4 Chronological changes in marine faunal remains

##### 4.4.1 Mollusc remains

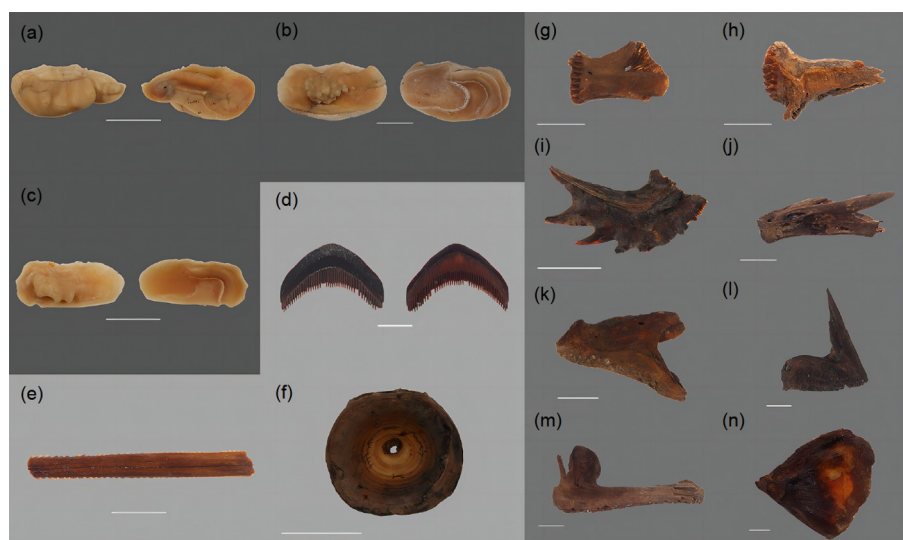
The NISP and MNI ratios of the different mollusc taxa in the sampling column indicate significant chronological changes (Figures 4, 5). Specifically, two relatively abundant taxa, the oysters and the blood cockles, show a negative correlation through the overall trend. Oysters decline noticeably and experience a low point at layer 19 (approx. 8,000 cal a BP), whereas blood cockles increase significantly at the end of this layer. Both oysters and blood cockles are stable in the cultural layer 17 (around 7,900 cal a BP), fluctuating slightly, and then decline in the cultural layer 11 (approx. 7,800 cal a BP). Furthermore, the ratios of black clams are negatively correlated with those of oysters. The proportions of black clams increase from the cultural layers 19 to 17 (about 8,100

to 7,900 cal a BP), then decline and remain stable. The cultural layer 16 (approx. 7,900 cal a BP) shows a considerable surge in Chinese razor clams, correlating with a minor decrease in oysters and subsequent fluctuations in the share of oysters. In general, the proportions of Chinese razor clams after the cultural layer 16 are much greater than that in the preceding cultural layer 16. The girdled horn shells are few in the cultural layers earlier than 11, but they increase immediately in the cultural layer 11 and become the most abundant mollusc in the cultural layer 10.

The proportion and the size distribution curves of blood cockles show remarkable similarity (Figures 5, 6). During the period when the ratios of blood cockles are higher, such as in the artificial layers of 19-4-6, 18-1-6, 16-2, 15-2, and 14-1, the shell sizes (SL and SH) are larger, implying a po-



**Figure 6** Size distribution of blood cockles from the sampling column at the Jingtoushan site. The maximum, minimum, quartile, mean, and median values are plotted in the chart.



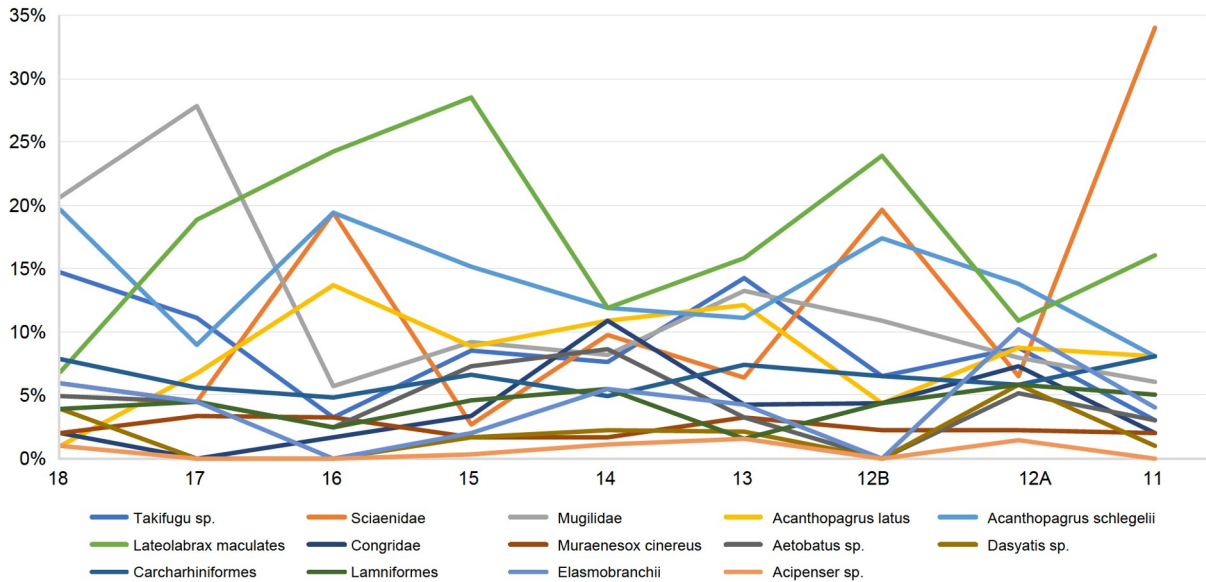
**Figure 7** Diagnostic fish bones and otoliths at the Jingtoushan site (scale bar: 1 cm). (a) sagittal otolith of *Larimichthys crocea*; (b) sagittal otolith of *Megalonibea fusca*; (c) sagittal otolith of *Miichthys miiuy*; (d) teeth of *Aetobatus* sp.; (e) caudal fin spine of *Dasyatis* sp.; (f) vertebra of Carcharhiniformes; (g) left dentary of *Takifugu* sp.; (h) left premaxilla of *Takifugu* sp.; (i) left preopercle of *Lateolabrax maculatus*; (j) right dentary of *Lateolabrax maculatus*; (k) left dentary of *Acanthopagrus latus*; (l) right premaxilla of *Acanthopagrus schlegelii*; (m) left premaxilla of Sciaenidae; (n) right opercle of Mugilidae.

sitive correlation between them.

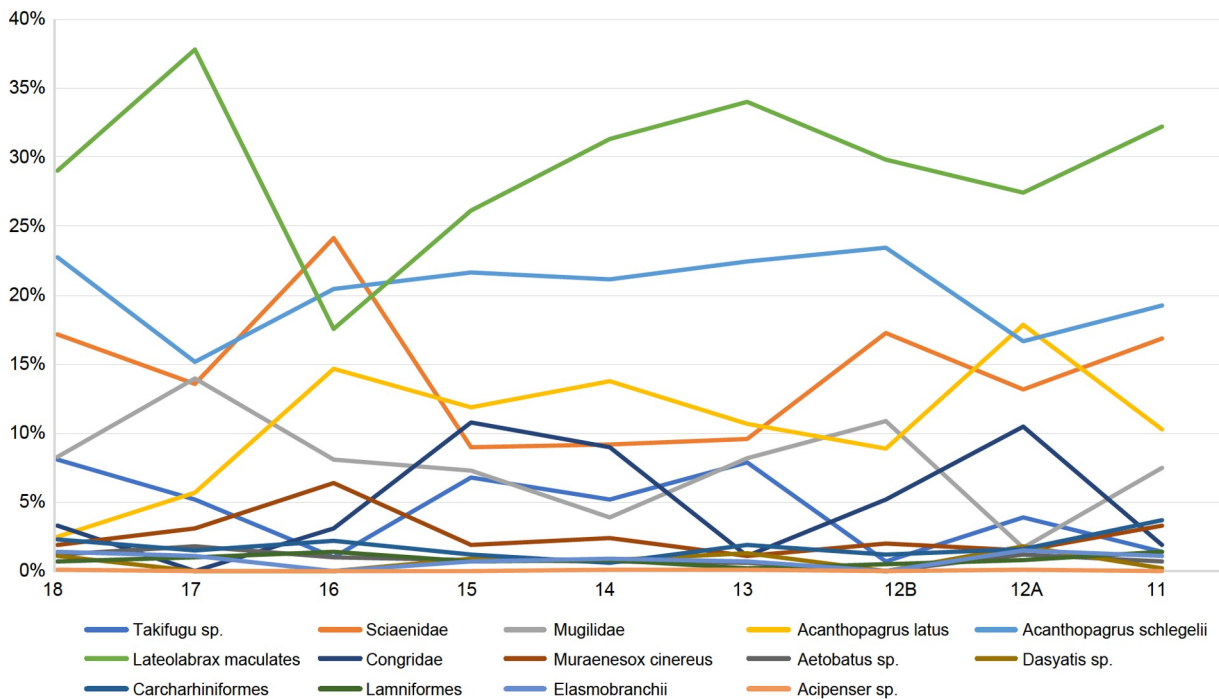
#### 4.4.2 Fish remains

The NISP and MNI proportions of fish remains from trench T509 change drastically from the cultural layers 18 to 11, but not synchronously between both quantification methods

(Figures 8, 9). MNI as secondary data, can be affected by the skeletal part survivorship of a species (Appendix 5) and may exaggerate the presence of rare species in the assemblage (Reitz and Wing, 2008). Since the fish remains in this study are from the same trench T509, NISP is used to discuss the chronological change of fish taxa instead of MNI.



**Figure 8** Relative proportions by NISP of fish remains from the cultural layers of trench T509 at the Jingtoushan site.



**Figure 9** Relative proportions by MNI of fish remains from the cultural layers of trench T509 at the Jingtoushan site.

According to radiocarbon dating results (Table 1), the cultural layer 18 of trench T509 refers to about 8,000 cal a BP and the cultural layers 17 to 12 are closely around 7,900 cal a BP. The cultural layer 11 is about 7,800 cal a BP, representing the middle to later phase of the deposit. Figure 8 indicates that a remarkable change of relative proportions occurs in the cultural layer 16 (approx. 7,900 cal a BP), represented by the decrease in the ratios of Chinese seabass, mullet, and pufferfish and an increase in the proportions of

drum fish, yellowfin seabream, blackhead seabream, and silver eel. The proportions do not change much from the cultural layers 15 to 13, but change significantly in the cultural layer 12A (approx. 7,800 cal a BP).

In sum, the taxonomic composition of molluscs and fish remains demonstrates chronological changes and is simultaneous to some degree. Since trench T509 only has the cultural layers 18 to 11, the composition of fish remains in earlier layers is still unknown. Therefore, we cannot presume



whether there was a significant shift of composition, the same as that shown in the mollusc assemblage in the layer 18. However, fish remains have a considerable change of proportions in the cultural layer 16. Correspondingly, the relative proportions of molluscs also change significantly, represented by the substantial increase of Chinese razor clams from the cultural layer 16 and the decrease in oyster ratios. Similarly, in the cultural layer 12A, the change of fish remains proportions corresponds to a peak in Chinese razor clams and a decrease in oysters. Although the NISP proportion of the significant shift in the mollusc remains occurs in the cultural layers 11 and 10, due to the lack of fish samples from the cultural layer 10, the relative variations could not be clarified.

## 5. Discussion

### 5.1 The palaeoenvironment of the settlement

Anthropological records of modern foraging tribes show that the foraging range of molluscs is usually no more than 5 km due to their low return rate. When the harvesting location of molluscs is far away, the foragers tend to process the shellfish *in situ* and only bring the flesh back to the settlement (Bigalke, 1973; Meehan, 1975, 1977; Gould, 1980; Voigt, 1982). Thus, the large number of molluscs at the Jingtoushan site possibly came from within a 5 km radius of the site. Through zooarchaeological analyses of the mollusc and fish remains excavated from the site, the taxa and relative proportions of these remains have been recorded. On this basis, together with mollusc and fish ecology, we try to reconstruct the palaeoenvironment around the Jingtoushan site and capture its temporal changes between 8,300 and 7,800 years ago. Moreover, we attempt to analyse the Jingtoushan people's exploitation of the environment and resources and the potential effects of past human activities on the area.

#### 5.1.1 *The settlement environment reflected by mollusc remains*

The molluscs have relatively consistent habitats, so that they can provide reliable information about the coastal palaeoenvironment and sea level changes near the Jingtoushan settlement. The Jingtoushan mollusc species mainly inhabit the intertidal zone, which can be further classified into muddy-sandy coasts, sandy-muddy coasts, and soft mudflats (muddy coasts) according to sediment composition. Oysters, oblique ark shells, and nerite snails live in the rocky reefs, while blood cockles, Chinese razor clams, black clams and girdled horn snails inhabit the muddy-sandy coasts and mudflats. Blood cockles and Chinese razor clams inhabit the mudflats, while black clams inhabit muddy-sandy coasts (Yao, 2007) (Appendix 6). It can be assumed that rocky reefs and muddy-sandy coasts are distributed near the Jing-

toushan site.

The distributions of molluscs in the intertidal zone also vary. For example, oysters often attach to the rocky reefs in the middle of the intertidal zones, blood cockles prefer the middle and lower intertidal zones of mudflats, and black clams and girdled horn shells inhabit the vicinity of the high-tide line of muddy-sandy shores (Shen et al., 2010; Li et al., 2018). The chronological changes in mollusc proportions indicate a negative correlation between oysters inhabiting rocky reefs and the muddy-sandy coasts where blood cockles, Chinese razor clams, and black clams inhabit. This reflects the change in the palaeoenvironment within the foraging range of the Jingtoushan settlement. The most significant proportional change occurs in the cultural layers 19 and 18 (about 8,100 to 8,000 cal a BP), possibly indicating a reduction in the rocky reefs and an expansion of the muddy-sandy shores instead.

After the cultural layer 16 (approx. 7,900 cal a BP), the proportions of mudflats inhabited by blood cockles and Chinese razor clams grow higher, more than the period before the cultural layer 19, probably indicating an increase in the mudflats during this time. Girdled horn snails live near the high-tide line; the farther away from the high-tide line, the fewer they are (Yang and Shen, 1992). The substantial increase of this taxa in the cultural layer 11 (7,800 cal a BP) implies that the resources near the high-tide line may have been exploited more often. Considering that molluscs may be commonly gathered within 5 km, the high-tide line could have possibly advanced towards the settlement from a distant area of the mollusc foraging range, such as around 5 km away from the site, causing easier access to these resources. At the same time, we can see a decrease in the proportions of oysters, blood cockles and black clams, reflecting a possible shrink in the intertidal zone. In sum, the change in mollusc proportions may be closely related to the changes in the intertidal environment due to the rise in sea level.

The rise of sea level in eastern China before 7,000 years has been studied (Zhao et al., 1994; Liu et al., 2004; Zheng et al., 2018). The occupation of the Jingtoushan site is in this timeframe. Research of the coastal palaeoenvironment in the Ningbo-Shaoxing Plain shows that the sea level kept rising and the shoreline moved inland since 8,000 a BP, coinciding with the late phase of Jingtoushan (Zheng et al., 2018; Lyu et al., 2021). The increasing sea level forced the intertidal zone to contract, and the high-tide line moved closer to coastal settlements. The transgression caused changes in the sediment, altering the distribution of rocky reefs, muddy-sandy and muddy coasts, which then led to alterations in the taxa of molluscs, further impacting the diets of the coastal populations that relied on marine resources.

#### 5.1.2 *The settlement environment reflected by fish remains*

In general, fish inhabit a more extensive range than molluscs

and migrate regularly. Thus, it is less precise to reconstruct the palaeoenvironment using fish remains than that of molluscs. By reviewing the biology and ecology of the fish species at Jingtoushan, we find that they mainly inhabit offshore and inshore regions (Appendix 7). Their restricted habitat suggests that these species can reflect the palaeoenvironment well.

Chinese seabass, the most abundant fish at Jingtoushan, is commonly found in the Bohai Sea, the Yellow Sea, the Yangtze River estuary and the East China Sea. It dwells in the middle and lower layers of brackish waters near the sea, as well as rocky reefs with strong currents (Zhao et al., 2016; Wu and Zhong, 2021). The blackhead seabream is a eurythermic and euryhalinity fish, that prefers rocky reefs, and clear waters with sandy and muddy seabeds. Adult individuals primarily feed on molluscs, small fishes, and shrimp (Zhao et al., 2016). The Yellowfin seabream is a small to medium-sized species which prefers warm temperatures; it primarily inhabits inshore areas with muddy-sandy seabed and occasionally enters estuaries or freshwater environments (Zhao et al., 2016). Silver eels are inshore and offshore demersal fish that live on muddy-sandy seabed or rocky reefs (Zhao et al., 2016; Wu and Zhong, 2021). Moreover, pufferfish are slow-swimming inshore and offshore demersal fish in warm waters, and the Jingtoushan inhabitant would have been able to catch them relatively easily (Wu, 2002; Zhao et al., 2016). Sturgeons are migratory fish that are widely distributed in inshore and freshwater rivers; they migrate upstream to the upper Yangtze River to spawn during the breeding seasons.

Although the mullet (*Mugilidae*) and drum (*Sciaenidae*) fish cannot be identified as species, in general, they inhabit the brackish waters in the tropical, subtropical and temperate zones, particularly along the coasts of estuarine and brackish bays (Yu and Cui, 2021). Drum fish are usually present in muddy-sandy offshores and epicontinental seas with riverine inflows, with few in the deep-sea areas unexposed to warm currents (Zhu et al., 1963). Conger eels are eurythermic fish that can survive in large areas, from temperate to subtropical and tropical zones, with muddy-sandy seabeds or rocky reefs (Zhao et al., 2016).

Elasmobranchii fish such as eagle rays, stingrays, ground sharks, and mackerel sharks have been unearthed at the Jingtoushan site. Eagle rays generally live in tropical or warm-temperate offshore seas, adapting to brackish environments and feeding on molluscs and crustaceans (Wu and Zhong, 2021). Stingrays usually inhabit offshore or inshore warm-temperate brackish or freshwater environments, often lurking in the shallow seas with muddy-sandy seabed, and feed on molluscs or crustaceans (Zhao et al., 2016; Wu and Zhong, 2021). Ground sharks are eurythermic inhabiting inshore, offshore or pelagic waters, and mackerel sharks inhabit warm-temperate offshore or pelagic waters; both taxa

can live in different sea depths (Zhao et al., 2016).

Examining the ecology and biological characteristics of fish and mollusc remains gives us an understanding of the settlement palaeoenvironment. The Jingtoushan settlement was located close to the sea, with muddy-sandy coasts and rocky reefs. It was dominated by a warm and humid climate during the 500-year occupation and the seawater salinity in this area was low due to the inflow of freshwater streams and the Yangtze River into the East China Sea. The coastal environment and ecosystem of the Jingtoushan area were complex and varied, providing plenty of resources and environment for the prehistoric populations to live.

## 5.2 Fishing economy and exploitation practices

The Jingtoushan people relied heavily on marine molluscs and fish for subsistence. Oysters, blood cockles, Chinese razor clams, and black clams were their primary mollusc resources for consumption, and they are still favoured now for nutrition and taste. According to ethnoarchaeological studies, molluscs are an important food source and are easy to collect. Women and children can be the primary members to fulfil the task, and the workforce of the community can be adequately allocated (Crook, 1992; Keegan et al., 2019). The gradual reduction of blood cockle size indicates that it could have been influenced by some level of survival pressure, which might be related to issues such as environmental change, community development, and population increase.

The most exploited fish at Jingtoushan are Chinese seabass, blackhead seabream, and yellowfin seabream, which inhabit inshore, suggesting that the coastal areas could be the primary fishing place for the Jingtoushan habitants. Fishing gear such as cover pots, which have been unearthed at Jingtoushan, is suitable for this coastal environment (Gabriel et al., 2005). The large number of big otoliths of drum fish and bones of cartilaginous fish suggests that the Jingtoushan people were capable of fishing larger fish such as drum fish, and ferocious fish such as ground sharks and mackerel sharks, representing their proficient fishing capability. Notably, plenty of pufferfish remains are retrieved from all cultural layers of the Jingtoushan site, indicating that these toxic fishes became a consistent marine food source for the Jingtoushan people. Pufferfish is an inshore demersal fish preying on molluscs, and usually contains high levels of tetrodotoxins in their internal organs, skin, and blood; the tetrodotoxins must be removed, and the fish must be boiled or salted before consumption (“Fishes of Fujian Province” Editorial Subcommittee, 1984). The Jingtoushan people are believed to have been proficient in handling toxic fish.

Moreover, pufferfish remains have been commonly found in coastal shell middens, particularly at sites of the Beixin and Dawenkou cultures on the Jiaodong Peninsula, such as Baishicun, Dazhongjia, Beiqian, and Geduiding in Shandong

Province (Cheng, 1992; The Institute of Archaeology, Chinese Academy of Social Sciences, 1999; Song and Wang, 2016; Song, 2022). Similar to the Jingtoushan site, the fish remains from these shell middens are composed mainly of inshore and offshore taxa such as blackhead seabreams, red seabreams (*Pagrus major*), and Chinese seabass. Pufferfish are slow-swimming fish that are easy to catch. The use of the toxic Tetraodontiformes fish can be dated back to the late Palaeolithic age (Boulanger et al., 2023). The toxic pufferfish became an important food source when people gained knowledge of these fish and were able to safely separate the toxic and edible parts. Additionally, seasonal fishing was possibly practiced by the Jingtoushan people targeting migratory fish, such as the Chinese seabass in spring when they came to the coast and estuary to feed, and the pufferfish during their spawning season, also in spring (Feng and Jiang, 1998; Zhao et al., 2016).

The ancient Jingtoushan people had developed a self-sufficient subsistence economy by exploiting both inshore and offshore resources. The species with higher economic value were purposefully targeted, indicating a well-planned fishing economy. This is further supported by the archaeological findings from the Jingtoushan site, such as the fishing nets, cover pots and traps, which were mainly used for inshore and offshore fishing of small to medium fish and molluscs in the shallow seas (Li, 1990). The Jingtoushan people seemed not to have been capable of seafaring over long distances. However, it was likely feasible for them to investigate neighbouring islands and coasts with the aid of sophisticated navigation techniques, such as canoes.

The fishing economy of the coastal shell middens in China shares standard features: for example, the mollusc taxa may vary from region to region, but are mostly indigenous species; the fish taxa are mainly inshore and offshore species, and only a few of them are pelagic species (Zhao, 2014). Clearly, the Jingtoushan fishing economy tallies with this pattern. Prior to 7,000 years ago, the subsistence economy of the coastal populations in China was fishing, hunting, and gathering, while agriculture was rarely practised (Zhang and Hung, 2016). However, evidence of rice cultivation has been reported at the Jingtoushan site (Dai et al., 2022), indicating a subsistence pattern of fishing-hunting-gathering supplemented by rice cultivation. Furthermore, compared to the Kuahuqiao culture of Zhejiang Province, the ancient Jingtoushan population was more adept at utilising marine resources. Although dolphin remains have been discovered in the Kuahuqiao culture, the fish remains primarily consist of freshwater taxa, and no marine molluscs have been found (Jiang, 2014). Additionally, the Hemudu culture, represented by the Tianloushan site, had sophisticated fishing practices but mainly in the freshwater (Zhang, 2015). The subsistence pattern of Jingtoushan is different from either of them, and it could be influenced by the coastal environment.

### 5.3 Interactions among marine resources, the palaeoenvironment, and the prehistoric community

The large number and diverse taxa of marine animal remains at the Jingtoushan site fully demonstrate the ancient coastal population's ability to exploit marine resources and adapt to the coastal environment in Neolithic China. The Jingtoushan community experienced a long period of prosperity and decline, and may have abandoned the settlement due to changes in the coastal environment.

Investigating the marine animal remains can assist us in comprehending the development of the Jingtoushan community. The mollusc taxa appear to have changed across different phases, potentially indicating alterations in the palaeoenvironment, as they were an important food source for the foragers. Marine geology studies have revealed that the sea level in eastern China experienced a fluctuating rise from 15,000 to 6,000 years ago (Feng and Wang, 1989; Yang, 2003; Zheng et al., 2018; Lyu et al., 2021). We suggest that in the early phase of the settlement, the sea level rose slowly, the fishing resources in the surrounding settlement were initially exploited, and the community gradually developed. During the middle stage of the settlement, the sea level was steady, providing a more favourable coastal habitat for the ancient population and leading to the prosperity of the community. Mollusc exploitation may have shrunk due to the rise of sea level and the population decline caused by over-exploitation; fishing was relied on more for subsistence. In the late phase, the sea level continued to rise, and the shoreline approached the settlement, forcing the Jingtoushan people to abandon it. Although fish resources are also wildlife resources, the fish taxa do not change significantly, and the NISP and MNI data do not show an apparent falling trend. This indicates that human activities had less effects on the fish in an open marine environment.

Fishing was a primary source of subsistence for the Jingtoushan people and was a necessary component of the community development. In addition, the Jingtoushan people hunted deer and pigs, gathered edible plants, and even cultivated rice for subsistence (Zhejiang Provincial Institute of Cultural Relics and Archaeology et al., 2021). This is similar to the Beiqian site on the Jiaodong Peninsula. It shows that the Jingtoushan people used their advantages of geographical location to exploit terrestrial and marine resources and adopt agricultural factors. Nevertheless, agricultural production could not provide long-term subsistence patterns to the community, which may have been caused by the alterations in the marine environment, the population pressure generated by settlement growth, or the interactions between the local foragers and the immigrant agricultural populations. Whether the Jingtoushan population, who had gained the skills of rice cultivation in the late phase of the site occupation, spread to surrounding areas through their advanced fishing practices



and seafaring capabilities, or if they stayed in the Ningbo-Shaoxing Plain and developed into the Hemudu culture, is not clear. This aspect needs to be explored in future studies.

## 6. Conclusion

This research used zooarchaeological methods to investigate the marine faunal remains from the Jingtoushan shell midden in the city of Yuyao in Zhejiang Province. At least 11 taxa of marine molluscs and 14 taxa of marine fish could be identified as a result. By examining the ecological and biological features of the mollusc and the fish, the study attempted to understand the interactions between the palaeoenvironment, fishing, and community development at the Jingtoushan site across the different phases. The results show that the Jingtoushan people mainly exploited marine resources in the inshore and offshore areas, which may have caused surviving pressure on the mollusc populations. The rise of sea level could be one of the reasons why the Jingtoushan people eventually gave up their settlement.

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**Conflict of interest** The authors declare that there are no conflicts of interest.

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