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Complete List of Authors:	Boulanger, Clara; National Museum of Ethnology, Department of Modern Society and Civilization; Muséum National d'Histoire Naturelle, Homme & Environnement; Australian National University College of Asia and the Pacific, Archaeology and Natural History Hawkins, Stuart; Australian National University, College of Asia and the Pacific Samper Carro, Sofia; Australian National University College of Asia and the Pacific, Archaeology and Natural History Ono, Rintaro; National Museum of Ethnology, Department of Modern Society and Civilization O'Connor, Sue; Australian National University, College of Asia and the Pacific
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# **Continuity and variability in prehistoric fishing practices by *Homo sapiens* in Island Southeast Asia: new ichthyofaunal data from Asitau Kuru, Timor-Leste**

C. Boulanger <sup>1 2 3 4</sup>; S. Hawkins <sup>4</sup>; S. C. Samper Carro <sup>4</sup>; R. Ono <sup>2</sup>; S. O'Connor <sup>4</sup>

<sup>1</sup> Japan Society for the Promotion of Science International Research Fellow

<sup>2</sup> Department of Modern Society and Civilization, National Museum of Ethnology, Osaka, Japan

<sup>3</sup> UMR 7194 Histoire Naturelle de l'Homme Préhistorique, Muséum National d'Histoire Naturelle, Paris, France

<sup>4</sup> Archaeology and Natural History, School of Culture, History and Language, College of Asia and the Pacific, Australian National University, Canberra ACT, Australia

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3 **Keywords:** ichthyoarchaeology, Anatomically Modern Human, Palaeolithic, marine  
4 environments, fishing techniques, modern behavior  
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8 **Abstract**  
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11 Human adaptations to marine resources were critical in the successful colonization of  
12 Island Southeast Asia (ISEA) and the Pacific since the Late Pleistocene. Fishing the dense  
13 biomass of ichthyofauna present in this maritime region required the cognitive capability to  
14 conceptualize fish ecology and develop methods and technologies to exploit these challenging  
15 underwater environments. This likely gave our species an edge over other hominin species in  
16 depauperate island landscapes. This paper reviews the limited number of archaeological sites  
17 in ISEA where fish bone assemblages and fishing gears have been recovered, incorporating  
18 new archaeological data from the site of Asitau Kuru (Jerimalai), Timor-Leste. Our findings  
19 indicate continuity in fishing behavior over several millennia with a near-shore exploitation of  
20 local marine habitats including trolling, line fishing and spearing. These data indicate the  
21 ecological plasticity of our species and the enduring fishing traditions passed on to generations  
22 through learned behavior.  
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## Introduction

Climate change and the discovery of new environments have at times been interpreted as the critical factors in the development of technological and cultural innovations by hominins (Behrensmeyer 2006; Potts 2012; Potts 2013). During the course of the evolution of *Homo*, the mastery of the sea has certainly been one of the last major advances in terms of confrontation with novel ecosystems in tropical Island Southeast Asia (ISEA).

Hominins first settled the region when *H. erectus* arrived in Indonesia by 1,300,000 years ago and the Philippines by 709,000 years ago via the establishment of land bridges and savannah corridors connecting mainland Asia with these continental islands on the Sunda shelf (Ingicco et al. 2018; Matsu'ura et al. 2020). More recently, novel species of archaic human, *H. floresiensis* on Flores by 100,000 years ago (Sutikna et al. 2016), and *H. luzonensis* on Luzon by 67,000 years ago (Détroit et al. 2019) have been identified, adding to the complexity of hominin evolution in the region. However, no evidence has so far shown any indication that those hominins ever exploited marine resources. The earliest and only evidence of aquatic interactions by archaic humans in ISEA was at the site where *H. erectus* was first discovered at Trinil on the island of Java, Indonesia ca. 600,000 years ago as indicated by the discovery of engraved abstract motifs on freshwater molluscs, which were also used as tools (Joordens et al. 2015). While archaic human species are capable of procuring sessile molluscs from river and coastal habitats by hand (Colonese et al. 2011), the development of technology and methods to procure marine fish requires cognitive capability that, to date, only *H. sapiens* have proven to possess (Roberts 2019; Shipton, O'Connor, and Kealy 2021; O'Connor et al. 2017).

A growing body of zooarchaeological research focused on ichthyofauna revealed unequivocally that modern humans, having first adopted fishing practices in South Africa during the Middle to Late Stone Age (van Niekerk 2011), left Africa ca. 100,000 years ago (Montinaro et al. 2021), rapidly arrived in ISEA ca. 73-65,000 years ago (Clarkson et al. 2017; Westaway et al. 2017) where they underwent substantial social transformations and adapted to oceanic regions punctuated by tropical islands with advanced fishing techniques by at least 42,000 years ago (O'Connor, Ono, and Clarkson 2011; Shipton et al. 2019; Kealy et al. 2020). The adaptation to coastal marine environments has signified to many scholars the flexibility in our species and indicated a cognitive capability that has been used as a marker for modern human settlement of ISEA (O'Connor et al. 2017). This was a paradigm shift in the evolution of our species and permitted fundamental changes in culture and subsistence that facilitated the colonization of the last frontier on planet earth – the colonization of the vast Pacific Ocean – reaching as far as New Zealand by 700 Before Present (BP) (Walter et al. 2000).

In this paper, we hypothesize that the diverse marine environments of ISEA encountered by multiple populations migrating under periods of climate and culture change since the late Pleistocene (Kaharudin et al. 2019; Kealy, Louys, and O'Connor 2018; Lambeck and Chappell 2001; Williams et al. 2018) are likely to have resulted in a significant amount of variability in fishing practices across space and time. We test this hypothesis by exploring variability in fishing behavior across the Wallacean, Philippines, and Ryukyu archipelagos, including new data from the Asitau Kuru site in Timor-Leste (Fig. 1).

### *Coastal prehistoric sites in Island Southeast Asia*

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Island Southeast Asia includes the greatest marine biodiversity hotspots in the world (Huang et al. 2018). The Indo-Pacific region counts more than 3,500 marine species living on the coasts of the Southeast Asian archipelagos (Froese and Pauly 2022), where a small number of prominent archaeological sites spanning the Pleistocene-Holocene periods have seen the recovery of significant quantities of fish bones and small amounts of remnant fishing gear (Fig. 1).

Human occupation in the Ryūkyū archipelago, situated between Taiwan and the island of Kyushu in Japan, has been recorded as early as 37,000 BP at Yamishita-cho Cave I, excavated in the 70's, along with fish remains (whose records have been lost), on Okinawa Island, Central Ryūkyū (Takamiya, Kin, and Suzuki 1975; Fujita 2021) (Takamiya et al. 1975, Fujita 2021) (Fig. 1). On the same island, human remains as well as one of the oldest known shell fishhooks dating to 23,000 to 20,000 BP, were discovered at Sakitori-do Cave. However, only nine unidentified fish remains have been found at the site, along with a few freshwater molluscs (Fujita et al. 2016). Human remains dated between 24,000 to 19,000 BP were also found at Shiraho-Saonetabaru, on Ishigaki Island, associated with a few marine fish remains and shells (Nakagawa et al. 2010) (Fig. 1).

In the Philippines, Southwestern Mindoro, the site of Bubog I, as well as the nearby sites of Bubog II and Bilat Cave, also produced evidence of early human occupation (Fig. 1). Bubog I is a stratified shell-midden with a chronology ranging from ca. 33,000 to 4,000 BP (Pawlik et al. 2014; Boulanger et al. 2019; Pawlik and Piper 2019; Boulanger 2021). Therefore, the Bubog I sequence provides a record of the important palaeoenvironmental and palaeogeographic changes that occurred at the end of the Pleistocene and during the mid-Holocene. Boulanger and co-authors (2019) and Pawlik and co-authors (2014) notably pointed out a major clear-cut shift in molluscan and crustacean resources along the stratigraphic profile, from a predominantly mangrove to a mainly marine origin. The fauna, including molluscs, crustaceans, and coastal and coral reef fishes (Pawlik et al. 2014; Boulanger 2015; Boulanger et al. 2019; Boulanger 2021) is associated with *Tridacna* shell adzes, one being securely dated to 7550-7250 cal. BP (Pawlik et al. 2015), as well as a fishing gorge from deposits below the shell midden dating between 33,000 and 28,000 cal. BP (Boulanger et al. 2019; Pawlik and Piper 2019). Two igneous pebbles with waisted modifications, possibly used as net-sinkers, were also recovered from the shell midden (Boulanger et al. 2019; Pawlik and Piper 2019).

In the south of ISEA, the depauperate terrestrial environments of most Wallacean islands conditioned access to terrestrial resources and fostered the development of subsistence strategies based on the acquisition of aquatic resources at many coastal sites (Hawkins et al. 2017). The Pleistocene inhabitants of Northern Wallacean archaeological sites, such as the site of Leang Sarru in the Talau Islands, Golo Cave in Gebe Island and the Goa Topogaro sites, in Central Sulawesi, seem to have relied almost exclusively on shellfish gathering as these sites show no evidence of specialization for fishing (Ono, Soegondho, and Yoneda 2009; Ono et al. 2020; Szabó, Brumm, and Bellwood 2007). In the Lesser Sunda Islands, nearby the coast of Timor-Leste, the Here Sorot Entapa (HSE) rockshelter, on the island of Kisar (Fig. 1), produced an interesting assemblage dated from 15,500 years ago to the Early Holocene ca. 9,500 years ago, followed by a hiatus and a mid to late Holocene occupation deposit from 4,900 to 1,800 cal. BP (Kaharudin et al. 2019; O'Connor et al. 2019). A great number of fish remains were

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3 identified, as well as remains of marine molluscs, crabs and urchins. Shell artefacts, shell  
4 fishhooks and coral artifacts were also found (O'Connor et al. 2019). The site of Tron Bon Lei,  
5 on the southwest coast of Alor Island (Fig. 1), yielded a similar assemblage dated between  
6 21,000 and 3,500 BP, mostly constituted of fish remains (Samper Carro et al. 2016).  
7 Furthermore, fishhooks associated with mortuary practices dated to around 12,000 BP were  
8 discovered at the same site (O'Connor et al. 2017). More recently, Kealy and co-authors (2020)  
9 highlighted the importance of marine inshore resources for the prehistoric community living at  
10 the site of Makpan, located on the west side of Alor Island (Fig. 1), from 40,208-36,454 cal.  
11 BP. A preliminary study of Makpan fish remains shows that the fish assemblage is similar to  
12 that of Tron Bon Lei's, both in terms of size and reefal taxa (Kealy et al. 2020). This assemblage  
13 also produced abundant fishing gears, that attests to the high degree of maritime specialization  
14 of these populations (Kealy et al. 2020; Langley et al. 2020). A few kilometers inland on the  
15 island of Timor, the analysis of the material excavated at the inland site of Laili (Fig. 1)  
16 produced the oldest date for human occupation in Wallacea, back to 44,600 BP, as well as  
17 evidence of coastal exploitation with the discovery of a few marine and freshwater fish remains  
18 (Boulanger, Hawkins, et al. in review; Boulanger 2021; Hawkins et al. 2017).  
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### 25 *The site of Asitau Kuru and Its environmental context*

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28 Asitau Kuru (previously called Jerimalai) is a small limestone shelter located within the  
29 Nino Konis Santana (NKS) National Park and Marine Park at the easternmost tip of Timor-  
30 Leste. It is in an uplifted coralline terrace running parallel to the coast at grid reference 8°24.8''  
31 S and 127°17.5'' E southeast of the village of Tutuala (O'Connor 2007) (Fig. 2). The shelter is  
32 ~75 m above mean sea level and about 1 km from the current shoreline (Meijer, Louys, and  
33 O'Connor 2019; Langley, O'Connor, and Piotto 2016). Asitau Kuru is one of the most  
34 archaeologically significant sites within the NKS National Park. The north coast of Timor has  
35 a steep offshore topography. Because of this, and the uplift of the coralline terraces, changing  
36 sea levels have had little impact on the distance of the site relative to the coastline over the  
37 period of human occupation, and the shelter preserves a record of coastal resource use back to  
38 ~42,000 years ago. Asitau Kuru was excavated in 2005 and again in 2017 and produced a rich  
39 assemblage including stone and shell artefacts, and abundant remains of marine fauna including  
40 turtle, fish, shellfish, crab and urchin (O'Connor 2007; Shipton et al. 2019).  
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45 The NKS Park was gazetted in 2007 for its pristine terrestrial and marine habitats, and  
46 is currently the largest area of terrestrial, coastal and marine habitat with protected status in  
47 Timor-Leste (Edyvane et al. 2009). The marine component of the NKS park is located within  
48 the 'Coral Triangle'; recognised as the global epicentre of tropical marine biodiversity (Veron  
49 et al. 2009), and comprises 55,660ha of marine habitat encompassing the north, east and south  
50 coasts of the eastern portion of Timor-Leste (Edyvane et al. 2009). The shoreline habitats along  
51 the north coast, including the region proximal to Asitau Kuru, are quite limited owing to the  
52 narrow coastal plain and steep coastal gradient. This has produced a coastline characterised by  
53 coastal cliffs and rocky headlands, interspersed with small sandy pocket beaches and narrow  
54 fringing reefs (Edyvane et al. 2009).  
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58 Due to the steep offshore coastal profile, the vast majority of the marine habitats within  
59 the NKS Marine Park (> 90%) are deepwater (> 100m depth) with limited lagoonal and reef  
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3 flat development. To date less than 2% of the marine park has been mapped, and mapping has  
4 been restricted to the shallow nearshore zone of the north east coast and Jaco Island (Edyvane  
5 et al. 2009, 33). The marine nearshore zones are characterised by narrow reef flat (often < 60m  
6 but can be up to ~900m wide in a few restricted areas), limited seagrass beds in the shallower  
7 more protected waters, and corals in deeper water. Mangrove habitat is entirely absent on the  
8 north and east coasts within the vicinity of Asitau Kuru (Boggs et al. 2009). As would be  
9 expected the marine fauna of the NKS Marine Park is highly diverse. A total of 432 fish species  
10 were recorded during a brief biological survey with estimated total fish diversity in the order of  
11 840 species (Edyvane et al. 2009, 42). The deepwater habitats and coastal upwellings of the  
12 waters near Asitau Kuru also provide for cetaceans (Edyvane et al. 2009, 44), and pelagic  
13 species such as dog tooth tuna (*Gymnosarda unicolor*) are found in abundance, and unusually  
14 close to shore (Edyvane et al. 2009, 55). A subsequent assessment, albeit covering more regions  
15 of Timor-Leste, indicated even higher fish species diversity (Erdmann and Mohan 2013).  
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20 Two 1x1 test pits, Square A and Square B, were excavated in 2005 (O'Connor 2007)  
21 and another 1x1 test pit adjoining the east wall of Square B was excavated in 2017 (Square C)  
22 by spits averaging 3 cm to a maximum depth of 1.83 m (Shipton et al. 2019). On the whole, the  
23 stratigraphic layers were constituted of homogenous sediments (Shipton et al. 2019) (Fig. 3).  
24 Four distinct phases of occupation were identified during the first 2011 excavation in Square A  
25 and B: Phase I from 42,000 to 38,000 cal. BP, Phase II from 17,000 to 9,000 cal. BP, Phase III  
26 from 6,500 to 5,500 cal. BP, and Phase IV from 5,500 cal. BP to modern (O'Connor, Ono, and  
27 Clarkson 2011) (Fig. 3). The upper layers of the stratigraphic profile were marked by the  
28 presence of ceramic sherds (O'Connor 2007; Shipton et al. 2019). The oldest and lowest  
29 radiocarbon sample from Square A is dated at  $42,696 \pm 435$  cal. BP. For Square B, the oldest  
30 date obtained is  $42,140 \pm 261$  cal. BP, placing the occupation at Asitau Kuru at greater than  
31 42,000 cal. BP (O'Connor 2007). In total, 74 absolute age estimates, eight Optically Stimulated  
32 Luminescence (OSL) and 54 radiocarbon dates on marine shells have been obtained for both  
33 excavations, which evidenced three broad phases of occupation in Square C (C. Shipton et al.  
34 2019): Phase 1, Layers 6-8/spits 42-61 (Pleistocene), including the oldest date for the site at  
35 between 46,529 and 43,085 cal. BP, Phase 2, Layers 3-5/spits 17-41 (early to middle Holocene),  
36 and Phase 3, Layers 1-2/spits 1-16 (Neolithic) (Shipton et al. 2019).  
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## Materials and Methods

All excavated sediment from the site was dry sieved and then wet sieved through a 1.5 mm mesh screen, ensuring good recovery of small bones and shell artifacts. All finds were then dried before being sorted and separated, and weighed into categories of bone, stone, shell, urchin, crab, charcoal, and seeds (Shipton et al. 2019). The Asitau Kuru vertebrate assemblage is dominated by fish (NISP Square A and B = 38,687; NISP Square C = 16,600) and marine turtle (Chelonioidae) in the Pleistocene levels. The high proportion of Scombridae (tunas, bonitos, mackerels) in the assemblage of the first excavation, comprising 23 distinct marine taxa, suggested that modern humans were capable of systematic pelagic fishing and long-distance sea travel from 42,000 years ago (O'Connor, Ono, and Clarkson 2011). However, the conclusions reached by this study are still debated today (Anderson 2013; O'Connor and Ono 2013). Marine molluscs, such as *Nerita* spp., *Strombus* spp., *Trochus* spp., *Turbo* spp. and chitons were also identified. Where the marine resources described above indicate a focused exploitation of this environment, the presence of large rodents (Muridae), suggests an opportunistic exploitation of the limited range of vertebrates found on Timor at the time (O'Connor 2007). Among the faunal assemblage, 231 avian bone fragments have also been counted. Quails (Phasianidae), buttonquails (Turnicidae) and pigeons (Columbidae) are the most abundant groups and were probably accumulated by avian predators (Meijer, Louys, and O'Connor 2019). Moreover, Marwick and co-authors (2016) and Shipton and co-authors (Shipton et al. 2019) respectively counted a total of 9752 stone artefacts in Square A and B, and 2476 knapped artefacts and four hammerstones in Square C. The artifacts were mostly made on chert of various colors, using three main reduction strategies evident in the cores: discoidal, multiplatform and bipolar (Shipton et al. 2019). Marwick and colleagues (2016) argued that the assemblage showed little technological change over the 44,000 years sequence, indicating long-term continuity in lithic technological practice. However, Shipton and colleagues (2019) detected subtle changes beginning in Phase 2, which included an increase in stone tools diversity, including the addition of artefacts made on obsidian which is exotic to the island. Flakes with gloss, and a large retouched chert blade also appear in Phase 2 indicating an expanded range of tool functions beginning at this time. Four types of artifacts made from marine shell have been recovered at Asitau Kuru: beads, fishhooks, scrapers and adzes, predominantly dated from the early to middle Holocene (Shipton et al. 2020). Two fishhooks made on *Rochia* sp. shell (previously *Tectus* sp.) were found from spits 17 and 19 (middle Holocene) of Square C, adding to the five other fishhooks recovered from Square B, dated from the terminal Pleistocene (between 23,000 and 16,000 years ago) to the middle Holocene (O'Connor, Ono, and Clarkson 2011; Shipton et al. 2020) (Fig. 4). Five worked and ochre stained artefacts made of *Nautilus pompilius* shell, recovered in contexts dating to between 38,000 and 42,000 cal. BP, were retrieved during the first excavation (Langley, O'Connor, and Piotto 2016), as well as utilized ochre pieces (Langley and O'Connor 2019; Shipton et al. 2020). Shell beads made of *Nassarius* spp. (Langley and O'Connor 2015; Shipton et al. 2020) and *Olivia* spp. were also found, with one *Oliva* bead from the original excavation being directly dated to 37,191 ± 1055 BP (Langley and O'Connor 2016; Shipton et al. 2020). A similar range of beads were also found at the other nearby archaeological sites of Matja Kuru 1, Matja Kuru 2 and Lene Hara (O'Connor 2010).



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3 The Asitau Kuru fish remains were identified to the lowest anatomical and taxonomic level  
4 possible (Tab. 2) by careful comparison with modern specimens housed in the Australian  
5 National University Archaeology and Natural History Pacific fish reference collection,  
6 representing 76 families, 168 genera and 219 species, over 663 specimens. The bones were  
7 quantified by Number of Identified Specimens (NISP) which provides basic bone counts and  
8 avoids issues of aggregation and the over representation of rare taxa, and Minimum Number of  
9 Individuals which reduces the risks of interdependence of fragmented bones (Lyman 2018).  
10 The Minimum Number of Elements (MNE), defined as “the minimum number of elements for  
11 different skeletal elements” (Bunn 1986) was also quantified. The fragmentation of the skeletal  
12 elements (FR) was also calculated. The FR allows to assess the degree of conservation of the  
13 latter by quantifying the impact of taphonomic processes on bone fragmentation. It is calculated  
14 by dividing the number of identified remains (NISP) and the Minimum Number of Elements  
15 (MNE) (Richardson 1980; Lyman 2008). Bones with traces of combustion, linked to the action  
16 of fire and cooking food, and cut marks were also reported. Concretions encrusting bone, due  
17 to the precipitation of dissolved carbonates were counted.

23 To evaluate the relationship between the three defined chronological periods in terms of  
24 biodiversity and foraged marine environments, quantification units were further used in several  
25 statistical ecological tests (Gotelli and Ellison 2004). Rarefaction, which is defined as the  
26 probabilistic relationship between the number of individuals (NISP) and the number of species,  
27 based on an average rarefaction curve, was validated by a two-sided Kolmogorov-Smirnov test  
28 (Grayson 1984; Lyman and Ames 2007). Beyond rarefaction (interpolation) from the effective  
29 number of taxa in our samples, we also computed predictions (extrapolations) of the number of  
30 taxa one would have found with larger samples using formulas and R package “iNEXT”  
31 (Chao et al. 2014; Hsieh, Ma, and Chao 2016). Taxon richness, diversity, and evenness were  
32 also estimated following Cruz-Uribe (1988) recommendations. All the tests were made using  
33 R freeware (R Core Team 2020), and its native packages.

37 In order to gain some insight into the range of potential fishing techniques and  
38 subsistence strategies that may have been employed at Asitau Kuru, we conducted informal  
39 interviews with a few of the older men and women who regularly fished and gleaned in the  
40 waters near Asitau Kuru. We did this with the help of a Tetum-speaking interpreter over a three-  
41 day period in the field in June 2019. Here, we focused on recording the activities of today’s  
42 fishers in their local environment at Valu Sere (Lautém, Tutuala), the closest beach location to  
43 Asitau Kuru. We were able to identify the fish taxa in the daily catch during this time, as well  
44 as using photographs in order to identify and discuss the fish that were caught throughout the  
45 year. These informal interviews were undertaken at the beach where the catch was brought in,  
46 and also at the house of the oldest and most experienced of the fishers known to our interpreter.

## Results

### *Zooarchaeological analysis*

Eight fish orders have been identified within the Square C assemblage belonging to the Teleostei infraclass. Within those orders, 23 families have been identified, as well as 30 genera, and 16 species (Tab. 1). The total NISP from Square C is 16,600. The majority of the remains have been counted in the early/middle Holocene phase (NISP = 13,860 (83.49%). The Neolithic phase counts 2,264 remains (13.64%), while the Pleistocene phase only counts 476 (2.87%). 3,046 (18.35%) bone fragments have been identified to the family level. 709 (4.27%) bones have been identified to the genus level. Finally, 239 (1.44%) fragments have been identified to the species level. Among those, 808 (4.87%) bones belong to the skull, 6,988 (42.09%) to the axial skeleton. 5,903 (35.56%) vertebrae have been counted for the whole assemblage (Tab. 2).

The dominant taxon of the assemblage is the Scombridae (NISP = 889). It is the dominant taxon in the early/middle Holocene phase (NISP = 776) and in the Pleistocene phase (NISP = 30). The second dominant taxon is the Carangidae (NISP = 517). It is the dominant taxa in the Neolithic phase (NISP = 102). The dominant genus of Carangidae is *Caranx* (NISP = 146). They are followed by Balistidae (NISP = 329), Acanthuridae (NISP = 258), Serranidae (NISP = 209), Lethrinidae (NISP = 122) and Lutjanidae (NISP = 122). Interestingly, nine hyperostosed cleithra of *Caranx sexfasciatus* have been identified. Thoses bones present an abnormal growth that is, for unknown reasons, common in Carangids (Fig. 5-A) (Meunier et al. 2008). The MNI is 132. The Scaridae are dominant (MNI = 23), followed by the Serranidae (MNI = 22), then the Balistidae (MNI = 20). The Carangidae (MNI = 18) and Scombridae (MNI = 6) have low MNI because they are essentially represented in the assemblage by postcranial elements and vertebrae (Fig. 5-B).

We counted a number of 3,257 partially or completely burnt bones representing 19.62% of Square C assemblage. No cut marks were observed. Concretions consistent with calcium carbonate were observed on 11,899 bones representing 71.68% of the assemblage. We counted 169 (1.02%) complete bones for 16,431 (98.98%) fragmentary bones with a fragmentation rate of 2.13% (Tab. 3).

Beyond indicating that fishing was limited in the three phases to about 15 different taxa, rarefaction curves further indicate that they can be compared with no risk for any sampling effort bias in any observed difference. The different taxa are consistently present throughout the stratigraphic profile, with the anecdotal occurrence of some of them, such as the Belonidae (needlefishes), the Diodontidae (pufferfishes), the Muraenidae (moray eels), the Ostraciidae (boxfishes) and the Tetraodontidae (globefishes) (Fig. 6). The other taxa are evenly distributed into the different strata and phases of occupation, with a peak between Spits 41 to 17, a limited occupation between 61 to 42, and no remains dated to the Last Glacial Maximum (LGM) (although radiocarbon samples and fish bone dated to the LGM were recovered in the original excavation of Squares A and B (Marwick et al. 2016:47) (Fig. 6). We therefore observed only a few differences between the early/middle Holocene phase (Spits 41 to 17), and the Neolithic phase (Spits 16 to 1), with respectively 18, and 16 identified taxa, and similar Shannon's diversity index, and evenness, while the NISP is quite different. However, we did observe differences between these two phases, and the Pleistocene phase (Spits 61 to 42), which can be

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3 explained by a low richness (only 7), and a low NISP in this latter phase, probably related to  
4 taphonomic processes such as carbonate concretions, that affected the assemblage, our  
5 identification, and therefore the evenness (Tab. 4).  
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7 Most of the identified families are reefal, we also find here taxa that are preferably found in  
8 some specific areas of the reef, from reef flats (e. g. Diodontidae) to rocky areas (e. g.  
9 Holocentridae, Muraenidae), and others that can be found in different parts of the reef,  
10 depending of their genus and species (e. g. Acanthuridae, Balistidae, Labridae, Lethrinidae,  
11 Lutjanidae, Ostraciidae, Pomacanthidae, Scaridae, Serranidae) (Fig. 7). However, they are not  
12 dominant in the assemblage. Indeed, the assemblage is dominated by the presence of  
13 Scombridae (tunas, mackerels, bonitos) and Carangidae (jacks, pompanos, jack mackerels,  
14 runners, scads), both coastal, and sometimes pelagic taxa, some of them having been identified  
15 to genus or species level (Fig. 7). This demonstrates the presence of a particular type of marine  
16 environment that could best be understood by undertaking some ethnoarchaeological  
17 investigation into today's habitats and catches.  
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### 23 *Ethnographic information relating to fish catch and fishing techniques at Asitau Kuru*

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25 Although most Timorese families are engaged in shifting slash and burn horticulture,  
26 subsistence fishing is still important to the communities within the NKS National Park  
27 (Edyvane et al. 2009, 52). Boat-based fishing is predominantly undertaken by men, while  
28 women and children more often collect fish, crabs and molluscs in the intertidal zone at low  
29 tide (Sandlund et al. 2001). However, at certain times of year when particular marine resources  
30 are abundant the whole community comes together to harvest them. Several authors have  
31 described traditional fishing and reef gleaning, as well as the ritual mass harvesting of marine  
32 resources that takes place at specific times of year, such as the sea worm harvest ('mechi') and  
33 sardine harvest (e. g. McWilliam 2002; Pannell and O'Connor 2010; Sandlund et al. 2001).  
34 Reef gleaning on very low spring tides also involves large numbers of the community including  
35 men, women and children who may be seen at night out on the reef flats with lanterns, knives,  
36 bamboo spears, and baskets (Pannell and O'Connor 2010). As well as these ritual and whole  
37 community events there are also small numbers of men who identify as fishermen and engage  
38 in fishing as their primary activity.  
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44 The Valu Sere fishermen have a very good knowledge of local marine environments and  
45 fishing in the district as they were born there and have fished in the channel separating Valu  
46 Sere and Jaco Island since their childhood. They have shacks at the back of Valu beach where  
47 they camp and store their boat engines and fish catch. The channel is deep (between 50 and  
48 100m), although it is only a few hundred meters wide (Fig. 8-A). The fishermen use boats with  
49 small outboards and prior to the independence of Timor-Leste they would regularly travel to  
50 the nearby island of Kisar (Fig. 2). Our informants said that they shift fishing spots depending  
51 on the tidal cycles and the strong currents and winds. Our informants noted the importance of  
52 several fishing techniques adapted to the local marine environment, the currents, and the type  
53 of fishes.  
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- 56 • Basket traps ('mechi'): at low tide, small coral fishes and some species of sardines  
57 (Clupeidae) are trapped into small rock or coral pools on the beach. Women use  
58 basket traps made of lontar palm leaves to catch small fishes, octopuses, and crabs  
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in these pools. A local woman used a poster entitled *Especies ikan nebee identifikadu no konsumu iha Timor Leste* (“Species that can be identified or consumed in Timor Leste”) to point out the species, *Naso literatus* (orangespine unicornfish, Acanthuridae), *Acanthurus lineatus* (lined surgeonfish, Acanthuridae), *Cheilinus fasciatus* (redbreasted wrasse, Labridae), *Parupeneus barberinus* (dash-and-dot goatfish, Mullidae), and *Myripristis murdjan* (pinecone soldierfish, Holocentridae), that she regularly catches in her traps (fig. 8-D).

- Spearing: until a few years ago, men used to spear fish using handmade spears and wooden handmade goggles (Edyvane et al. 2009, 53). Scaridae (parrotfishes) and Acanthuridae (surgeonfishes, unicornfishes) were fished in some areas of the channel, in waters between 12 and 15 m deep. However, this technique is not much used anymore today because of the increase in numbers of dangerous saltwater crocodiles. The crocodiles are not hunted as they are sacred and revered as the reincarnation of the souls of their ancestors (de Almeida 1963). Furthermore, it appeared that some species such as *Cheilinus undulatus* and other species of wrasses, caught by spearing, have been overfished and are rare today.
- Netting: is used to catch fish that are schooling such as the Mugilidae (mulletts), and the Clupeidae (herrings, shads, sardines, hilsa, menhadens), but also sometimes small tunas, on the other side of Jaco Island, where the currents are less strong.
- Angling: large groupers (Serranidae) of the genus *Epinephelus*, Carangidae (jacks, pompanos, jack mackerels, runners, scads), and Elopidae (tenpouders) are caught using modern metal hooks and baits made of plastic and resin from the beach or from boats. Rocks are tied to the line near the hook to weight the line when it is thrown or dropped.
- Trolling from boats (between 3 and 5m deep): this is perhaps the most commonly used and efficient technique practiced by the Valu Sere fishermen to catch Scombridae (tunas, mackerels, bonitos), Carangidae, Sphyraenidae (barracudas), that feed at the surface, and some species of Lutjanidae (snappers) (Fig. 8-B), as the currents are very strong in the channel and make netting almost impossible.

The Valu Sere fishermen catch all kind of tuna species in the channel. We were unable to define what species were caught exactly as they declared that they caught all Timorese Scombridae species based on photographs that we provided. They are caught by trolling with lures using feathers, local plants, small fishes (Clupeidae, Belonidae, Hemirhamphidae), or cephalopods. However, all these species are not present in the channel at the same time of the year, depending on migration patterns. According to them, *Thunnus albacares* (yellowfin tuna) can be caught during the dry season. *Katsuwonus pelamis* (skipjack tuna) is more present right after the rainy season, and the catches are generally larger during this season. On the other hand, some other species such as *Auxis thazard* (frigate tuna) and *Gymnosarda unicolor* (dogtooth tuna) can be caught at any time in the year. Some species were said to be harder to catch. This is the case with *Scomberomorus commerson* (narrow-barred Spanish mackerel), as they reach very large proportions. A fisherman reported that once he almost caught a several meters long fish that based on his identification of the photographs was probably a blue marlin (Istiophoridae). In a general way, the deeper one fishes in the channel, the bigger the fishes one catches. The species

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3 *Lutjanus argentimaculatus* (mangrove red snapper) is also commonly caught in a deep black  
4 coral area, as well as some species of Serranidae (sea basses, groupers) (Fig. 8-B).  
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6 Most fishes are eaten, even pufferfishes (Diodontidae) and boxfishes (Ostraciidae) that are  
7 both known to secrete powerful toxins produced by small organisms living in the reef  
8 (Boulanger et al. in review). Boxfishes and triggerfishes (Balistidae) are mainly caught during  
9 the rainy season. They are peeled as their skin is very thick. Moray eels (Muraenidae), whose  
10 consumption may cause ciguatera poisoning (Swift and Swift 1993), are also eaten during  
11 ceremonies. Ciguatera toxins are produced by marine dinoflagellates associated with coral reefs,  
12 and produces gastrointestinal, and neurological symptoms that can be debilitating and  
13 prolonged (Swift and Swift 1993). Stingrays (Myliobatoidei) are also consumed. However,  
14 globefishes (Tetraodontidae) and stonefishes (Synanceiidae) are known as highly poisonous  
15 and they are immediately thrown back to the water whenever they are caught.  
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## Discussion

The additional data produced by analyses of Square C combined with ethnographic observations at Asitau Kuru has added significantly to the debate about inshore versus deep sea fishing (O'Connor, Ono, and Clarkson 2011). The 23 fish families identified at Asitau Kuru are a testament to human exploitation of the significant biodiversity zone in the Coral Triangle and their utilization of a large range of fishing techniques since 42,000 years ago (Shipton et al. 2019).

Given the right conditions, spearing was probably practiced, primarily for Labridae (wrasses) and Scaridae (parrotfishes), which rarely take a baited hook. De Almeida (1963) described this technique as the most popular among the locals (who he observed using handmade harpoons and arrows), along with line and trap fishing. It is likely that most of the herbivorous taxa (such as the Pomacanthidae) were caught using spears as netting is, and probably was, very limited in the channel because of the strong currents. Interestingly, de Almeida (1963) does not mention the use of this technique. The Mugilidae (mulletts) could have probably been caught this way, but their presence at the site is limited. Thus, this technique would have been only used occasionally or farther from the site. Basket traps were potentially also used to catch smaller specimens that might not have been recovered in archaeological assemblages because of taphonomic processes.

Line fishing seems to have been one of the main techniques used at the site and was probably more favored by the prehistoric fishermen than today's fishermen. This is shown by the presence of Carangidae, and more specifically the species *Caranx sexfasciatus* (bigeye trevally), and *Caranx melampygus* (bluefin trevally), that can be caught from the beach, but also some other reef taxa, such as the Lethrinidae (emperors, emperor breams, pigface breams), Lutjanidae (snappers), and Serranidae (sea basses, groupers). This hypothesis is reinforced by the discovery of shell fishhooks from the terminal Pleistocene to middle Holocene contexts at Asitau Kuru (Fig. 4) (O'Connor, Ono, and Clarkson 2011; Shipton et al. 2020), as well as similar artefacts discovered at Lene Hara (O'Connor and Veth 2005), Here Sorot Entapa (O'Connor et al. 2019), Tron Bon Lei (O'Connor et al. 2017), and Makpan (Langley et al. 2020; Kealy et al. 2020). The hooks found at Asitau Kuru are J-shaped jabbing hooks, which require the line to be pulled sharply when the fish bites to secure it. They are regarded as less well suited for deepwater fishing, windy conditions or in situations where coral is likely to snag the hook. In these circumstances circular rotating hooks are thought to be superior (e. g. O'Connor et al. 2017), however none have thus far been recovered at Asitau Kuru. The nacreous shell hooks have the advantage of being able to be used without bait; the natural lustre of the shell being sufficient to attract fish (Anell 1955).

In an earlier publication, O'Connor and co-authors (2011) stated that bone points made on the spines of large fish were recovered at Asitau Kuru. "Their function is uncertain but they clearly represent a component of a composite tool, such as fine barbs for fish spears, or part of complex hooks for trolling." Since this time the bone assemblage has been more thoroughly examined and this preliminary view reassessed. Bone points do occur in the Asitau Kuru assemblage and are mostly light and slender, and likely to have formed prongs or barbs in composite hafted fishing spears. An example of a point made on the barb of a sting ray has been



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3 found at nearby Matja Kuru 2 (MK2) (Fig. 4). No examples of bone artefacts which might have  
4 been used as lures have been identified, however a possible lure made on *Nautilus* shell was  
5 found at MK2 and directly dated to 9190+/-50 (0ZG899) (O'Connor et al. 2021, 32). This  
6 artefact raises the possibility that trolling may have been practiced in Timor-Leste at this time.  
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9 Many of the bone artefacts from Asitua Kuru are so modified that it is not possible to tell  
10 what taxa or bone they are made on. A few examples of bone artefacts from Asitau Kuru and  
11 the MK2 sting ray barb point are reproduced here (Fig. 4), and the complete bone artefact  
12 assemblage will be published in full shortly. While spearing can be used for catching  
13 Scombridae, such as *Acanthocybium solandri* (wahoo) and *Katsuwonus pelamis* (skipjack tuna),  
14 Carangidae, such as *Elagatis bippinulata* (rainbow runner), and Sphyraenidae (barracudas) the  
15 bone points found in the Asitau Kuru assemblage are quite fine and fragile and do not seem  
16 suited for the capture of such fast, powerful fish. Trolling may also have been carried out using  
17 baits, near or at the surface of the water. The manufacture of strong fiber line is implied by the  
18 presence of the hooks (O'Connor, Ono, and Clarkson 2011). However, lines were presumably  
19 quite short, but efficient enough to catch smaller fish swimming at the surface of the sea over  
20 deep water. This could possibly explain why some taxa that are commonly fished at Valu Sere  
21 today, are not represented in the Asitau Kuru assemblage, such as large specimens of *Lutjanus*  
22 *argenteimaculatus* (mangrove red snapper, Lutjanidae) that probably favor deeper reef areas.  
23 However, the size of the Scombridae, between 40 to 100 cm long, presently caught in waters  
24 near the site seems to be similar to the ones caught during prehistoric times. These are, today,  
25 fished by locals from boats in a deeper area of the channel.  
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29 In summary, Asitau Kuru presents only limited change in terms of fishing strategies  
30 employed over the 44,000 years sequence. Currently it appears that fishhooks first appear in  
31 the terminal Pleistocene, ca. 17,000 years ago, coinciding with an increase in fish remains and  
32 occupation intensity more generally. In the Square C excavation presented here there is a  
33 significant increase in fish remains in the early to mid-Holocene compared to the Pleistocene  
34 or the Neolithic deposits. However, despite these fluctuations in the quantities of fish bone there  
35 is considerable continuity over time in the fish taxa which dominate the assemblage. This  
36 continuity could be the result of the steepness of the coastal profile producing shorelines and  
37 coastal environments that did not change dramatically with changes in sea level, thus resulting  
38 in insignificant changes in fish ecology and fishing behavior over time.  
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42 Comparisons between archaeological assemblages from different palaeolithic sites across  
43 ISEA show that not all sites contained significant evidence for fishing (Fig. 1; Tab. 5). Indeed,  
44 only a limited number of sites produced evidence of fishing, some of them exhibiting large  
45 assemblages of fish bones while in others only a few fish bones were recovered. In the Ryūkyū  
46 Islands, fish bones are rarely recovered (e. g. Fujita et al. 2016), while some sites in the  
47 Philippines had only slightly more significant fish bone assemblages (Boulanger 2021;  
48 Boulanger et al. 2019). Most of the Lesser Sunda Island sites produced evidence of fishing,  
49 with some sites producing thousands of fish bones (O'Connor, Ono, and Clarkson 2011;  
50 O'Connor et al. 2019; Samper Carro et al. 2016; Kealy et al. 2020). This discrepancy could  
51 indicate a greater marine adaptation in the insular region of Wallacea, it could also reflect  
52 differential preservation issues by region and/or disparities in recovery methods as larger mesh  
53 sizes return fewer fish bones and assemblages with lower diversity (Nagaoka 2005; Densmore  
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2009; Nagaoka 1994; Vale and Gargett 2002). Wallacean archaeological sites typically have been wet sieved with fine mesh sizes thus aiding significantly the recovery of smaller fish bones (Boulanger 2021; Samper Carro et al. 2016; O'Connor et al. 2019) (Tab. 5).

Discussion on these archaeological sites indicates that humans in Island Southeast Asia and in the Wallacea mostly exploited near-shore environments. Inter-site differences are therefore probably directly related to local environmental disparities, and climate-mediated environmental changes, but also, in some cases, to taphonomic bias. It is interesting to note that the representativity of taxa at all sites is similar to that usually identified from archaeological sites in the Remote Pacific islands (see, for example, list of fish taxa in Butler 1994), even though far more genera and species are represented within those families in the Coral Triangle area. The Mindoro sites, such as Bubog I, exhibit a relatively low occupation intensity throughout time (Boulanger et al. 2019; Boulanger 2021), compared to Wallacean coastal sites like Here Sorot Entapa (O'Connor et al. 2019), Tron Bon Lei (Samper Carro et al. 2016) and Asitau Kuru. The surrounding coral reef was exploited, as well as possibly the mangrove swamps during low sea level periods at Bubog I (Boulanger 2021; Boulanger et al. 2019). In contrast, Here Sorot Entapa and Asitau Kuru delivered large assemblages with an occupation that seems to have fluctuated throughout their sequences, and that exhibit a long-term continuity in terms of foraged habitats. Here Sorot Entapa's exploitation focused on the extensive but narrow limestone coral reef terraces surrounding Kisar Island (O'Connor et al. 2019), while Asitau Kuru's exploitation was concentrated on the easily accessible deep channel located between the site and Jaco Island. At Tron Bon Lei, Samper Carro and co-authors (2016) suggested a shift from carnivorous/open-water taxa during the terminal Pleistocene to smaller herbivorous/omnivorous taxa after the early Holocene. This change in taxonomic relative abundance could be explained by the use of different fishing techniques, culinary preferences, prey availability related to environmental changes, or changes in social organization over time (Samper Carro et al. 2016).

The hypothesis of the *H. sapiens* 'generalist specialist niche' stipulates that humans have a degree of ecological plasticity making our species capable of adapting to any kind of environment (Roberts and Stewart 2018). *H. sapiens* fishing practices clearly fit into this model as modern humans appear to have adapted with great flexibility to a variety of specific local marine habitats throughout ISEA. The implication is that it took significant cognitive capability to plan fishing expeditions requiring knowledge of sea floors, and the ichthyofauna that populate them gained by millennia of learned experiences. This also allowed the development of efficient technologies that optimized productivity and permitted a sustainable diet for human populations in depauperate terrestrial environments. Continuity of fishing practices in different marine habitats across time and space in ISEA indicates strong cultural transmission across generations of established islanders. We argue here, due to the high concentration of protein in fish populations in these marine environments (Joordens et al. 2014), that some of these human populations, particularly in the Lesser Sunda Islands where diversity is most abundant, engaged in hyper-specialized foraging in coastal marine habitats.

This hyper-specialized adaptation to various marine habitats appears to have resulted in inter-site variability in fish assemblages from ISEA archaeological sites, with occurrences of predators at Asitau Kuru, representatives of the Cirrhitidae (hawkfishes), Holocentridae (squirrelfishes and soldierfishes) and small specimens of Balistidae (triggerfishes) at Here Sorot

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3 Entapa (O'Connor et al. 2019), and perhaps mangrove taxa (like the juveniles of parrotfishes)  
4 at Bubog I (Boulanger 2021; Boulanger et al. 2019) (Tab. 5). Comparisons with archaeological  
5 and ethnographic data in the Pacific, shows an opportunistic exploitation of marine resources,  
6 coupled with our own observations in Timor-Leste allowed us to make inferences on  
7 established fishing techniques. The ethnography revealed that a wide range of techniques likely  
8 produced the fish bone assemblages in ISEA. These hypotheses are corroborated by the  
9 discovery of fishing gear including fishhooks, fishing gorges, and net sinkers (Tab. 5).

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11 Most of the prehistoric fishing in ISEA could have been conducted from the near-shore,  
12 however, the use of boats is likely, and probably became more prominent in the Terminal  
13 Pleistocene. Because of the rare preservation of boats in archaeological records, the origins of  
14 boat technologies are still debated (Erlandson and Fitzpatrick 2006). The development of  
15 maritime networks is demonstrated from the Terminal Pleistocene/early Holocene by the  
16 appearance of exotic obsidian artefacts, both in the Philippines (Neri et al. 2015; Pawlik 2021),  
17 and in Wallacea (O'Connor et al. 2023; Reepmeyer et al. 2019; Reepmeyer, O'Connor, and  
18 Brockwell 2011). This period also coincides with the manufacture of shell adzes dating between  
19 the early and middle Holocene, in the Philippines (Pawlik et al. 2015; Pawlik 2021), and in  
20 Timor-Leste (Shipton et al. 2020). Their principal function has been argued to relate to the  
21 manufacture of dugout canoes, as suggested by the presence of hafting residue and use-wear  
22 scars indicating their use in heavy-duty woodworking tasks (Shipton et al. 2020). We can thus  
23 conclude that the type of fishing practiced by these Australo-Melanesian populations likely  
24 included the use of boats, whether for fishing tunas and other fast-swimming fish in the deep  
25 channel between Valu Sere and Jaco Island, or for fishing small coral fishes in the reef  
26 surrounding Kisar Island. Marine resources were extremely well managed, and it was probably  
27 not necessary for those populations to be engaged in more risky offshore fishing.

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29 Furthermore, while zooarchaeological, and more particularly ichthyoarchaeological studies,  
30 generally tend to decipher marine exploitation by inferring fishing techniques, it is also  
31 interesting to try to understand the social or ritual significance of fishing practices (Colley 1990),  
32 as it implies modernity of human behavior. This is often difficult to establish, with the best  
33 example of fishing within the social realm demonstrated at Tron Bon Lei (Alor Island), where  
34 symbolic behavior was inferred from the discovery of the oldest-known fishhooks associated  
35 with mortuary practices, and thus displaying the intrinsic connection of these Pleistocene island  
36 communities to the sea, in both life and death (O'Connor et al. 2017).

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## Figure captions

Figure 1. Map of Island Southeast Asia showing the archaeological sites where marine fish remains (NISP > 100) have been found as well as its biogeographical lines of delineation and the extent of the continent shelves at -130 m.

Figure 2. Map of Timor-Leste and nearby islands showing the position of Asitau Kuru, as well as the extent of the continent shelves at -120 m.

Figure 3. East wall of the stratigraphic profile of Asitau Kuru Square C, constituted of eight distinct layers colored using the Munsell Color Charts, according to Shipton and co-authors (2020).

Figure 4. A. Modified stingray barb from Matja Kuru 2, Square C, Spit 27. B. Close-up of polished lateral barbs (white rectangle in A). C. Example of modern stingray barb. Image purchased from iStock. D. Example of four bone points identified in Asitau Kuru, Square A. E. Early Holocene fishhook from Asitau Kuru (Square A, Spit 26) (Shipton et al. 2020). F. Middle Holocene fishhook from Asitau Kuru (Square C, Spit 19) (Shipton et al. 2020).

Figure 5. A. Caudal vertebrae of Scombridae recovered from Spit 58, Trench C, showing the level of carbonate concretions coating the bones in the lower part of the stratigraphy, as well as comparative modern specimens of *Katsuwonus pelamis*' caudal vertebrae (Scombridae) from Japan. B. Part of a *Caranx sexfasciatus* left cleithrum recovered from Spit 34, Trench C, exhibiting hyperostosis with *Caranx sexfasciatus* comparative modern hyperostosed cleithrum from Timor-Leste.

Figure 6. Percentage of NISP (= 16,600) per family and per spit at Asitau Kuru.

Figure 7. Percentage of NISP per taxa ecological settings at Asitau Kuru. Here, "Generalist" refers to fishes that can be found on the reef but also in the mangrove swamps, estuarine and sometimes pelagic areas (often as juveniles); "Predator" refers to carnivorous fishes; "Reefal" refers to all fish taxa inhabiting coral reefs, from sandy bottoms to rocky areas.

Figure 8. A. Valu Sere, the channel, and on the other side, Jaco Island. B. Fish catch of a day: a trevally (Carangidae), a barracuda (Sphyraenidae), a small tuna (Scombridae), and a mangrove red snapper (Lutjanidae). C. Woman showing us basket traps made of lontar palm leaves. D. A woman doing the mechi at low tide. Tutuala, Timor-Leste, 2019.



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3 **Tables captions**  
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5 Table 1. Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI)  
6 at Asitau Kuru.  
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9 Table 2. Minimum Number of Elements (MNE) at Asitau Kuru.  
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12 Table 3. Number and percentage of cultural and taphonomic disturbances at Asitau Kuru.  
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15 Table 4. Taxon richness, diversity and evenness at Asitau Kuru.  
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18 Table 5. Synthesis of aquatic environments and associated artefacts for each of the sites cited  
19 in our review where fish remains have been found, with the exception of Sakitari-do, where no  
20 fish bones have been retrieved but the oldest known fish hook.  
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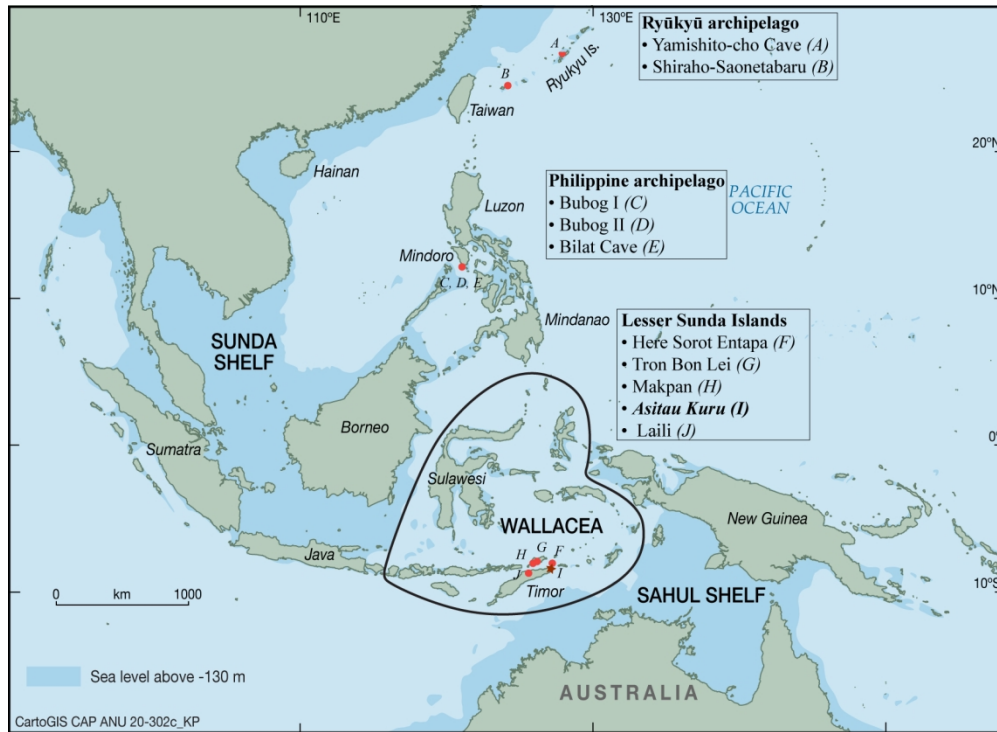


Figure 1. Map of Island Southeast Asia showing the archaeological sites where marine fish remains (NISP > 100) have been found as well as its biogeographical lines of delineation and the extent of the continent shelves at -130 m.

150x109mm (300 x 300 DPI)



Figure 2. Map of Timor-Leste and nearby islands showing the position of Asitau Kuru, as well as the extent of the continent shelves at  $-120$  m.

150x66mm (300 x 300 DPI)

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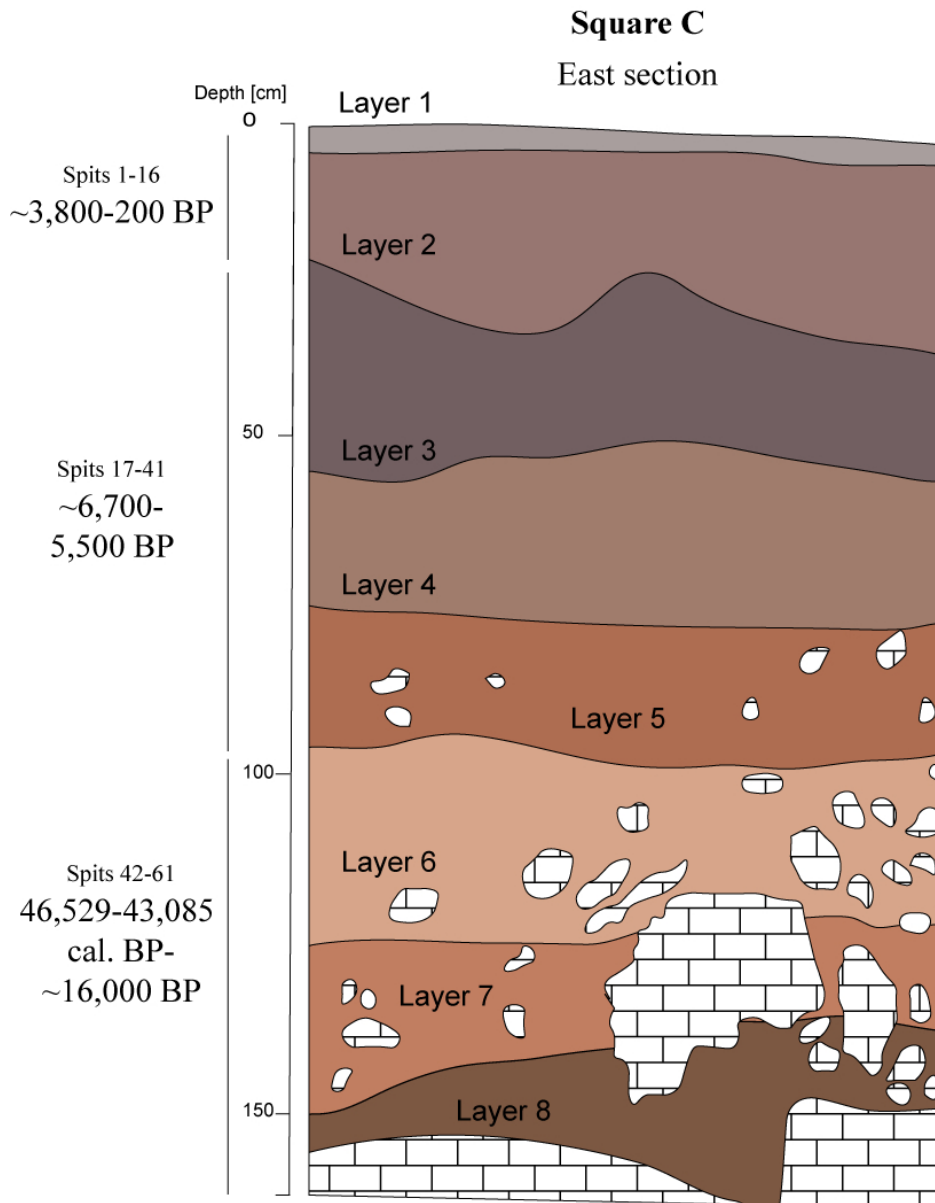


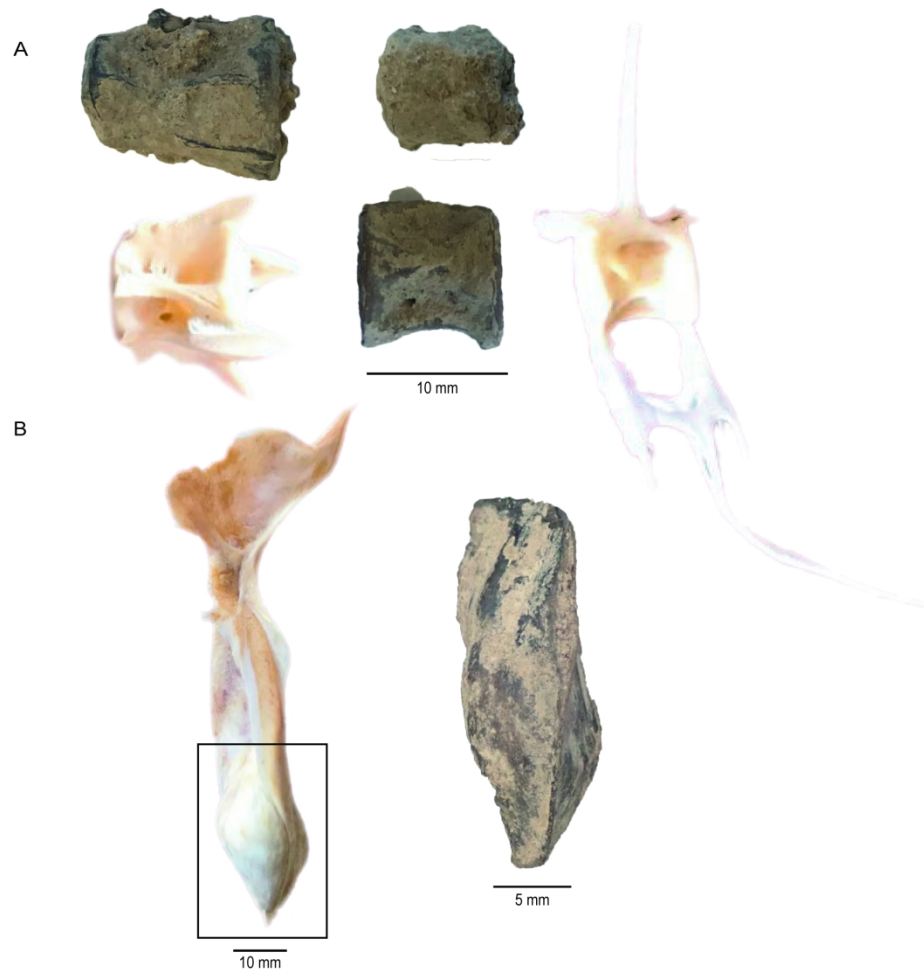
Figure 3. East wall of the stratigraphic profile of Asitau Kuru Square C, constituted of eight distinct layers colored using the Munsell Color Charts, according to Shipton and co-authors (2020).

69x88mm (300 x 300 DPI)



Figure 4. A. Modified stingray barb from Matja Kuru 2, Square C, Spit 27. B. Close-up of polished lateral barbs (white rectangle in A). C. Example of modern stingray barb. Image purchased from IStock. D. Example of four bone points identified in Asitau Kuru, Square A. E. Early Holocene fishhook from Asitau Kuru (Square A, Spit 26) (Shipton et al. 2020). F. Middle Holocene fishhook from Asitau Kuru (Square C, Spit 19) (Shipton et al. 2020).

447x260mm (300 x 300 DPI)



38 Figure 5. A. Caudal vertebrae of Scombridae recovered from Spit 58, Trench C, showing the level of  
39 carbonate concretions coating the bones in the lower part of the stratigraphy, as well as comparative  
40 modern specimens of *Katsuwonus pelamis*' caudal vertebrae (Scombridae) from Japan. B. Part of a *Caranx*  
41 *sexfasciatus* left cleithrum recovered from Spit 34, Trench C, exhibiting hyperostosis with *Caranx*  
42 *sexfasciatus* comparative modern hyperostosed cleithrum from Timor-Leste.

43 196x192mm (300 x 300 DPI)

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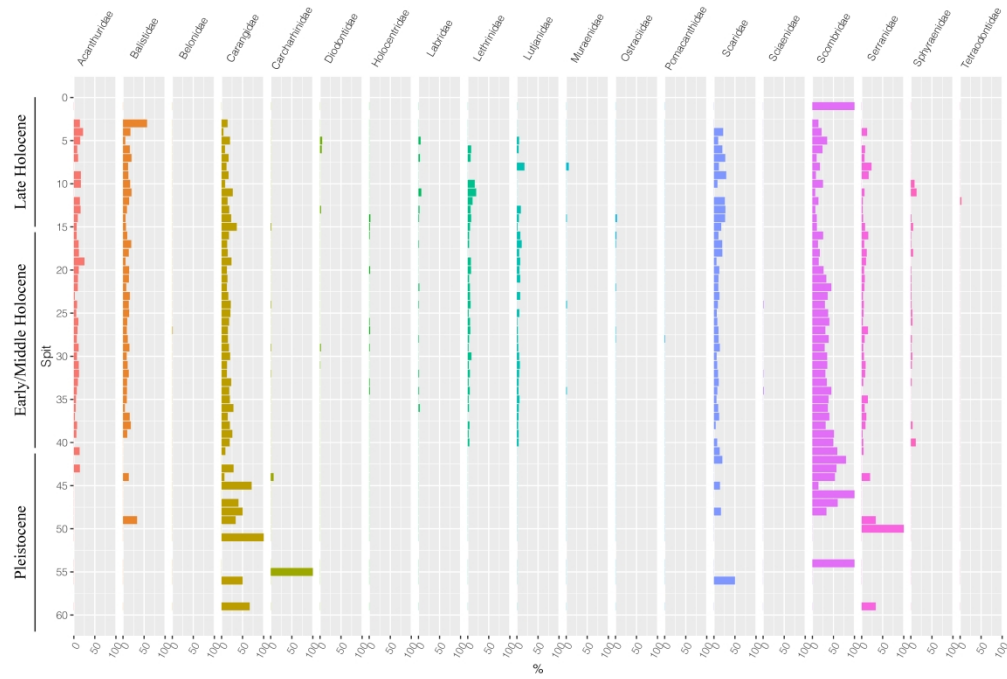


Figure 6. Percentage of NISP (= 16,600) per family and per spit at Asitau Kuru.

304x210mm (300 x 300 DPI)

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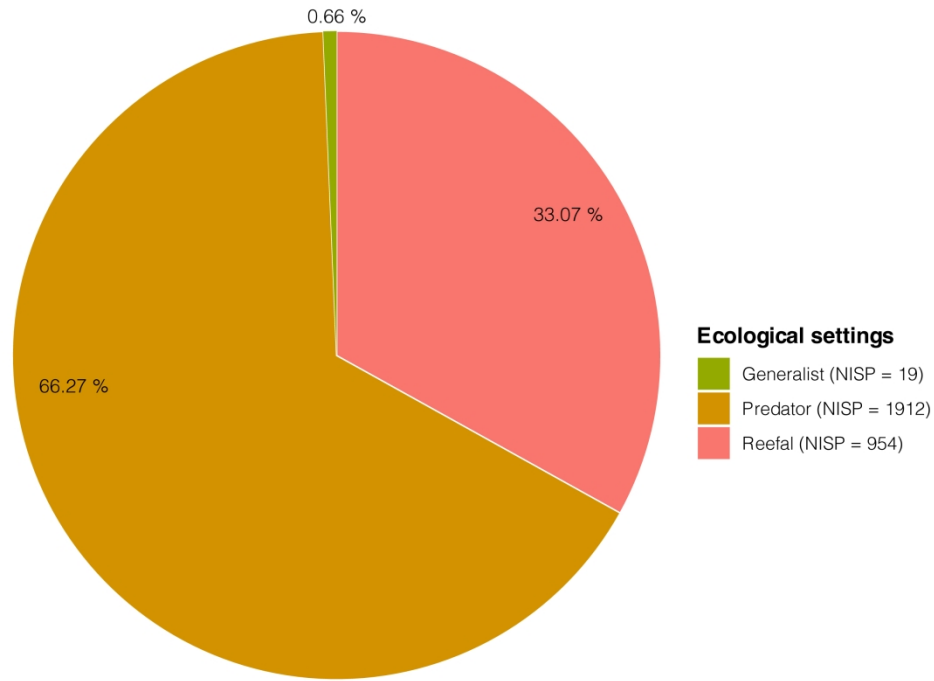


Figure 7. Percentage of NISP per taxa ecological settings at Asitau Kuru. Here, "Generalist" refers to fishes that can be found on the reef but also in the mangrove swamps, estuarine and sometimes pelagic areas (often as juveniles) ; "Predator" refers to carnivorous fishes ; "Reefal" refers to all fish taxa inhabiting coral reefs, from sandy bottoms to rocky areas.

258x210mm (300 x 300 DPI)



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B



C



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Figure 8. A. Valu Sere, the channel, and on the other side, Jaco Island. B. Fish catch of a day: a trevally (Carangidae), a barracuda (Sphyraenidae), a small tuna (Scombridae), and a mangrove red snapper (Lutjanidae). C. Woman showing us basket traps made of lontar palm leaves. D. A woman doing the mechi at low tide. Tutuala, Timor-Leste, 2019.

162x208mm (300 x 300 DPI)

Subclass	Order	Family	Subfamily	
Elasmobranchii	Carcharhiniformes	Carcharhinidae		
Neopterygii	Anguilliformes	Muraenidae	Muraeninae	
		Beloniformes	Belonidae	
		Beryciformes	Holocentridae	Holocentrinae
				Myripristinae
	Clupeiformes	Clupeidae		
		Mugiliformes	Mugilidae	
	Perciformes	Acanthuridae		Acanthurinae
				Nasinae
		<i>cf.</i> Acanthuridae		
		Carangidae	Caranginae	
				Naucratinae
				Scomberoidinae
		<i>cf.</i> Carangidae		
		<i>cf.</i> Gerreidae		
		<i>cf.</i> Haemulidae		
	Labridae		Bodianinae	
			Cheilininae	
	<i>cf.</i> Labridae			
	Lethrinidae		Lethrininae	
			Monotaxinae	
	<i>cf.</i> Lethrinidae			
	Lutjanidae		Lutjaninae	



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*cf.* Lutjanidae  
Pomacanthidae  
Scaridae  
Scarinae

Sparisomatinae

*cf.* Scaridae  
Sciaenidae  
Scombridae  
Scombrinae

*cf.* Scombridae  
Serranidae  
Epinephelinae

*cf.* Serranidae  
Sphyraenidae  
Epinephelinae

Tetraodontiformes Balistidae



*cf.* Balistidae  
Diodontidae

Ostraciidae  
Tetraodontidae  
*cf.* Tetraodontidae

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Indet. (Teleostei)

**Total**

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Species	Vernacular name	Pleistocene	
		(Spits 42-61)	
		NISP	MNI
	Requiem sharks	<b>3</b>	<b>1</b>
cf. <i>Gymnothorax</i> sp.	Moray eels	<b>0</b>	<b>0</b>
	Needlefishes	<b>0</b>	<b>0</b>
	Squirrelfishes, soldierfishes	<b>0</b>	<b>0</b>
<i>Sargocentron</i> sp.	Squirrelfishes	0	-
<i>Myripristis</i> sp.	Soldierfishes	0	-
cf. <i>Myripristis</i> sp.		0	-
	Herrings, shads, sardines, hilsa, menhadens	<b>0</b>	<b>0</b>
	Mulletts	<b>0</b>	<b>0</b>
	Surgeonfishes, tangs, unicornfishes	<b>1</b>	<b>1</b>
<i>Acanthurus</i> sp.	Surgeonfishes	0	-
cf. <i>Acanthurus</i> sp.		0	-
<i>Naso</i> sp.	Unicornfishes	0	-
cf. <i>Naso</i> sp.		0	-
		<b>0</b>	-
	Jacks, pompanos, jack mackerels, runners, scads	<b>19</b>	<b>1</b>
<i>Caranx</i> sp.		2	1
cf. <i>Caranx</i> sp.		1	-
<i>Caranx melampygus</i>	Bluefin trevallies	0	-
<i>Caranx sexfasciatus</i>	Bigeye trevallies	0	-
<i>Elagatis bipinnulata</i>	Rainbow runners	0	-
cf. <i>Seriola</i> sp.	Amberjacks	0	-
<i>Scomberoides</i> sp.	Queenfishes	0	-
cf. <i>Scomberoides</i> sp.		2	-
		<b>4</b>	-
	Mojarras	<b>0</b>	-
	Grunts	<b>0</b>	-
	Wrasses	<b>0</b>	<b>0</b>
<i>Bodianus</i> sp.	Hogfishes	0	-
<i>Cheilinus</i> sp.		0	-
cf. <i>Cheilinus</i> sp.		0	-
cf. <i>Cheilinus undulatus</i>	Humphead wrasses	0	-
		<b>0</b>	-
	Emperors, emperor breams, pigface breams	<b>0</b>	<b>0</b>
<i>Lethrinus</i> sp.	Emperors	0	-
cf. <i>Lethrinus</i> sp.		0	-
<i>Monotaxis</i> sp.		0	-
<i>Monotaxis grandoculis</i>	Humpnose big-eye breams	0	-
		<b>1</b>	-
	Snappers	<b>0</b>	<b>0</b>
<i>Lutjanus</i> sp.		0	-
cf. <i>Lutjanus</i> sp.		0	-

1				
2			<b>1</b>	-
3		Marine angelfishes	<b>0</b>	<b>0</b>
4		Parrotfishes	<b>5</b>	<b>1</b>
5				
6	<i>Cetoscarus</i> sp.		0	-
7	<i>Chlorurus</i> sp.		0	-
8	cf. <i>Chlorurus</i> sp.		0	-
9				
10	<i>Hipposcarus longiceps</i>	Pacific longnose parrotfishes	0	-
11	<i>Scarus</i> sp.		0	-
12	cf. <i>Scarus</i> sp.		0	-
13				
14	<i>Scarus rubroviolaceus</i>	Ember parrotfishes	0	-
15	<i>Calotomus</i> sp.		0	-
16			<b>1</b>	-
17				
18		Drums, croackers	<b>0</b>	<b>0</b>
19		Mackerels, tunas, bonitos	<b>30</b>	<b>1</b>
20	<i>Acanthocybium solandri</i>	Wahoos	0	-
21	cf. <i>Acanthocybium solandri</i>		0	-
22				
23	<i>Katsuwonus pelamis</i>	Skipjack tunas	1	1
24	cf. <i>Katsuwonus pelamis</i>		0	-
25			<b>2</b>	-
26				
27		Sea basses, groupers	<b>6</b>	<b>3</b>
28	cf. <i>Cephalopholis</i>		0	-
29	cf. <i>Epinephelus</i>		0	-
30				
31	<i>Plectropomus</i> sp.		0	-
32			<b>1</b>	-
33		Barracudas	<b>0</b>	<b>0</b>
34				
35	<i>Sphyraena</i> sp.		0	-
36	<i>Sphyraena barracuda</i>	Great barracudas	0	-
37		Triggerfishes	<b>3</b>	<b>1</b>
38				
39	<i>Balistapus undulatus</i>	Orange-lined triggerfishes	0	-
40	cf. <i>Balistapus undulatus</i>		0	-
41				
42	<i>Balistoides</i> sp.		0	-
43	<i>Balistoides conspicillum</i>	Clown triggerfishes	0	-
44	cf. <i>Balistoides</i>		0	-
45	<i>Canthidermis maculata</i>	Rough triggerfishes	0	-
46	cf. <i>Canthidermis maculata</i>		0	-
47				
48	<i>Pseudobalistes flavimarginatus</i>	Yellowmargin triggerfishes	0	-
49	cf. <i>Pseudobalistes flavimarginatus</i>		0	-
50			<b>1</b>	-
51				
52		Porcupinefishes	<b>0</b>	<b>0</b>
53				
54	<i>Diodon</i> sp.		0	-
55	<i>Diodon</i> cf. <i>holocanthus</i>	Longpsined porcupinefishes	0	-
56	<i>Diodon hystrix</i>	Spot-fin porcupinefishes	0	-
57	<i>Diodon</i> cf. <i>hystrix</i>		0	-
58				
59		Boxfishes, cofferfishes, cowfishes, trunkfishes	<b>0</b>	<b>0</b>
60		Pufferfishes	<b>0</b>	<b>0</b>
			<b>0</b>	-

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Early/mid-Holocene		Neolithic		Total NISP	Total MNI
(Spits 17-41)		(Spits 1-16)			
NISP	MNI	NISP	MNI		
3	1	1	1	7	3
3	1	2	1	5	2
1	1	0	0	1	1
9	1	4	1	13	2
0	-	1	1	1	-
1	1	0	-	1	-
1	-	0	-	1	-
0	0	0	0	0	0
0	0	0	0	0	0
205	2	52	2	258	5
44	1	11	1	55	-
5	-	2	-	7	-
37	1	12	1	49	-
6	-	2	-	8	-
15	-	2	-	17	-
396	15	102	2	517	18
111	6	33	1	146	8
4	-	1	-	6	-
1	1	0	-	1	-
8	4	1	1	9	-
8	1	0	-	8	-
1	-	0	-	1	-
3	1	6	1	9	-
1	-	0	-	3	-
38	-	6	-	48	-
1	-	0	-	1	-
1	-	0	-	1	-
10	2	5	1	15	3
0	-	1	1	1	-
1	1	0	-	1	-
0	-	1	-	1	-
2	-	0	-	2	-
2	-	1	-	3	-
92	2	30	2	122	4
18	2	14	1	32	-
0	-	2	-	2	-
1	1	1	1	2	-
6	1	0	-	6	-
10	-	7	-	18	-
100	11	22	2	122	13
16	5	6	2	22	-
1	-	0	-	1	-

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2	<b>18</b>	-	<b>5</b>	-	<b>24</b>	-
3	<b>1</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>1</b>
4	<b>231</b>	<b>9</b>	<b>98</b>	<b>13</b>	<b>334</b>	<b>23</b>
5	0	-	1	1	1	-
6	19	4	3	2	22	-
7	3	-	3	-	6	-
8	1	1	0	-	1	-
9	29	3	11	3	40	-
10	4	-	0	-	4	-
11	1	1	0	-	1	-
12	1	1	1	1	2	-
13	<b>8</b>	-	<b>2</b>	-	<b>11</b>	-
14	<b>3</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>3</b>	<b>1</b>
15	<b>776</b>	<b>3</b>	<b>83</b>	<b>2</b>	<b>889</b>	<b>6</b>
16	11	1	1	1	12	-
17	1	-	0	-	1	-
18	86	1	4	1	91	3
19	8	-	2	-	10	-
20	<b>4</b>	-	<b>3</b>	-	<b>9</b>	-
21	<b>160</b>	<b>15</b>	<b>43</b>	<b>4</b>	<b>209</b>	<b>22</b>
22	2	-	3	-	5	-
23	1	-	1	-	2	-
24	1	1	0	-	1	-
25	<b>11</b>	-	<b>0</b>	-	<b>12</b>	-
26	<b>39</b>	<b>1</b>	<b>9</b>	<b>1</b>	<b>48</b>	<b>2</b>
27	8	1	9	1	17	-
28	28	1	3	1	31	-
29	<b>268</b>	<b>8</b>	<b>58</b>	<b>11</b>	<b>329</b>	<b>20</b>
30	2	1	0	-	2	-
31	2	-	<b>0</b>	-	2	-
32	10	2	3	1	13	-
33	6	1	1	1	7	-
34	20	-	0	-	20	-
35	14	3	2	1	16	-
36	11	-	3	-	14	-
37	1	1	2	1	3	-
38	6	-	4	3	10	-
39	<b>8</b>	-	<b>3</b>	-	<b>12</b>	-
40	<b>3</b>	<b>2</b>	<b>3</b>	<b>1</b>	<b>6</b>	<b>3</b>
41	0	-	1	1	1	-
42	1	1	0	-	1	-
43	1	1	0	-	1	-
44	1	-	0	-	1	-
45	<b>4</b>	<b>1</b>	<b>5</b>	<b>1</b>	<b>9</b>	<b>2</b>
46	<b>0</b>	<b>0</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>
47	<b>1</b>	-	<b>0</b>	-	<b>1</b>	-

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<b>13860</b>	<b>77 2264</b>	<b>46 16600</b>	<b>132</b>

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<b>Cranial bones</b>	<b>NR</b>	<b>Postcranial bones</b>	<b>NR</b>	<b>Special bones</b>
Neurocranium	1	First vertebra	88	Dorsal pterygiophore (Acanthuridae)
Basioccipital	2	Precaudal vertebra	1127	Caudal spine (Acanthuridae)
Vomer	22	Caudal vertebra	1616	First dorsal spine (Balistidae)
Ethmoid	8	Urostyle	85	Pterygial carina (Balistidae)
Dentary	99	Hypural	11	Dermal spine (Diodontidae)
Premaxilla	82	Indet. vertebra	2976	Anal pterygiophore (Carangidae)
Jaw fragment	21	Pterygiophore	98	Caudal spine (Scombridae)
Tooth	33	Dorsal spine	292	
Maxilla	66	Pectoral spine	7	
Quadrate	84	Indet. spine	324	
Articular	38	Scale	33	
Palatin	31			
Pharyngeal plate	29			
Lateral pharyngeal	47			
Indet. pharyngeal	3			
Epibranchial	1			
Opercle	15			
Preopercle	2			
Subopercle	1			
Cleithrum	63			
Scapula	49			
Postcleithrum	21			
Supracleithrum	26			
Hyomandibular	33			
Ceratohyal	9			
Urohyal	17			
Epihyal	3			
Basipterygium	1			
Otolith	1			
Indet.	8804			
<b>Total</b>	<b>9612</b>		<b>6657</b>	

1	
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3	<b>NR</b>
4	<u>38</u>
5	1
6	47
7	17
8	1
9	224
10	3
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47	<b>331</b>
48	<b>16600</b>
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NISP	Complete bones	Fragmentary bones	Calcinated	Cutmarked	Concretions
16600	169 (1,02%)	16431 (98,98%)	3257 (19,62%)	0 (0,00%)	11899 (71,68%)

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Fragmentation rate
2.13%

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<b>Stratigraphy</b>	<b>Chronological phases</b>	<b>Taxon richness</b>	<b>Total NISP</b>
Spits 16 to 1	Neolithic	16	518
Spits 41 to 17	Early/mid-Holocene	18	2300
Spits 61 to 42	Pleistocene (from 46 kya)	7	67

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<b>Shannon's diversity index</b>	<b>Evenness</b>
2.183	0.787
1.978	0.684
1.468	0.754

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Location	Site	Age of the fish remains assemblages	Site type	Richness (family)	NISP
Okinawa, Japan	Yamashito-cho I	Back to 37,000 BP	Cave	Unknown	Unknown
Okinawa, Japan	Sakitaro-do	36,500 to 13,000 cal. BP	Cave	NA	9
Ilin, Philippines	Bubog I	33,277- 31,783 cal. BP to 4,240-4,081 cal. BP	Rockshelter	19	1445
Ilin, Philippines	Bubog II	9,530-9,320 cal. BP to Pre-Spanish era	Rockshelter	19	1382
Mindoro, Philippines	Bilat	13,574-13,561 cal. BP to 8,192-8,043 cal. BP	Cave	14	678
Kisar, Indonesia	Here Sorot Entapa	15,500 to 1,800 BP	Rockshelter	27	105780
Alor, Indonesia	Tron Bon Lei	21,584-21,029 cal. BP to 3,561-3,455 cal. BP	Rockshelter	14	39349
Alor, Indonesia	Makpan	40,360-38,585 cal. BP to recent time	Cave	At least 8	NA
<b>Tutuala, Timor-Leste</b>	<b>Asitau Kuru</b>	<b>46,529-43,085 cal. BP to Neolithic</b>	<b>Rockshelter</b>	<b>23</b>	<b>55287</b>
Laleia, Timor-Leste	Laili	43,704-41,429 cal. BP to 8,555-8,316 cal. BP	Rockshelter	6	491

Predominant taxa	Local aquatic environments	Artefacts
Unknown	Kokuba-gawa River	Sandstone cobbles
	Coral reef	
Unidentified	Yuhi-gawa River	Shell jabbing hooks
	Coral reef	Seashell artifacts & beads
Reef taxa such as Diodontidae,	Coral reef	Net sinkers
Scaridae and Acanthuridae	Ilin Mindoro/channel	Bipoint fishing gorge
	Mangrove swamps	Shell adze
	Coral reef	Preform of a shell adze
	Ilin Mindoro/channel	
	Coral reef	Shell adze
	Ilin Mindoro/channel	
Small Balistidae, Serranidae,	Narrow coastal reef terraces	Shell jabbing hooks,
Labridae and Holocentridae	Limited access to the beach	beads & ornaments
	Rocky coral reef	Obsidian flakes
Balistidae, Acanthuridae and	Easy access to the beach	Shell jabbing hooks
Scaridae	Rocky coral reef	Shell beads & ornaments
Reef taxa (the fish assemblage has	Easy access to the beach	Shell jabbing hooks
only been sorted and weighed)	Easy access to the beach	Shell beads & ornaments
Scombridae, Carangidae and reefal	<b>Valu Sere/Jaco deep channel</b>	<b>Bone points and shell</b>
taxa such as Scaridae		<b>fish hooks, shell adzes</b>
	<b>Coral reef with strong courants</b>	<b>beads &amp; ornaments</b>
Anguillidae and a few coastal fish	Laleia river	Obsidian flakes
taxa	Coral reef at 4.3 km	Lithic artefacts

Halieutic subsistence strategies	Recovery method	References
Unknown	Unknown	<i>In</i> Fujita 2021 Takamiya et al. 1975
Very limited fishing activity	Water screening (0.5 cm to 3 mm)	Fujita et al. 2016
Predominant exploitation of the coral reef with the use of a large variety of fishing techniques such as angling, spearing, netting, hand-gathering and fish traps	Sieving (2 mm mesh)	Pawlik et al. 2014, 2015 Boulanger et al. 2019 Boulanger 2021
	Sieving (2 mm mesh)	Pawlik et al. 2014, 2015 Boulanger 2021
	Sieving (2 mm mesh)	Pawlik et al. 2014, 2015 Boulanger 2021
Continuity in reef fishing strategies with a decline of diversity during the mid-Holocene	Dry-sieved and wet-sieved (1.5 mm mesh)	O'Connor et al. 2019
Shift from carnivorous/open-water taxa during the terminal Pleistocene to herbivorous/omnivorous taxa during the Holocene	Dry-sieved and wet-sieved (1.5 mm mesh)	O'Connor et al. 2017 Samper Carro et al. 2016
Probable exploitation of the nearby coral reef	Dry-sieved and wet-sieved (1.5 mm mesh)	Langley et al. 2020 Kealy et al. 2020
Exploitation of local marine environments implying the use of trolling, angling and spearing	Dry-sieved and wet-sieved (1.5 mm mesh)	<b>O'Connor et al. 2011</b>
		<b>Shipton et al. 2019</b>
Exploitation of both marine and freshwater habitats over time	Dry-sieved and wet-sieved (1.5 mm mesh)	Hawkins et al. 2017 <u>Boulanger et al. in review</u>