

1                   **30,000 years of fishing in the Philippines:**  
2                   **New ichthyoarchaeological investigations in**  
3                   **Occidental Mindoro**

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40 **Keywords:** ichthyoarchaeology; *Homo sapiens*; Island Southeast Asia; coastal adaptation;  
41 marine environments; fishing; Pleistocene; Holocene

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44 **Highlights:**

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46 • Study of three Late Pleistocene to Holocene ichthyoarchaeological assemblages  
47 recovered in Occidental Mindoro, Philippines.

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49 • Use of expanded skeletal element identification protocols to the lowest taxonomic level  
50 possible combined with rarefaction, statistical tests and diversity indices.

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52 • Exploitation of near-shore environments with temporal variations in fishing practices  
53 reflecting significant periods of climate mediated habitat change.

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55 • Understanding coastal adaptation of *Homo sapiens* in Island Southeast Asia over 30,000  
56 years.

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62 **Abstract**

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64 Marine adaptations are considered to have been significant factors in the evolution of our  
65 species (*Homo sapiens*). As humans dispersed from Africa around 100 kya, marine resources  
66 provided essential nutrients in island environments of the tropical Southeast Asian seas. The  
67 Philippine archipelago has revealed significant evidence of early human settlement during this  
68 period of coastal migration. Yet, despite being a global marine biodiversity hotspot, few studies  
69 have investigated prehistoric marine adaptations there. In this study, we focus on the analysis  
70 of fish bones from three sites in Occidental Mindoro, Philippines: Bubog I, Bubog II, and Bilat  
71 Cave with the aim of enhancing the understanding of *H. sapiens*' coastal adaptations and  
72 maritime interactions since at least 32,000 BP. We utilized expanded skeletal element  
73 identification protocols to determine the lowest taxonomic level possible, combined with  
74 diversity indices. The analyses indicate that *H. sapiens* on Mindoro mostly exploited near-shore  
75 environments, with temporal variations in fishing practices reflecting differences in site  
76 occupation intensity and periods of climate-mediated habitat change. Inter-site variations in  
77 fishing practices are likely related to disparities in local marine habitats. Spatiotemporal  
78 differences in marine environments influenced the development of diverse fishing methods and  
79 technologies, demonstrating a detailed knowledge of local aquatic environments and the  
80 adaptability of modern humans in Island Southeast Asia since the Pleistocene.

## 1. Introduction

The study of fish remains from archaeological sites (ichthyoarchaeology) in the Asia-Pacific tropical island region is of global significance for reconstructing *Homo sapiens* interactions with diverse marine environments (Boulanger, 2021; Boulanger et al., 2022; Butler, 1994; Colley, 1990). Many recent studies demonstrate shifting fishing strategies in response to changing marine environments during periods of climate and culture change dating back to 46 kya (Boulanger et al., 2022, 2019; Colley, 1987; O'Connor et al., 2019; Ono et al., 2019; Ono and Intoh, 2011; Samper Carro et al., 2016). Coastal archaeological cave sites east of Huxley's line associated with Pleistocene *H. sapiens* indicate open water crossings to the oceanic islands of Southeast Asia, representing the earliest known period of human maritime adaptation (Clarkson et al., 2017). These marine adaptations are considered to have been significant factors in the survival of our species during dispersal from Sunda to Sahul as other hominin species became extinct (O'Connor et al., 2017; Shipton et al., 2021).

The Philippines archipelago is situated at the apex of the Coral triangle (Allen, 2008; Randall, 1998), yet despite its outstanding fish biodiversity, few ichthyoarchaeological studies have been conducted on these islands. Three main factors have contributed to this paucity of data. Firstly, preservation conditions vary throughout the Asia-Pacific. In Island Southeast Asia (ISEA), complex geological and sea level changes, necessitates a reliance on cave sites for zooarchaeological inquiry, which often act as traps for vertebrate deposition (Louys et al., 2017). Secondly, extensive and detailed comparative reference collections are only in their early stages of development (Boulanger, 2021). Comparative anatomy and other classical methods used in ichthyoarchaeology to reconstruct fishing techniques and palaeoenvironments, such as osteometry (Chaix and Desse, 1994) or sclerochronology (Panfili et al., 2002) depend on diverse and well-curated modern reference collections.

Asia-Pacific fishes are notoriously difficult to identify to species as large families often limit identification to the family level, making ecological reconstructions less detailed (Boulanger, 2021; Lambrides and Weisler, 2013). This is problematic for interpretations of human interactions with marine habitats which one considers diverse families such as scombrids have many species sharing different habitats and life histories, including changes in habitats for breeding and spawning behaviors, some of which could be caught close to shore while others are found in pelagic habitats (Anderson, 2013). Thirdly, matching ethnoarchaeological accounts of traditional fishing practices to ichthyofaunal assemblages is often complex. Scholars have attempted classification of contemporary Pacific islander fishing techniques in specific marine habitats, which varied by geographic region in the Asia-Pacific (Butler, 1994; Giovas et al., 2016; Johannes, 1981; Kirch and Dye, 1979; Masse, 1986; Ono, 2010; Ono et al., 2009).

However, in ISEA, very few studies on traditional fishing practices have been conducted. Umali and Warfel (1949), in a report dedicated to coral reef fishing in the Philippines, described the fishing methods commonly used by contemporary fishers. Fishing using traditional techniques had already declined in society at the time of their study, with the introduction of new modern methods and materials that included explosives, poisons, diving and spearing, fish pots, lines, reef drag seine and various drive-in-nets (Bohol and Japanese). This doubtlessly caused dramatic modifications to local ecologies and does not allow us to make direct

125 ethnological comparisons with archaeological material from the Philippines. Nevertheless,  
126 many authors seem to agree that Pacific fishing strategies are diverse and highly specialized,  
127 aimed at capturing specific species, and are adapted to a variety of ecological conditions.  
128 Therefore, local fishing communities choose the techniques that are the most appropriate and  
129 efficient in their environment and with the available resources (Boulanger, 2021; Boulanger et  
130 al., 2022; Giovas et al., 2017; Ono and Clark, 2012; Walter, 1989).

131 The early development of fishing in ISEA appears to have focused on a variety of fish near  
132 the edge of the reef shelf, indicating that fishing methods and technology were being employed  
133 to adapt to a range of marine and freshwater habitats (Boulanger, 2021; Boulanger et al., 2023,  
134 2022). In Wallacea, which has never been connected to a continental landmass (Kealy et al.,  
135 2016), archaeological excavations of coastal cave sites in the Lesser Sunda Islands, including  
136 eastern Indonesia and Timor-Leste, have revealed the highest abundances of fish remains in  
137 ISEA (Boulanger, 2021; Boulanger et al., 2022; Kealy et al., 2020; O'Connor et al., 2019, 2011;  
138 Samper Carro et al., 2016). Further, shell fishhooks were recovered in burial contexts at Tron  
139 Bon Lei on Alor in Indonesia by 12 kya indicating the importance of maritime culture in socio-  
140 ritualized treatment of the dead by the end of the Pleistocene (O'Connor et al., 2017). Later,  
141 between 4,000-2,900 BP, populations speaking languages related to the Austronesian family,  
142 spread from Taiwan and Southeast Asia throughout ISEA. Their subsistence mode combining  
143 food production and near shore marine foraging indicates the noteworthy maritime adaptations  
144 that Neolithic cultures engaged in (Bedford et al., 2007; Bouffandeau et al., 2018; Butler, 1994;  
145 Fitzpatrick et al., 2011; Fitzpatrick and Kataoka, 2005; Giovas et al., 2017, 2016; Kirch and  
146 Dye, 1979; Lambrides et al., 2018; Ono, 2004, 2003; Ono et al., 2019; Ono and Intoh, 2011;  
147 Walter, 1989; Weisler and Green, 2013).

148 This paper builds on these developments by incorporating ichthyoarchaeological data from  
149 Bubog I (Boulanger et al., 2019), combined with unpublished detailed analysis of this site, and  
150 new data from Bubog II, located on the small island of Ilin, and Bilat Cave, which is situated  
151 on the coast of Mindoro facing Ilin (Fig. 1). The study utilizes a wide range of skeletal elements  
152 to the lowest taxonomic level possible and focuses on how this analysis facilitates a more  
153 detailed understanding of *H. sapiens* fishing practices at Occidental Mindoro, Philippines over  
154 the last 30,000 years. The study seeks to understand the variations in marine habitat and  
155 temporal changes in culture spanning the transition from Pleistocene to Holocene and  
156 encompassing the Austronesian expansion ca. 4,000 cal. BP, and beyond.

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## 159 **2. Archaeological background**

160

161 Mindoro is the seventh largest island in the Philippines by land area with a total of 10,571  
162 km<sup>2</sup>, located to the southwestern coast of Luzon, in the Southwest corner of the South China  
163 Sea (Fig. 1). The limestone formations in the southern part of Occidental Mindoro have been  
164 the target of archaeological explorations since 2010 (Pawlik et al., 2014; Porr et al., 2012). Due  
165 to its geographic situation, the island may have served as a stepping-stone for migration to the  
166 Philippine archipelago via the central Sunda Shelf route to Palawan (Porr et al., 2012), where  
167 the earliest evidence for the presence of *H. sapiens* at Tabon Cave is AMS-dates to ca. 39-  
168 33,000 BP (Choa, 2018), while less secure U-series dated the human remains to as early as ca.

169 47,000 BP (Détroit et al., 2004; O’Connell et al., 2018). This study focuses on two sites located  
170 on Ilin, Bubog I and Bubog II, and one site, Bilat Cave, in Sta. Teresa, Magsaysay at the  
171 southwestern end of Mindoro, separated from Ilin Island by a ca. 900 to 1,300 m wide channel  
172 (Fig. 1). These sites have produced evidence of a variety of human activities, including fish  
173 bone assemblages that, based on their chronology and long sequence, are crucial to  
174 understanding how changes in landforms and sea levels might have influenced the mobility of  
175 human populations and changing subsistence behaviors (Neri et al., 2015; Pawlik et al., 2015,  
176 2014; Pawlik and Fuentes, 2023; Pawlik and Piper, 2019).

177

## 178 **2.1. Bubog I**

179

180 Bubog I rockshelter is located at a grid reference of 12°10’16”N, 121°07’52”E, at the  
181 southeast end of Ilin Island (Fig. 1), approximately 30 m above mean sea level, and about 180  
182 m from the present shoreline. The main rockshelter consists of a broad, bright, and spacious  
183 northeast-facing platform, measuring approximately 20 m in length with a maximum width  
184 from the lip of the overhang to the rear limestone wall of about 4 m, and a height of around 10  
185 m. The archaeological record consists of twelve well-stratified layers and a shell midden  
186 (Layers 9 to 1) with a total depth of ca. 1.5 m and Pleistocene deposits of about 2 m recently  
187 discovered underneath the shell midden (Pawlik, 2019; Pawlik et al., 2014). The stratigraphic  
188 sequence is anchored to an absolute chronology by 16 radiocarbon dates, ranging from 33,040-  
189 31,736 cal. BP at the bottom of Layer 9 to 4,848 to 4,651 cal. BP in Layer 2, with an important  
190 hiatus within Layer 9 (Pawlik et al., 2014; Pawlik and Piper, 2019). It provides records of the  
191 important palaeoenvironmental and palaeogeographic changes that occurred at the end of the  
192 Pleistocene and during the mid-Holocene.

193 Pawlik and co-authors (2014) notably pointed out a major shift in mollusks from Layers 7-  
194 6, around 6000 BP, transitioning from a predominantly mangrove to a mainly marine origin.  
195 The malacofauna from Bubog I indicates the presence of mangrove bivalves (*Polymesoda*  
196 (*Geloina*) *coaxans*, *Terebralia sulcata*), and mangrove crabs (*Cardisoma carnifex*, *Scylla* sp.)  
197 in Layers 9 and 8, and the presence of marine gastropods (*Lambis* sp., *Strombus* sp., *Turbo* sp.,  
198 *Lunella* sp., *Trochus* sp., and *Conus* sp.) and marine bivalves (e.g., *Tridacna* sp., *Hippopus* sp.)  
199 in Layers 6 to 3 (Lim, 2016; Pawlik et al., 2014). This clearly reflects the adaptation of  
200 subsistence strategies to changing landscapes (Boulanger, 2015; Boulanger et al., 2019; Lim,  
201 2016; Pawlik et al., 2014). The rest of the fauna consists of fish remains, micromammal remains  
202 such as murids (Reyes, 2019; Reyes et al., 2017), and a few large mammals including the native  
203 pig of Mindoro (*Sus oiveri*), as well as few remains of tamaraw, an endemic water buffalo  
204 (*Bubalus mindorensis*), and two endemic deer species (*Rusa marianna* and *Cervus alfredi*)  
205 (Boulanger, 2015; Boulanger et al., 2019; Pawlik and Piper, 2019). The interpretation for a shift  
206 in subsistence strategies in relation to changing paleo-landscape is consistent with results  
207 obtained from the macrobotanical analysis, with the lower layers (Layers 9 to 5) rich in  
208 mangrove forest taxa such as Rhizophoraceae which were rapidly replaced in the upper layers  
209 by secondary forest taxa (Carlos et al., 2018).

210 The faunal material was associated with a lithic industry mostly composed of unmodified  
211 pebbles with wear traces, which were used as hammerstones to extract meat from the mollusks.  
212 Among the relatively few flaked artefacts were seven obsidian flakes found at the base of the

213 shell midden in Layer 9 and below the midden in the silty deposits of Layer 10 (Pawlik, 2021;  
214 Pawlik et al., 2014). As Palawan is non-volcanic, the obsidian would have been acquired  
215 remotely and transported to sites (Neri et al., 2015; Pawlik and Fuentes, 2023). In addition, a  
216 *Tridacna* shell adze was also recovered and directly AMS-dated to 7,341-7,012 cal. BP (Pawlik  
217 et al., 2015), as well as flaked shell artefacts made of *Tridacna*, *Conus* and *Geloina* shells. From  
218 the terrestrial deposits below the shell midden, an almost complete fishing gorge was recovered  
219 in Layer 10, dated by association to before 30,000 years ago. Another bone point and potential  
220 fishing gorge fragment have also been found in Layer 5, together with a heavily fragmented  
221 modified bone artefact and a modified suid canine with wear traces (Pawlik et al., 2015). Two  
222 igneous pebbles with waisted modifications possibly used as net-sinkers were also recovered  
223 from the shell midden (Boulanger et al., 2019; Pawlik and Piper, 2019). Moreover, the  
224 excavation of Trench 4 in 2013 led to the discovery of a buried gracile mature individual  
225 directly dated to ca. 5,000 years ago (Pawlik et al., 2019). From underneath the burial, a single  
226 AMS date of 35,034-33,847 cal. BP on *Terebralia* shell provides the currently earliest  
227 radiocarbon date for Bubog I.

## 228 229 **2.2. Bubog II**

230  
231 Bubog II rockshelter is located at a grid reference of 12°10'25"N, 121°07'42"E, about  
232 250 m north of Bubog I (Fig. 1), at an elevation of 45 m above mean sea level. The rockshelter  
233 faces southeast and has a level rectangular platform ca. 6 m in width, surrounded by high ceil-  
234 ings and walls to the north, south, and west, and two large rock falls to the east. The site has a  
235 shell midden that is similar in structure, though less extensive, than the midden in Bubog I, with  
236 a stratigraphic profile of 14 distinct layers in the eastern Trench 2, AMS-dated from 9,536-  
237 9,316 cal. BP to the 16th-17<sup>th</sup> Century AD and the beginning of the colonial period (Fig. 2).  
238 The earliest available dates for Bubog II of 10,785-10,562 cal. BP were retrieved from Trench  
239 3 in the center of the habitation platform (Pawlik, 2021; Pawlik et al., 2014; Pawlik and Piper,  
240 2019). The fauna and the lithic assemblages are similar, albeit in smaller numbers, to those in  
241 Bubog I (Pawlik, 2021; Pawlik et al., 2014; Pawlik and Piper, 2019).

242 A total of 42 gastropod genera and twelve bivalve genera were identified at Bubog II  
243 (Pawlik et al., 2014). Fish and large mammal remains were also found. Micromammals such as  
244 rats (murids), bats (Chiroptera) and shrews (Soricidae) were also present, but less numerous  
245 and less diversified than in Bubog I (Reyes, 2019). A small assemblage of 27 lithic artefacts,  
246 consisting of nine complete but damaged pebbles used as hammers, one with a waisted  
247 modification like the ones from Bubog I, two pebbles fragments and 16 flakes and shattered  
248 pieces were recovered throughout the sequence (Pawlik et al., 2014). A large preform of a  
249 *Tridacna* shell adze was found in Layer 5 of Trench 3, directly dated to 8,970-8,600 cal. BP  
250 (Pawlik and Piper, 2019).

## 251 252 **2.3. Bilat Cave**

253  
254 Bilat Cave is located directly at the coast of Sta. Teresa, Magsaysay at a grid reference  
255 of 12°14'482"N and 121°07'642"E. The cave is situated at an elevation of approximately 2-3  
256 m above mean sea level and composed of three connecting chambers, which were still used by

257 fishers for storage. The first chamber faces the landside to the northeast and contains a levelled  
258 platform of approximately 18 m in length and about 6 m in width. A large, but relatively shallow  
259 shell midden (compared to Bubog I) covered the surface of the entrance area. The northern  
260 chamber is connected to two other chambers to the south and west, which both have openings  
261 to the sea, facing the Ilin Strait (Fig. 1). They are almost at sea level, and the present cave floors  
262 show signs of occasional flooding. The cave was probably flooded during the Holocene climatic  
263 optimum around ca. 6,000 BP when sea levels rose to approximately 3 to 5 m higher than  
264 present (Sathiamurthy and Voris, 2006; Voris, 2000). Two excavation trenches were set up in  
265 Chamber 1, Trench 1 with a size of 3x2 m, and Trench 2 with a size of 4x1 m. Excavation of  
266 Trench 1 reached the water table at a depth of 100-90 cm above sea level in Squares C and D,  
267 while in Square A, a 100x50 cm shell sampling column was exposed, and shell samples were  
268 taken in controlled units. Several AMS-dates on charcoal and shell provided a chronology  
269 ranging from the Last Glacial Maximum (LGM) until the present day or 287-3 cal. BP (Fig. 2).  
270 A charcoal sample from a stratified context in Square 1A, at the bottom of the shell midden at  
271 2.30-2.20 m above sea level, returned an AMS-date of 8,185-8,033 cal. BP (Pawlik and Piper,  
272 2019). The deeper strata of squares C and D, Layer 3, provided a date on charcoal associated  
273 with a lithic flake in Layer 3 of 13,790-13,596 cal. BP, while two samples of *Melanoides* shells  
274 from Layer 4 delivered radiocarbon dates of 21,891-21,367 and 21,252-20,745 cal. BP,  
275 respectively, indicating human presence during the terminal Pleistocene and LGM (Pawlik and  
276 Piper, 2019).

277 The excavation produced remains from terrestrial and marine vertebrates, several flaked  
278 cherts as well as unmodified but used pebble artefacts and their fragments. Trench 2 produced  
279 an edge-ground *Tridacna* shell adze, similar in form and age to the one found in Bubog I, di-  
280 rectly dated to 7,292-6,984 cal. BP, suggesting a cultural connection to the Bubog sites across  
281 the Ilin Strait and, in the context of the shell adze preform from Bubog II, a local manufacture  
282 of this type of tool during the early to mid-Holocene (Pawlik et al., 2015; Pawlik and Piper,  
283 2019).

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### 286 **3. Material and methods**

287

#### 288 ***3.1. Recovery procedure***

289

290 The majority of the excavated sediments were sieved through a 2 mm mesh screen on  
291 sites. All artefacts and ecofacts were removed, bagged, and recorded. A bag of 15 L of sediment  
292 from each stratigraphic horizon was transported to the beach where it was wet sieved through  
293 a 1 mm and 2 mm sieve rack in the sea. A bag of 5 L of sediment from each unit was floated in  
294 fresh water. The light fraction was poured into a 0.5 mm sieve, and the organic remains  
295 collected (Pawlik et al., 2014). This whole process of washing the sediment was repeated three  
296 times. The recovery strategy remained consistent throughout the excavated stratigraphic  
297 sequence of the three sites to ensure temporal and spatial comparability within and between  
298 excavated contexts. All fish remains from all excavation trenches were sorted from the  
299 vertebrate assemblage after sieving.

300



### 3.2. *Comparative anatomy*

The Mindoro assemblages have been identified to the lowest anatomical and taxonomical level, thanks to the extensive modern reference collection housed at the Muséum national d'Histoire naturelle (UMR 7209 "Archéozoologie et Archéobotanique - Sociétés, Pratiques et Environnements"), comprised of 448 complete individual Indo-Pacific fish skeletons, from 73 families, 175 associated genera, and 320 species. All elements were considered for identification. This permitted a more detailed analysis of the assemblage of Bubog I, which was previously performed using the reference collection of the University of the Philippines Diliman where 36 families are represented (Boulanger et al., 2019).

### 3.3. *Quantitative analysis*

Following taxon identification, the different skeletal elements were counted to estimate taxon frequencies using a range of standard quantification methods (Grayson, 1984). Here we use three main methods as follows: the NISP (number of identified specimens) (Payne, 1975), which can be severely affected by differential fragmentation (Lyman, 2008); the MNE (minimum number of elements), defined as the minimum number of elements for different skeletal elements (Bunn, 1986); and the MNI (minimum number of individuals). The MNI corresponds to the smallest number of individual animals necessary to account for all the NISP of a specific taxon in an assemblage (White, 1953). MNI can reduce the effects of fragmentation on quantification of relative abundance and is determined by combining the laterality or anatomical position of the elements (Poplin, 1976). In this paper, we opted to compute the NISP, MNE and MNI per layer of each archaeological site.

### 3.4. *Analysis of cultural and taphonomical disturbances*

We took into account several types of anthropic and natural actions that may have had an impact on the assemblage, such as traces of combustion. Discolorations ranging from black to light-gray indicated potential heating, either from cooking or incidental firing (Lebon, 2008). We also considered potential cut marks, discernible by their shape, on fishbone surfaces caused by tools during preparation or consumption, as well as concretions present in the sediments coming from the precipitation of dissolved carbonates from speleothem. The fragmentation of the skeletal elements (FR) was also determined, allowing to assess the degree of preservation of the latter by quantifying the impact of taphonomic processes on bone fragmentation. FR is calculated by dividing NISP by MNE (Lyman, 2008; Richardson, 1980).

### 3.5. *Rarefaction, richness, diversity, and evenness*

To evaluate the relationship between the defined chronological periods at each site in terms of foraged marine environments, quantification units were further used in indices. Additionally, we utilized rarefaction curves to ascertain whether an adequate number of taxa had been identified for conducting a comparison among the three sites. Rarefaction is defined as the probabilistic relationship between the number of individuals (NISP) and the number of

345 taxa, based on an estimated rarefaction curve from the sample (Grayson, 1984; Lyman and  
346 Ames, 2007). Practically, rarefaction provides the expected species richness in random  
347 subsamples, therefore allowing to compare two samples of different sizes by comparing the  
348 shape of the curves. The larger the sampling is, the larger the number of taxa will be. Yet, such  
349 an inflation curve is asymptotic and effort grows very fast before reaching a plateau with  
350 declining returns with increasing sampling effort. In other terms, at first, each new sample has  
351 a high probability to represent a new unseen before taxon within the assemblage, but after a  
352 certain estimated number of samples, the probability to find a new taxon is weak. Rarefaction  
353 curves would therefore indicate whether differences in the number of taxa in the different sites  
354 result from a different sampling effort, or size of the assemblages. Beyond rarefaction  
355 (interpolation) from the effective number of taxa in our samples, we also computed predictions  
356 (extrapolations) of the number of taxa one would have found with larger samples using Chao  
357 and co-authors (2014) and Hsieh and co-authors (2016) formulas. Differences among distinct  
358 assemblages within the same site were assessed using a Chi-squared test for homogeneity based  
359 on the NISP, following the methodology outlined by Grayson (1984). As the sample sizes are  
360 small, the p-values were computed for a Monte Carlo test (Hope, 1968), which were then  
361 corrected using a Bonferroni correction for multiple tests (Dunn, 1961).

362 Because the absence of certain taxa in one of the assemblages could not be  
363 accommodated within this specific test due to its calculation method, taxon richness, diversity,  
364 and evenness were also estimated following Cruz-Uribe (1988) recommendations. Richness is  
365 defined as the number of taxa (e.g. family) in a certain stratum. Additionally, to mitigate the  
366 influence of potential differences in sample size, we calculated the Menhinick's Richness Index  
367 which accounts for the number of taxa in a sample divided by the square root of the number of  
368 individuals in the sample. Higher values of Menhinick's index indicate greater taxa richness,  
369 meaning the community or sample contains a more diverse array of species. Conversely, lower  
370 values indicate lower species richness, with fewer unique species represented (Magurran,  
371 1988). Diversity accounts for the frequency of each taxon in the same stratum, which is  
372 summarized by the Shannon's Diversity Index which is richness dependent. The index has a  
373 lower limit of 0, which corresponds to a few species with a variable number of specimens per  
374 taxon and has no upper boundary. A large Shannon's Diversity Index corresponds to several  
375 species being represented by a more even number of specimens one from the other. The Pielou's  
376 Evenness Index, which is commonly used to measure evenness, ranges from 0 and 1 with  
377 indicating complete inequality (i.e., only one taxon has all the individuals) and 1 indicating  
378 perfect equality (i.e., all taxa have the same number of individuals. All the indices, rarefaction  
379 curves and Chi-squared test were made using R freeware (R Core Team, 2020), and its native  
380 packages.

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## 4. Results

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### 4.1. Bubog I

386

387 At Bubog I, 19 families are represented, as well as 22 genera, and 12 species (Tab. 1).  
388 The NISP up to the subclass level (Elasmobranchii) or infraclass level (Teleostei) is 1,445.

389 Most of the fragments were identified from Layer 9 to 4, totalling 1,025 specimens (70.93%).  
390 Layer 9 had the highest NISP with 233 specimens (16.12%), while Layer 7 only had 129 fish  
391 specimens, likely due to stratigraphic disruption caused by rock falls. Of the bone fragments,  
392 405 (28.08%) were identified to the family level, 73 (5.05%) to the genus level, and 17 (1.18%)  
393 to the species level, with the majority of bones (70.66%) belonging to the axial skeleton (Tab.  
394 4; Tab. A1). Numerous bones (NISP = 1,038), comprising 71.83% of the site's assemblage,  
395 showed traces of calcining, ranging from black to light-grey coloration, indicating potential  
396 cooking or incidental firing (Tab. 4).

397 The Bubog I assemblage can be divided into two broad periods based on a change in the  
398 proportions of mangrove crustaceans between Layers 12 to 7 and 6 to 1 (Boulangier, 2015;  
399 Boulangier et al., 2019). For comparison purposes, we aggregated the data from these two layers  
400 (Tab. 5). After applying the Chi-squared test, they appear to be statistically different ( $\chi^2 = 77.236$ ,  
401  $p = 9.999\text{e-}05$ ).

#### 402 **4.2. Bubog II**

403  
404  
405 At Bubog II, we identified 19 families, 18 genera, and five species from the fishbone  
406 assemblage (Tab. 2; Tab. A2). The total NISP up to the subclass level (Elasmobranchii) or  
407 infraclass level (Teleostei) is 1,382. The majority of the remains were identified within Layers  
408 8 to 1, totaling 1,187 specimens (85.89%). In terms of taxon identification, 309 bone fragments  
409 (22.36%) were identified to the family level, 111 (8.03%) to the genus level, and 18 (1.30%) to  
410 the species level, with the majority of remains belonging to the axial skeleton (768 specimens,  
411 55.57%) (Tab. 4; Tab. A2). Only 13.46% of the bones (186 specimens) were partially or entirely  
412 covered with black to light-grey traces of combustion, indicating potential cooking or incidental  
413 firing (Tab. 4).

414 The Bubog II fishbone assemblage is similar to the Bubog I assemblage in terms of size  
415 and the variety of faunal spectra (Tab. 1; Tab. 2). Based on radiocarbon dates, two main cultural  
416 phases have been identified at Bubog II: an early/mid-Holocene phase spanning Layers 14 to  
417 7, followed by a Late Holocene to protohistoric phase covering Layers 6 to 1 (Pawlik et al.,  
418 2014; Pawlik and Piper, 2019). For comparative analysis, we aggregated these two layers  
419 together (Tab. 5). After applying the Chi-squared test, they appear to be statistically different  
420 ( $\chi^2 = 35.203$ ,  $p = 0.0036$ ).

#### 421 422 **4.3. Bilat Cave**

423  
424  
425 At Bilat Cave, we identified at least 14 families, 15 genera, and six species (Tab. 3;  
426 Tab. A3). The total NISP up to the subclass level (Elasmobranchii) or infraclass level (Tele-  
427 ostei) is 678. The majority of the remains were found in Spits 5 and 4, accounting for 443  
428 specimens (65.33%). Out of the identified remains, 171 (25.22%) were classified to the family  
429 level, 70 (10.32%) to the genus level, and 12 (1.77%) to the species level (see Table 3). As  
430 expected, most of the bones (NISP = 456) (67.25%) belong to the axial skeleton, with 358  
431 vertebrae identified (see Table 4 and Table A3). A total of 547 bones were found to be partially  
432 or entirely covered with traces of combustion, representing 80.68% of the assemblage at the

433 site (Tab. 4). In Spit 6, we also observed the presence of a terminal Pleistocene requiem shark  
434 (Carcharhinidae) vertebra, which may have been used as an ornamental artifact. However, the  
435 preservation of this specimen is not sufficient to determine its anthropological nature or identify  
436 potential characteristic traces of shaping (Boulanger et al., 2020) (Fig. A4).

437 The Bilat Cave assemblage is proportionally smaller compared to the other Mindoro  
438 assemblages (Tab. 3; Tab. 4). The site has been divided into two broad chronological periods:  
439 a terminal Pleistocene phase and an early to mid-Holocene phase. No evidence of a Neolithic  
440 occupation was found at Bilat (Pawlik and Piper, 2019). As a result, we compared these two  
441 layers aggregated together (Tab. 5). After applying the Chi-squared test, they appear to be sta-  
442 tistically different ( $\chi^2 = 25.734, p = 0.027597$ ).

443

444

## 445 5. Discussion

446

447 Beyond indicating that fishing activities targeted approximately 17 different taxa, the  
448 rarefaction and extrapolation curves, further reveal insights into the diverse marine  
449 environments at the three archaeological sites - Bubog I, Bubog II, and Bilat Cave. These curves  
450 evidence that at the smallest NISP sample size which is Bilat Spits 9-5, the other site groups  
451 had a similar number of taxa. Furthermore, any additional sampling effort would only have  
452 resulted in the identification of a maximum of three new taxa. Therefore, one can conclude that  
453 any differences in terms of diversity between each of these groups are not related to the size of  
454 the assemblages but to subsistence behaviors.

455 The zooarchaeological analysis of the fish bone assemblages in Mindoro has provided  
456 valuable insights into the taxonomic diversity of the ancient fish exploitation. The thorough  
457 identification of skeletal elements, with a notable focus on vertebrae, has allowed for the  
458 detection of less common taxa, including Clupeidae and Mullidae. However, when examining  
459 the overall richness across sites, we observed both inter- and intra-site variability, which  
460 appeared relatively normal considering that the three are located within the Mindoro Strait, but  
461 low considering the geographic location of the sites within the Coral Triangle. This  
462 phenomenon could be influenced by two main factors. Firstly, the smaller sizes of the samples  
463 compared to other ichthyoarchaeological assemblages in the broader Southeast Asian region  
464 (Boulanger et al., 2022) might introduce a preservation bias. This means that the relatively  
465 smaller sample sizes could impact the representation and diversity of fish taxa in the  
466 assemblages. Secondly, the similarity of local environments at Bubog I, Bubog II, and Bilat  
467 Cave under comparable localized climatic conditions may also play a role in shaping the  
468 observed pattern. These similar environmental conditions could lead to overlapping fish  
469 communities across the sites, which might contribute to the relatively limited variation in  
470 richness observed. Despite the fact that not all periods are preserved at the three sites, the  
471 chronostratigraphies of Bubog I, Bubog II, and Bilat Cave complement each other. By  
472 analyzing them collectively, we gain a broader perspective that allows us to interpret the results  
473 at the scale of the Mindoro Strait as a whole, revealing valuable information about changes in  
474 fishing practices over time in response to shifts in the paleoecological conditions that occurred  
475 in the region (Pawlik et al., 2014).

476

### 5.1. Late Pleistocene (from 32,000 BP) and Last Glacial Maximum (LGM)

Between 32,000 years BP and approximately 8,000 BP, a period characterized by rising sea levels up to about -40 m, Ilin Island and Mindoro were connected (Pawlik et al., 2014) (Fig. 5). During this time, the coastal waters of Bubog I witnessed the regular exploitation of fishes from eight different families (Tab. 1). The assemblage included various species such as surgeonfishes, tangs, unicornfishes (Acanthuridae), and a diverse array of parrotfish species (Scaridae), which are commonly found in reef environments (Allen and Steene, 1999) (Fig. 6). The favorable marine conditions resulting from the land connection between Ilin Island and Mindoro provided ample opportunities for ancient coastal populations to engage in fishing activities. The abundance and diversity of fish species from different families suggest a thriving marine ecosystem, likely teeming with various resources that were essential for the sustenance of human communities during this period. Notably, surgeonfishes, tangs, and unicornfishes are known for their adaptability to reef habitats (Froese and Pauly, 2022), making them well-suited for exploitation in such coastal areas. Additionally, the presence of numerous parrotfish species indicates a rich and productive reef environment, as parrotfishes play crucial roles in maintaining coral reef health through their grazing and bioerosion (Froese and Pauly, 2022). However, wherever they are found archaeologically, parrotfish tend to be one of the dominant families of fishes identified in the Pacific (e.g. Bouffandeau et al., 2018; Fleming, 1987; Lambrides and Weisler, 2015; Rurua et al., 2020). This dominance is often related to the robusticity of their pharyngeal clusters (Boulanger et al., 2019; Fleming, 1987).

Among the identified coastal taxa, grunts (*Pomadasys* sp., Haemulidae) and mullets (Mugilidae) were certainly consumed at Bubog I (Fig. 6). These fish typically prefer brackish and estuarine environments but can also be found in association with reef habitats (Froese and Pauly, 2023). Additionally, evidence suggests that the ancient inhabitants of Bubog I gathered brackish crabs (*Cardisoma carnifex* and *Scylla* sp.) and mollusks (*Polymesoda (Geloina) coaxans* and *Terebralia sulcata*) from mangrove swamps and brought them back to the site (Boulanger, 2015; Boulanger et al., 2019; Lim, 2016; Pawlik et al., 2014; Pawlik and Piper, 2019). This indicates the presence and exploitation of the mangrove environment in the Mindoro Strait during that time. Indeed, mangrove swamps play a crucial role in the subsistence strategies of coastal populations in tropical areas, particularly for shell gathering (Burgos and Dillais, 2012; Guillaud and Burgos, 2018). However, evidence of their exploitation in the archaeological record remains limited (Boulanger et al., 2019). These environments also serve as nurseries for many fish species, making them vital for ecosystem health. It is likely that both anadromous (fish that migrate from the sea to freshwater for breeding) and catadromous (fish that migrate from freshwater to the sea for breeding) taxa were collected from mangrove swamps by ancient inhabitants, although distinguishing between them in the fossil record may not be feasible. The exploitation of mangrove habitats at Bubog demonstrates the adaptability of coastal population to diverse environments and their ability to utilize a wide range of marine resources to meet their subsistence needs.

The discovery of bonito (Scombridae) remains in Layers 9 and 10 at Bubog I is particularly intriguing (Boulanger et al., 2019; Pawlik and Piper, 2019). Bonitos, including the species *Euthynnus affinis*, are known to be pelagic fish that primarily inhabit open waters. However, it

521 appears that they occasionally ventured into the external edges of the reef at Bubog I, possibly  
522 for opportunistic hunting or foraging for prey (Froese and Pauly, 2022). Given their predatory  
523 nature, catching bonitos would have required specific fishing skills and specialized tools. A  
524 bone fishing gorge was found in Layer 10, indicating the presence of fishing equipment  
525 probably used for hunting such fish (Boulanger et al., 2019). The fishing gorge was likely  
526 employed as a lure and hook mechanism, which demonstrates the ingenuity and resourcefulness  
527 of ancient fishing practices at Bubog I (Fig. 6).

528 At Bubog I, during the initial phase of occupation (Fig. 6), the fish bone assemblage reveals  
529 a variety of exploited environments. The NISP is relatively low, totaling 89, and the taxonomic  
530 richness reaches about 12 identified families. However, the Menhinick's Richness Index is  
531 higher in this earlier phase than in the most recent one, indicating a greater taxa richness. In  
532 contrast, the second phase of occupation shows a higher NISP of 294 and a richness of 15 taxa.  
533 Interestingly, the Shannon's Diversity Index and evenness are higher during the oldest period  
534 (Tab. 5). Several factors could account for these observed differences. Firstly, the lower NISP  
535 and richness during the earliest period might be attributed to the longer travel required to access  
536 the coast. This could have been due to the larger landmass and the land connection between Ilin  
537 Island and Mindoro that existed until approximately 8,000 BP, as illustrated in Figure 5. This  
538 land connection could have affected the availability and accessibility of certain marine  
539 resources, leading to a more limited range of fish species exploited during that time. Secondly,  
540 the zooarchaeological analysis itself may have influenced the results. The presence of calcium  
541 carbonate concretions coating the bones, particularly between Layers 12 to 7 (Tab. 4), might  
542 have hindered the detailed identification of some fish remains. These concretions could have  
543 obscured important diagnostic features, resulting in less precise taxonomic identifications  
544 during this phase of occupation. In summary, the differences in NISP, richness, Menhinick's  
545 Richness Index, Shannon's Diversity Index, and evenness between the two phases of  
546 occupation at Bubog I can be attributed to a combination of environmental factors and  
547 taphonomic processes. The changing marine conditions and the potential challenges in bone  
548 preservation and identification during the earlier period highlight the complexity of interpreting  
549 and understanding the fishing practices and subsistence strategies of ancient coastal populations  
550 in the Mindoro Strait.

551

## 552 ***5.2. End of the Pleistocene and early Holocene***

553

554 The archaeological evidence from Bilat Cave indicates human occupation dating back to  
555 around 22,000 cal. BP during the Last Glacial Maximum (LGM). At that time, Bilat was located  
556 several kilometers inland from the coast (Fig. 5). Over the transition from the Pleistocene to the  
557 early Holocene, roughly between 13,500 to 8,000 BP, there was a relatively rapid rise in sea  
558 level (Pawlik et al., 2014). This sea-level rise eventually led to partial flooding of the cave  
559 during the mid-Holocene, and today the cave sits at an elevation of 2-3 meters above sea level  
560 (Pawlik, 2019; Pawlik and Fuentes, 2023). Despite the changes in sea level and the distance to  
561 the coast and marine resources, the zooarchaeological analysis at Bilat Cave has revealed that  
562 all 14 identified families of fish remains are from reef fishes (Fig. 6). Interestingly, there were  
563 no significant changes in terms of the foraged environments observed along the stratigraphic  
564 profile. The richness of identified taxa remained the same in Spits 9 to 5 and Spit 4 to 1, with a

565 total of 12 taxa identified. In this context, a higher Menhinick's Richness Index during the initial  
566 phase of site occupation indicates a comparable level of richness for a smaller NISP (Number  
567 of Identified Specimens) in Spits 9 to 5 compared to that in Spits 4 to 1. Notably, mangrove  
568 swamp or brackish water taxa were absent, suggesting the lack of such habitats in the area  
569 during the occupation, likely due to the steeply dropping profile of the southern coast of  
570 Mindoro.

571 The archaeological record shows that the earliest phase of occupation at the site was  
572 followed by a stratigraphic hiatus, and then a peak of occupation in Spits 4 to 1 (NISP = 101).  
573 This could possibly be explained by the sea-level rise during this period, which would have  
574 resulted in shorter distances to the coast, improving foraging efficiency and settlement  
575 conditions (Fig. 5). This period of increased occupation intensity also coincided with an  
576 increase in diversity and evenness of identified taxa (Tab. 5). Interestingly, no remains were  
577 identified to the family level between Spits 8 and 9, likely due to disturbance caused by the  
578 bedrock (Tab. 3; Tab. 5). Among the identified taxa in the assemblage, common reef species  
579 like parrotfishes (Scaridae) are present throughout the stratigraphic profile (Fig. 6). However,  
580 other taxa with known ecology and feeding behaviors suggest that a variety of different habitats  
581 within the coral reef were exploited by ancient inhabitants of the cave. For example, goatfishes  
582 (Mullidae) were likely favored in sandy and muddy bottoms, while rocky areas were likely  
583 frequented by nocturnal fishes like moray eels (Muraenidae). Predatory species were often  
584 found on the external edges of the reef, such as requiem sharks (Carcharhinidae) and  
585 needlefishes (Belonidae), which typically inhabit the sea bottom and hunt small prey near the  
586 water's surface (Fig. 6).

## 588 *5.2. Mid-Holocene to pre-Spanish period*

589  
590 Around 7,500 BP, at Bubog I, Layer 8 exhibits a notable decline in the consumption of taxa  
591 associated with mangrove swamps. This decline coincides with the formation of an estuary  
592 between the two islands after 8,000 BP and the disappearance of paleo-lakes (Pawlik et al.,  
593 2014) (Fig. 5), which corresponds to the beginning of the occupation of Bubog II. The decrease  
594 in evenness between Bubog I Layers 12 to 7 and Layers 6 to 1 may be attributed to the migration  
595 of fishermen to Bubog II following rock falls, particularly in Layer 7, or due to different uses  
596 of the site (Tab. 5). Nevertheless, the relatively low variations observed despite the rock falls  
597 and abrupt climate changes encountered during the Last Glacial Maximum (LGM) suggest a  
598 continuity in fishing practices over time, as seen at Bubog II as well.

599 At the Bubog II site, the diversity of identified families remains relatively stable,  
600 encompassing 14 families within Layers 14 to 7 and 15 families within Layers 6 to 1. There's  
601 an elevated Menhinick's Richness Index during the initial phase of occupation due to a  
602 significantly smaller NISP, which is more than twice as small. Similarly, the Shannon's  
603 Diversity Index and evenness are higher for Layers 14 to 7 and lower for Layers 6 to 1 (Tab.  
604 5), indicating no significant cultural changes throughout its occupation from Layers 14 to 7 to  
605 Layers 6 to 1. The exploitation of local reef habitats remained a constant feature. Various reef  
606 fish families were prevalent at Bubog II, including surgeonfishes, tangs, unicorn fishes  
607 (Acanthuridae), and parrotfishes (Scaridae), although their NISP may have been somewhat  
608 overestimated due to taphonomic biases (Boulanger et al., 2019; Fleming, 1987). Additionally,

609 specific taxa were associated with distinct ecosystems within the coral reef. For example,  
610 hawkfishes (Cirrhitidae) and moray eels (Muraenidae) were found in rocky areas, while  
611 porcupinefishes (Diodontidae) typically inhabit sandy bottoms. Occasional catches of  
612 predators, such as needlefishes (Belonidae), jacks, pompanos, jack mackerels, runners, and  
613 scads (Carangidae), along with requiem sharks (Carcharhinidae), likely occurred on the external  
614 edge of the reef. Other species like herrings, shads, sardines, hilsa, menhadens (Clupeidae), and  
615 breams, porgies (Sparidae) were also part of the assemblage. The presence of such a diverse  
616 range of taxa and the continuity in fishing practices at both Bubog I and Bubog II suggest the  
617 importance of marine resources and the exploitation of various reef habitats by ancient coastal  
618 populations in the Mindoro Strait over millennia.

619  
620

## 621 **6. Conclusion**

622

623 The ichthyoarchaeological methods and protocols employed in this study allowed for  
624 the detailed analysis of exploited marine habitats from three archaeological sites at Occidental  
625 Mindoro, Philippines, identifying fish remains to the lowest possible taxonomic level. How-  
626 ever, the high biodiversity of the Coral Triangle and morphological variability at the family  
627 level presented challenges in reconstructing fish ecology in the Indo-Pacific region, especially  
628 given the old age of the sites and the highly fragmentary conditions of the archaeological ma-  
629 terial.

630 Despite these difficulties, the study revealed both similarities and a few differences at  
631 inter- and intra-site levels in Mindoro's prehistory, suggesting that populations that practiced  
632 similar fishing strategies inhabited the Ilin Strait for over 30,000 years. Throughout the occu-  
633 pation of the sites, *Homo sapiens* on Mindoro predominantly relied on near-shore marine envi-  
634 ronments for their subsistence. Differences between sites likely arose due to variations in local  
635 marine habitats influenced by climate-mediated changes. As a result, a diverse range of fishing  
636 practices such as netting, spearing, angling, and hand-gathering (Boulanger, 2015, 2021; Bou-  
637 langer et al., 2019) were employed to exploit a wide variety of fish taxa, reflecting the excep-  
638 tional richness and biodiversity of the Coral Triangle.

639 Evidence such as waisted pebbles, possibly used as fishing weights, suggests the use of  
640 net or trap fishing techniques (Boulanger et al., 2019; Pawlik, 2021). The presence of woody  
641 vines at Bubog II during the Holocene occupation indicates the use of baskets, while fish weirs,  
642 similar to those used in the modern shallow parts of Ilin Channel and surrounding mangrove  
643 areas, were likely utilized (Boulanger, 2021). The construction of dugout canoes may have fa-  
644 cilitated these fishing activities, possibly made using Holocene shell adzes found at each site  
645 (Pawlik et al., 2015; Shipton et al., 2020).

646 Compared to other coastal sites in the Coral Triangle, such as Makpan (Kealy et al.,  
647 2020), Tron Bon Lei (Samper Carro et al., 2016), Here Sorot Entapa (O'Connor et al., 2019;  
648 Boulanger, 2021), and Asitau Kuru (Boulanger, 2021; Boulanger, Hawkins, Ono, et al., 2023),  
649 the Mindoro sites of Bubog I, Bubog II, and Bilat Cave show relatively low occupation intensity  
650 over time. It is possible that the inhabitants of Bubog preferred open coastal areas and only  
651 sought shelter in rock shelters during adverse weather conditions, relying more on opportunistic  
652 fishing. This is supported by the smaller sizes of the assemblages and the presence of taxa



653 secreting powerful toxins, such as moray eels and pufferfish, which were nonetheless exploited  
654 (Boulanger et al., 2023). Despite this, the wide range of taxa represented at the three sites sug-  
655 gests the use of specific subsistence strategies tailored to each environment. These strategies  
656 persisted over time, demonstrating a detailed understanding of the aquatic environments near  
657 the archaeological sites and the development of sophisticated fishing techniques, which further  
658 reflects the behavioral complexity and modernity of *Homo sapiens* in the Philippines during  
659 prehistoric times (Pawlik, 2010, 2012, 2021; Pawlik and Fuentes, 2023).  
660  
661

662 **References**

663

664 Allen, G.R., 2008. Conservation hotspots of biodiversity and endemism for Indo-Pacific coral  
665 reef fishes. *Aquat. Conserv. Mar. Freshw. Ecosyst.*

666

667 Anderson, A., 2013. Inshore or offshore? Boating and fishing in the Pleistocene. *Antiquity* 87,  
668 879–879. <https://doi.org/10.1017/S0003598X0004953X>

669

670 Bedford, S., Sand, C., Connaughton, S.P. (Eds.), 2007. *Oceanic Explorations: Lapita and West-*  
671 *ern Pacific Settlement*. ANU Press, Canberra.

672

673 Bouffandeau, L., Béarez, P., Bedford, S., Valentin, F., Spriggs, M., Nolet, É., 2018. Fishing at  
674 Arapus-Mangaasi, Efate, Vanuatu (2800–2200 BP): New methodological approaches and re-  
675 sults. *J. Archaeol. Sci. Rep.* 18, 356–369. <https://doi.org/10.1016/j.jasrep.2018.01.025>

676

677 Boulanger, C., 2021. *Aquatic resources exploitation and adaptation of Anatomically Modern*  
678 *Human in Island Southeast Asia: palaeoenvironmental and cultural implications* (PhD disser-  
679 tation). Muséum national d’Histoire naturelle, Australian National University, Paris, Canberra.

680

681 Boulanger, C., 2015. *Etude des comportements de subsistance d’un site australo-mélanésien :*  
682 *Bubog I (île d’Ilin, Mindoro, Philippines), ca. 11000-4000 ans BP Ichtyofaune, crustacés dé-*  
683 *capodes et grands mammifères* (Master’s thesis). Muséum national d’Histoire naturelle, Paris.

684

685 Boulanger, C., Hawkins, S., Ono, R., O’Connor, S., 2022. Continuity and variability in prehis-  
686 toric fishing practices by *Homo sapiens* in Island Southeast Asia: new ichthyofaunal data from  
687 Asitau Kuru, Timor-Leste. *World Archaeol.* 54, 288–316.

688

689 Boulanger, C., Hawkins, S., Shipton, C., Ingicco, T., Sémah, A.-M., O’Connor, S., 2023. Inland  
690 fishing by *Homo sapiens* during early settlement of Wallacea. *Front. Environ. Archaeol.* 2.

691

692 Boulanger, C., Ingicco, T., Piper, P.J., Amano, N., Grouard, S., Ono, R., Hawkins, S., Pawlik,  
693 A.F., 2019. Coastal Subsistence Strategies and Mangrove Swamp Evolution at Bubog I Rock-  
694 shelter (Ilin Island, Mindoro, Philippines) from the Late Pleistocene to the mid-Holocene. *J.*  
695 *Isl. Coast. Archaeol.* 0, 1–21. <https://doi.org/10.1080/15564894.2018.1531957>

696

697 Bronk Ramsey, C., 2009. Bayesian Analysis of Radiocarbon Dates. *Radiocarbon* 51, 337–360.  
698 <https://doi.org/10.1017/S0033822200033865>

699

700 Bunn, H.T., 1986. Patterns of skeletal representation and hominid subsistence activities at Ol-  
701 duvai Gorge, Tanzania, and Koobi Fora, Kenya. *J. Hum. Evol.* 15, 673–690.  
702 [https://doi.org/10.1016/S0047-2484\(86\)80004-5](https://doi.org/10.1016/S0047-2484(86)80004-5)

703

704 Burgos, A., Dillais, P., 2012. Les femmes, les coquillages et la mangrove. *Tech. Cult.* 326–337.

705

706 Butler, V.L., 1994. Fish Feeding Behaviour and Fish Capture: The Case for Variation in Lapita  
707 *Fishing Strategies*. *Archaeol. Ocean.* 29, 81–90.

708

709 Carlos, J.B., Paz, V.J., Escobin, R.P., Conda, J.M., Rameros, M.D.R., Pawlik, A.F., 2018. Ar-  
710 chaeological evidence of woody vines at Bubog 2, Ilin Island, Mindoro, Philippines. *Archaeol.*  
711 *Anthropol. Sci.* <https://doi.org/10.1007/s12520-018-0722-7>

712 Chaix, L., Desse, J., 1994. L'os et sa mesure. Archéozoologie et archéométrie. *Hist. Mes.* 9,  
713 339–363.  
714

715 Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014.  
716 Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in  
717 species diversity studies. *Ecol. Monogr.* 84, 45–67. <https://doi.org/10.1890/13-0133.1>  
718

719 Choa, O., 2018. *A geochemical history of Tabon Cave (Palawan, Philippines) : environment,*  
720 *climate, and early modern humans in the Philippine archipelago* (PhD dissertation). Muséum  
721 national d'Histoire naturelle, Paris.  
722

723 Clarkson, C., Jacobs, Z., Marwick, B., Fullagar, R., Wallis, L., Smith, M., Roberts, R.G., Hayes,  
724 E., Lowe, K., Carah, X., Florin, S.A., McNeil, J., Cox, D., Arnold, L.J., Hua, Q., Huntley, J.,  
725 Brand, H.E.A., Manne, T., Fairbairn, A., Shulmeister, J., Lyle, L., Salinas, M., Page, M., Con-  
726 nell, K., Park, G., Norman, K., Murphy, T., Pardoe, C., 2017. Human occupation of northern  
727 Australia by 65,000 years ago. *Nature* 547, 306. <https://doi.org/10.1038/nature22968>  
728

729 Colley, S.M., 1990. The Analysis and Interpretation of Archaeological Fish Remains. *Archaeol.*  
730 *Method Theory* 2, 207–253.  
731

732 Colley, S.M., 1987. Fishing for Facts. Can We Reconstruct Fishing Methods from Archaeolog-  
733 ical Evidence? *Aust. Archaeol.* 16–26.  
734

735 Cruz-Uribe, K., 1988. The use and meaning of species diversity and richness in archaeological  
736 faunas. *J. Archaeol. Sci.* 15, 179–196. [https://doi.org/10.1016/0305-4403\(88\)90006-4](https://doi.org/10.1016/0305-4403(88)90006-4)  
737

738 Déroit, F., Dizon, E., Falguères, C., Hameau, S., Ronquillo, W., Sémah, F., 2004. Upper Pleis-  
739 tocene *Homo sapiens* from the Tabon cave (Palawan, The Philippines): description and dating  
740 of new discoveries. *Comptes Rendus Palevol* 3, 705–712.  
741 <https://doi.org/10.1016/j.crpv.2004.06.004>  
742

743 Dunn, O.J., 1961. Multiple Comparisons among Means. *J. Am. Stat. Assoc.* 56, 52–64.  
744 <https://doi.org/10.1080/01621459.1961.10482090>  
745

746 Fitzpatrick, S.M., Giovas, C.M., Kataoka, O., 2011. Temporal trends in prehistoric fishing in  
747 Palau, Micronesia over the last 1500 years. *Archaeol. Ocean.* 46, 6–16.  
748 <https://doi.org/10.1002/j.1834-4453.2011.tb00094.x>  
749

750 Fitzpatrick, S.M., Kataoka, O., 2005. Prehistoric fishing in Palau, Micronesia: evidence from  
751 the Northern Rock Islands. *Archaeol. Ocean.* 40, 1–13. <https://doi.org/10.1002/j.1834-4453.2005.tb00574.x>  
752

753

754 Fleming, M.A., 1987. *The Scaridae family in Pacific prehistory* (Thesis). University of Otago.  
755 Froese, R., Pauly, D., 2023. FishBase [WWW Document]. URL [www.fishbase.org](http://www.fishbase.org) (accessed  
756 11.25.22).  
757

758 Giovas, C.M., Fitzpatrick, S.M., Kataoka, O., Clark, M., 2016. Prey body size and anthropo-  
759 genic resource depression: The decline of prehistoric fishing at Chelechol ra Orrak, Palau. *J.*  
760 *Anthropol. Archaeol.* 41, 132–146.  
761

- 762 Giovas, C.M., Lambrides, A.B.J., Fitzpatrick, S.M., Kataoka, O., 2017. Reconstructing prehis-  
763 toric fishing zones in Palau, Micronesia using fish remains: A blind test of inter-analyst corre-  
764 spondence. *Archaeol. Ocean.* 52, 45–61. <https://doi.org/10.1002/arco.5119>  
765
- 766 Grayson, D.K., 1984. *Quantitative Zooarchaeology: Topics in the Analysis of Archaeological*  
767 *Faunas*, Academic Press. ed, Studies in Archaeology. New York.  
768
- 769 Guillaud, D., Burgos, A., 2018. Les sens de la forêt. Usages et évolutions de la forêt humide et  
770 de la mangrove de Siberut et Nias, Sumatra, Indonésie. *Nouv. Archéologie* 41–47.  
771 <https://doi.org/10.4000/nda.4223>  
772
- 773 Heaton, T.J., Köhler, P., Butzin, M., Bard, E., Reimer, R.W., Austin, W.E.N., Ramsey, C.B.,  
774 Grootes, P.M., Hughen, K.A., Kromer, B., Reimer, P.J., Adkins, J., Burke, A., Cook, M.S.,  
775 Olsen, J., Skinner, L.C., 2020. Marine20—The Marine Radiocarbon Age Calibration Curve (0–  
776 55,000 cal BP). *Radiocarbon* 62, 779–820. <https://doi.org/10.1017/RDC.2020.68>  
777
- 778 Hope, A.C.A., 1968. A Simplified Monte Carlo Significance Test Procedure. *J. R. Stat. Soc.*  
779 *Ser. B Methodol.* 30, 582–598.  
780
- 781 Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation  
782 of species diversity (Hill numbers). *Methods Ecol. Evol.* 7, 1451–1456.  
783 <https://doi.org/10.1111/2041-210X.12613>  
784
- 785 Johannes, R.E., 1981. *Words of the lagoon: fishing and marine lore in the Palau district of*  
786 *Micronesia*, University of California Press. ed. Berkeley.  
787
- 788 Kealy, S., Louys, J., O’Connor, S., 2016. Islands Under the Sea: A Review of Early Modern  
789 Human Dispersal Routes and Migration Hypotheses Through Wallacea. *J. Isl. Coast. Archaeol.*  
790 11, 364–384. <https://doi.org/10.1080/15564894.2015.1119218>  
791
- 792 Kealy, S., O’Connor, S., Mahirta, Sari, D.M., Shipton, C., Langley, M.C., Boulanger, C.,  
793 Kaharudin, H.A.F., Patridina, E.P.B.G.G., Algifary, M.A., Irfan, A., Beaumont, P., Jankowski,  
794 N., Hawkins, S., Louys, J., 2020. Forty-thousand years of maritime subsistence near a changing  
795 shoreline on Alor Island (Indonesia). *Quat. Sci. Rev.* 249, 106599.  
796 <https://doi.org/10.1016/j.quascirev.2020.106599>  
797
- 798 Kirch, P.V., Dye, T.S., 1979. Ethno-archaeology and the development of Polynesian fishing  
799 strategies. *J. Polyn. Soc.* 88, 53–76.  
800
- 801 Lambrides, A., Weisler, M., Charleux, M., 2018. New taxonomic records and regional trends  
802 for the Marquesan prehistoric marine fishery, Eiao Island, Polynesia. *J. Pac. Archaeol.* 9, 44–  
803 62.  
804
- 805 Lambrides, A.B.J., Weisler, M.I., 2013. Assessing Protocols for Identifying Pacific Island Ar-  
806 chaeological Fish Remains: The Contribution of Vertebrae. *Int. J. Osteoarchaeol.* 25, 838–848.  
807 <https://doi.org/10.1002/oa.2354>  
808
- 809 Lim, K.K.A., 2016. *Coastal adaptation of prehistoric Mindoro: The Archaeomalacology of*  
810 *Bubog I, Ilin Island from the Terminal Pleistocene to the Mid Holocene* (Master’s thesis). Uni-  
811 versity of the Philippines Diliman, Quezon City.

812  
813 Louys, J., Kealy, S., O'Connor, S., Price, G., Hawkins, S., Aplin, K., Rizal, Y., Zaim, J., Ma-  
814 hirta, Tanudirjo, D., Santoso, W.D., Hidayah, A.R., Trihascaryo, A., Wood, R., Bevitt, J., Clark,  
815 T., 2017. Differential preservation of vertebrates in Southeast Asian caves. *Int. J. Speleol.* 46.  
816 <https://doi.org/https://doi.org/10.5038/1827-806X.46.3.2131>  
817  
818 Lyman, R.L., 2008. *Quantitative Paleozoology*. Cambridge University Press, Cambridge.  
819  
820 Lyman, R.L., Ames, K.M., 2007. On the use of species-area curves to detect the effects of  
821 sample size. *J. Archaeol. Sci.* 34, 1985–1990. <https://doi.org/10.1016/j.jas.2007.01.011>  
822  
823 Magurran, A.E., 1988. *Ecological Diversity and Its Measurement*. Springer Netherlands, Dor-  
824 drecht. <https://doi.org/10.1007/978-94-015-7358-0>  
825  
826 Masse, W.B., 1986. A millennium of fishing in the Palau Islands, Micronesia, in: Pacific An-  
827 thropological Records. Presented at the Traditional Fishing in the Pacific: Ethnographical and  
828 Archaeological Papers from the 15th Pacific Science Congress, Bishop Museum Press, Hono-  
829 lulu, pp. 85–119.  
830  
831 Neri, L.A.M., Pawlik, A.F., Reepmeyer, C., Mijares, A.S.B., Paz, V.J., 2015. Mobility of early  
832 islanders in the Philippines during the Terminal Pleistocene/Early Holocene boundary: pXRF-  
833 analysis of obsidian artefacts. *J. Archaeol. Sci.* 61, 149–157.  
834 <https://doi.org/10.1016/j.jas.2015.05.005>  
835  
836 O'Connell, J.F., Allen, J., Williams, M.A.J., Williams, A.N., Turney, C.S.M., Spooner, N.A.,  
837 Kamminga, J., Brown, G., Cooper, A., 2018. When did Homo sapiens first reach Southeast  
838 Asia and Sahul? *Proc. Natl. Acad. Sci. U. S. A.* 115, 8482–8490.  
839 <https://doi.org/10.1073/pnas.1808385115>  
840  
841 O'Connor, S., Mahirta, Kealy, S., Boulanger, C., Maloney, T.R., Hawkins, S., Langley, M.C.,  
842 Kaharudin, H.A.F., Suniarti, Y., Husni, M., Tanudirjo, D., Wattimena, L., Handoko, W., Alifah,  
843 Louys, J., 2019. Kisar and the Archaeology of Small Islands in the Wallacean Archipelago. *J.*  
844 *Isl. Coast. Archaeol.* 14, 198–225.  
845  
846 O'Connor, S., Mahirta, Samper-Carro, S.C., Hawkins, S., Kealy, S., Louys, J., Wood, R., 2017.  
847 Fishing in life and death: Pleistocene fish-hooks from a burial context on Alor Island, Indonesia.  
848 *Antiquity* 91, 1451–1468. <https://doi.org/10.15184/aqy.2017.186>  
849  
850 O'Connor, S., Ono, R., Clarkson, C., 2011. Pelagic fishing at 42,000 years before the present  
851 and the maritime skills of modern humans. *Science* 334, 1117–1121.  
852 <https://doi.org/10.1126/science.1207703>  
853  
854 Ono, R., 2010. Ethno-archaeology and early Austronesian fishing strategies in near-shore en-  
855 vironments. *J. Polyn. Soc.* 119, 269–314.  
856  
857 Ono, R., 2004. Prehistoric Fishing at Bukit Tengkorak, East Coast of Borneo Island. *N. Z. J.*  
858 *Archaeol.* 24, 77–106.  
859  
860 Ono, R., 2003. Prehistoric Austronesian Fishing Strategies: A comparison between Island  
861 Southeast Asia and the Lapita Cultural Complex. Cah. Archéologie En Nouv.-Caléd., Pacific

862 Archaeology: assessments and prospects. Proceedings of the International Conference for the  
863 50th anniversary of the first Lapita excavation 15, 191–201.

864

865 Ono, R., Clark, G., 2012. A 2500-year record of marine resource use on Ulong Island, Republic  
866 of Palau. *Int. J. Osteoarchaeol.* 22, 637–654. <https://doi.org/10.1002/oa.1226>

867

868 Ono, R., Hawkins, S., Bedford, S., 2019. Lapita maritime adaptations and the development of  
869 fishing technology: A view from Vanuatu, in: Bedford, S., Spriggs, M. (Eds.), *Debating Lapita:  
870 Distribution, Chronology, Society and Subsistence*, Terra Australis. ANU Press, Canberra, pp.  
871 415–438.

872

873 Ono, R., Intoh, M., 2011. Island of Pelagic Fishermen: Temporal Changes in Prehistoric Fishing  
874 on Fais, Micronesia. *J. Isl. Coast. Archaeol.* 6, 255–286.  
875 <https://doi.org/10.1080/15564894.2010.540531>

876

877 Ono, R., Morrison, A., Addison, D., 2009. *Prehistoric Marine Resource Use in the Indo-Pacific  
878 Regions*, Terra Australis. ANU Press, Canberra.

879

880 Panfili, J., de Pontual, H., Troadec, H., Wright, P.J. (Eds.), 2002. *Manual of fish  
881 sclerochronology*, IFREMER. ed. Plouzané.

882

883 Pawlik, A., Crozier, R., Fuentes, R., Wood, R., Piper, P., 2019. Burial traditions in early Mid-  
884 Holocene Island Southeast Asia: new evidence from Bubog-1, Ilin Island, Mindoro Occidental.  
885 *Antiquity* 93, 901–918. <https://doi.org/10.15184/aqy.2018.190>

886

887 Pawlik, A.F., 2021. Technology, adaptation, and mobility in maritime environments in the Phil-  
888ippines from the Late Pleistocene to Early/Mid-Holocene. *Quat. Int.* 596, 109–123.  
889 <https://doi.org/10.1016/j.quaint.2020.11.007>

890

891 Pawlik, A.F., 2019. *Field report on the archaeological excavations on Ilin Island and Sta Te-  
892 resa, Mindoro Occidental, Philippines - Update and campaign from 07-21 July 2019*. Ateneo  
893 de Manila University, Quezon City.

894

895 Pawlik, A.F., Fuentes, R.B., 2023. Prehistoric Hunter-Gatherers in the Philippines—Subsist-  
896ence strategies, adaptation, and behaviour in maritime environments. *Front. Earth Sci.* 11.

897

898 Pawlik, A.F., Piper, P.J., 2019. The Philippines from c. 14,000 to 4,000 cal. BP in Regional  
899 Context. *Camb. Archaeol. J.* 29, 1–22. <https://doi.org/10.1017/S0959774318000306>

900

901 Pawlik, A.F., Piper, P.J., Faylona, M.G.P.G., Padilla, S.G., Carlos, J., Mijares, A.S.B., Vallejo,  
902 B., Reyes, M., Amano, N., Ingicco, T., Porr, M., 2014. Adaptation and foraging from the Ter-  
903minal Pleistocene to the Early Holocene: Excavation at Bubog on Ilin Island, Philippines. *J.  
904 Field Archaeol.* 39, 230–247. <https://doi.org/10.1179/0093469014Z.00000000090>

905

906 Pawlik, A.F., Piper, P.J., Wood, R.E., Lim, K.K.A., Faylona, M.G.P.G., Mijares, A.S.B., Porr,  
907 M., 2015. Shell tool technology in Island Southeast Asia: an early Middle Holocene *Tridacna*  
908 adze from Ilin Island, Mindoro, Philippines. *Antiquity* 89, 292–308.  
909 <https://doi.org/10.15184/aqy.2015.3>

910

911 Payne, S., 1975. Partial recovery and sample bias. *Archaeozoological Stud.* 7–17.

912  
913 Poplin, F., 1976. A propos du nombre de restes et du nombre d'individus dans les échantillons  
914 d'ossements. *Cah. Cent. Rech. Préhistoriques* 5, e75.  
915  
916 Porr, M., Mijares, A.S.B., Pawlik, A.F., Piper, P.J., Padilla, S., 2012. North of the Southern Arc  
917 — The Mindoro Archaeological Research Program: A summary of the 2010 and 2011 field-  
918 work activities. *Aust. Archaeol.* 75, 110–117.  
919  
920 R Core Team, 2020. *R: A language and environment for statistical computing*.  
921  
922 Randall, J.E., 1998. Zoogeography of shore fishes of the Indo-Pacific region. *Zool. Stud.* 37,  
923 227–268.  
924  
925 Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Ramsey, C.B., Butzin, M.,  
926 Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton,  
927 T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G.,  
928 Pearson, C., Plicht, J. van der, Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Tur-  
929 ney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S.M., Fogtman-  
930 Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto,  
931 M., Sookdeo, A., Talamo, S., 2020. The IntCal20 Northern Hemisphere Radiocarbon Age Cal-  
932 ibration Curve (0–55 cal kBP). *Radiocarbon* 62, 725–757.  
933 <https://doi.org/10.1017/RDC.2020.41>  
934  
935 Reyes, M.C., 2019. *Micromammals of Ilin Island and Bulalacao sites, Southern Mindoro, Phil-*  
936 *ippines: Insights on paleoecology and taphonomy from Terminal Pleistocene to Holocene ma-*  
937 *terials* (Master's thesis). University of the Philippines Diliman, Quezon City.  
938  
939 Reyes, M.C., Ingicco, T., Piper, P.J., Amano, N., Pawlik, A.F., 2017. First fossil evidence of  
940 the extinct Philippine cloud rat *Crateromys paulus* (Muridae: Murinae: Phloeomyini) from Ilin  
941 Island, Mindoro, and insights into its Holocene abundance. *Proc. Biol. Soc. Wash.* 130, 84–97.  
942 <https://doi.org/10.2988/17-00012>  
943  
944 Rurua, V., Béarez, P., Hermann, A., Conte, E., 2020. Length and weight reconstruction of  
945 *Chlorurus microrhinos* (Scaridae) from isolated cranial bones and vertebrae. *Cybium Int. J. Ich-*  
946 *thyol.* 44, 61–68. <https://doi.org/10.26028/cybium/2020-441-008>  
947  
948 Samper Carro, S.C., O'Connor, S., Louys, J., Hawkins, S., Mahrta, M., 2016. Human maritime  
949 subsistence strategies in the Lesser Sunda Islands during the terminal Pleistocene–early Holo-  
950 cene: New evidence from Alor, Indonesia. *Quat. Int., Southeast Asia: human evolution, disper-*  
951 *sals and adaptation* 416, 64–79. <https://doi.org/10.1016/j.quaint.2015.07.068>  
952  
953 Sathiamurthy, E., Voris, H.K., 2006. Maps of Holocene Sea Level Transgression and Sub-  
954 merged Lakes on the Sunda Shelf. *Trop. Nat. Hist.* 1–44.  
955  
956 Shipton, C., O'Connor, S., Kealy, S., 2021. The biogeographic threshold of wallacea in human  
957 evolution. *Quat. Int.* <https://doi.org/10.1016/j.quaint.2020.07.028>  
958  
959 Umali, A.F., Warfel, H.E., 1949. *Reef Fishing in the Philippines*, Fish and Wildlife Service  
960 United States Department of the Interior. ed, Fishery Leaflet. Manila.  
961

- 962 Voris, H.K., 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems  
963 and time durations. *J. Biogeogr.* 27, 1153–1167. [https://doi.org/10.1046/j.1365-](https://doi.org/10.1046/j.1365-2699.2000.00489.x)  
964 [2699.2000.00489.x](https://doi.org/10.1046/j.1365-2699.2000.00489.x)
- 965  
966 Walter, R., 1989. Lapita fishing strategies: A review of the archaeological and linguistic evi-  
967 dence. *Pac. Stud.* 13, 127–149.
- 968  
969 Weisler, M.I., Green, R.C., 2013. Mangareva Fishing Strategies in Regional Context: an Anal-  
970 ysis of Fish Bones from Five Sites Excavated in 1959. *J. Pac. Archaeol.* 4, 73–89.
- 971  
972 White, T.E., 1953. A Method of Calculating the Dietary Percentage of Various Food Animals  
973 Utilized by Aboriginal Peoples. *Am. Antiq.* 18, 396–398. <https://doi.org/10.2307/277116>  
974  
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976 **Acknowledgements**

977

978 We thank the members of the Mindoro Archaeological Research Team, the National Museum  
979 of the Philippines, and the municipalities and people of San Jose and Magsaysay in Occidental  
980 Mindoro. This research and the authors received support from the University of Western Aus-  
981 tralia, National Geographic Society, POSCO TJ Park Foundation, Ateneo de Manila University,  
982 University of the Philippines OVPAA and the University of the Philippines Diliman OVCRD.  
983 We acknowledge the CartoGIS Services (ANU College of Asia and the Pacific, The Australian  
984 National University) for providing all base maps (Creative Commons Attribution-ShareAlike  
985 4.0 international license (CC BY SA). We also thank the UMR7209 laboratory (Muséum Na-  
986 tional d'Histoire Naturelle) and Philippe Béarez for giving us access to the fish osteological  
987 reference collection they patiently built year after year. We thank Simon Puaud for his help  
988 with the Hirox digital microscope and Léa Bouteille for her precious advice. Finally, we would  
989 like to thank the reviewers for their comments that helped improve the manuscript.

990 **Author contributions**

991

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995 **Sémah:** Conceptualization, Supervision, Writing- review & editing. **Stuart Hawkins:** Writing-

996 original draft. **Rintaro Ono:** Writing- review & editing. **Marian C. Reyes:** Review & editing.

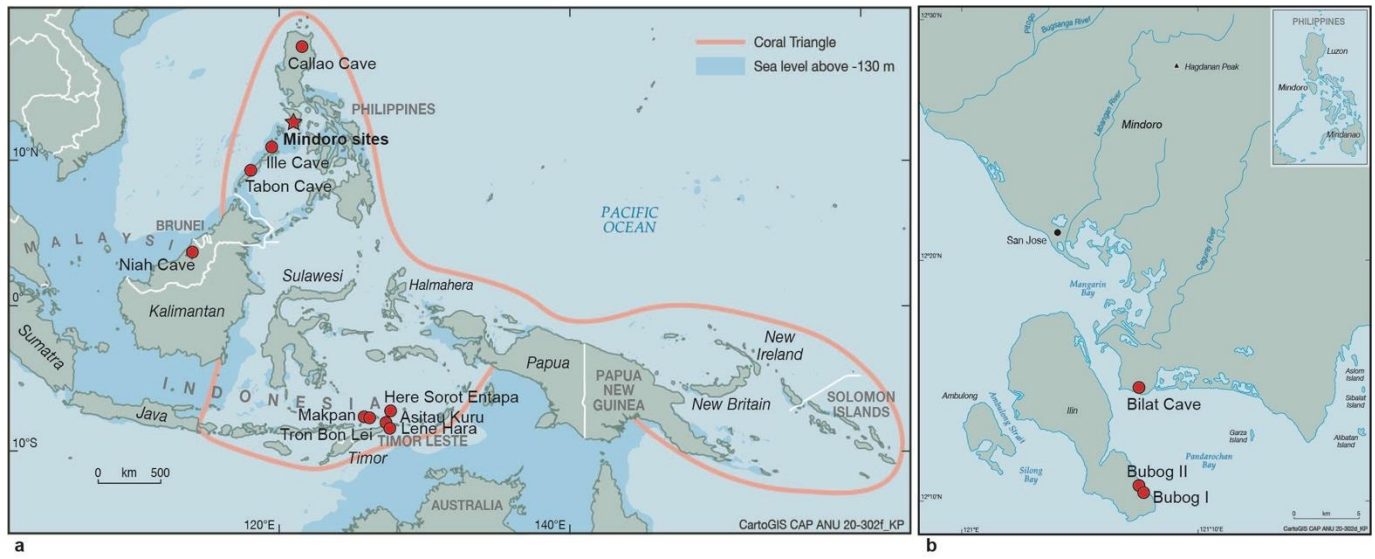
997 **Alfred Pawlik:** Funding acquisition, Investigation, Project administration, Writing-review &

998 editing.

999

1000 **Figures and captions**

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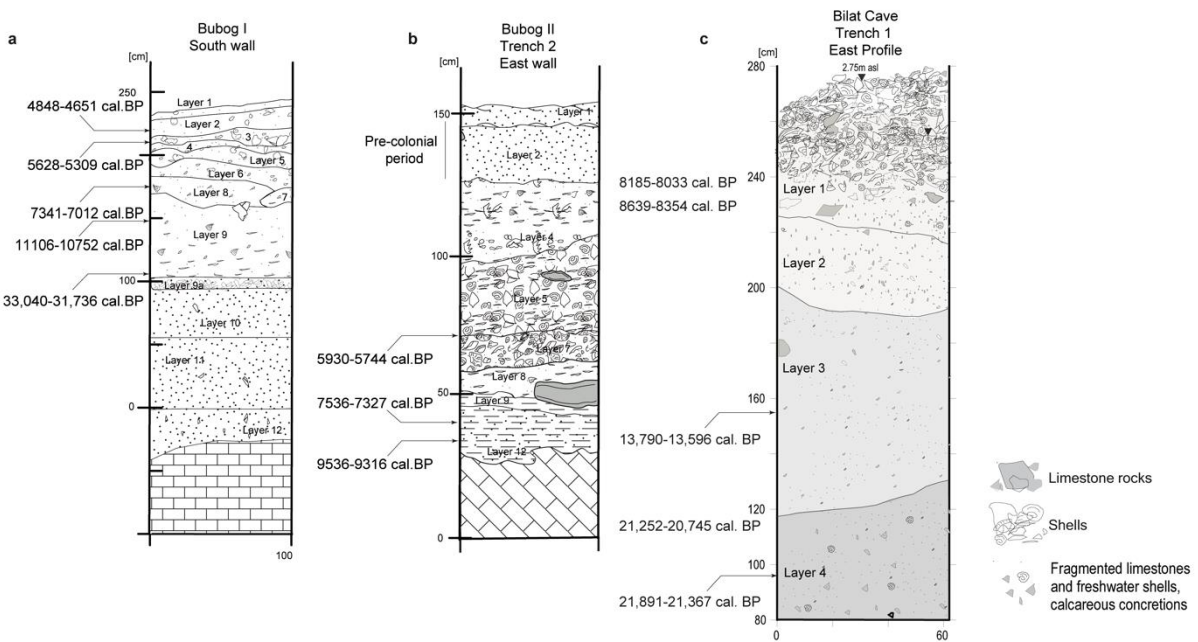
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Figure 1. a. Map of Island Southeast and the Coral Triangle showing the position of the main sites mentioned in the text. b. Map of Southwest Mindoro showing the position of Ilin Island, Bubog I, Bubog II and Bilat Cave.



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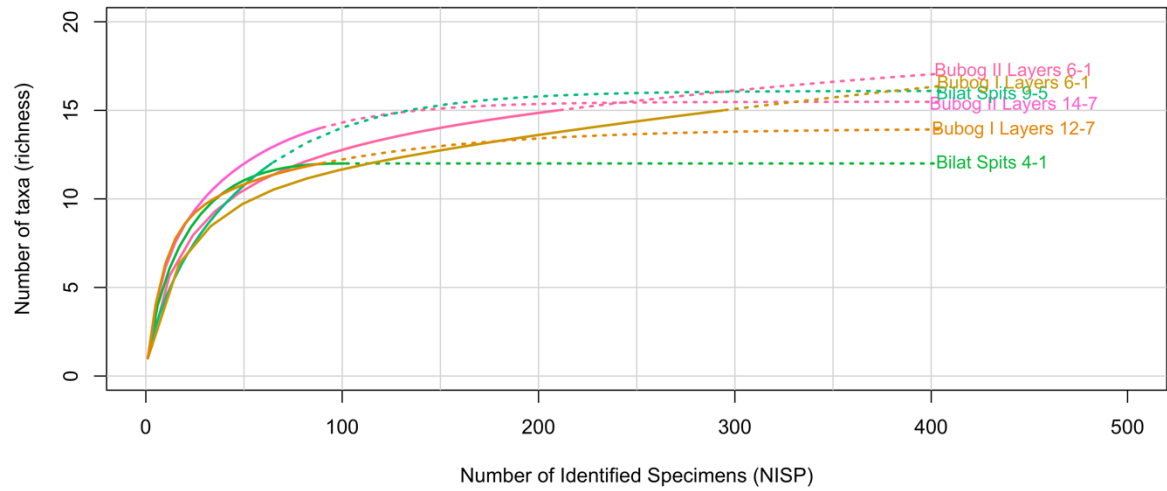
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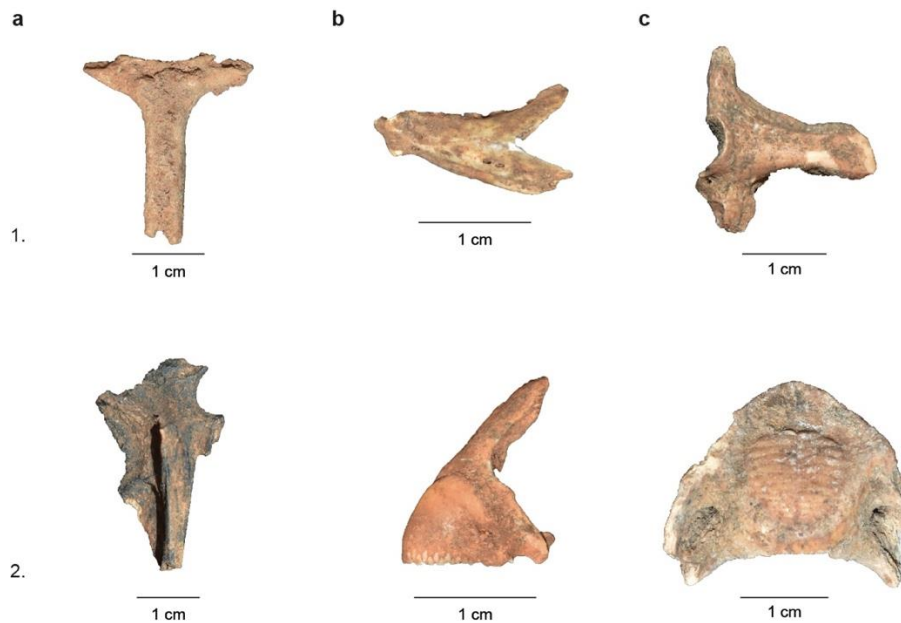
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Figure 2. Stratigraphic profiles of a. Bubog I, b. Bubog II (Trench 2) and ca. Bilat Cave shell midden and associated datings (Boulanger et al., 2019; Pawlik and Piper, 2019). Radiocarbon dates cited were calibrated with OxCal 4.4 (using the most recent calibration curves of IntCal20 (file version intcal20.14c) for dating charcoal, and Marine 20 (file version marine20.14c) for dating marine shells and reported as modelled data at 95.4% confidence intervals (Bronk Ramsey, 2009; Heaton et al., 2020; Reimer et al., 2020). Dates published before 2020 were corrected accordingly where necessary.

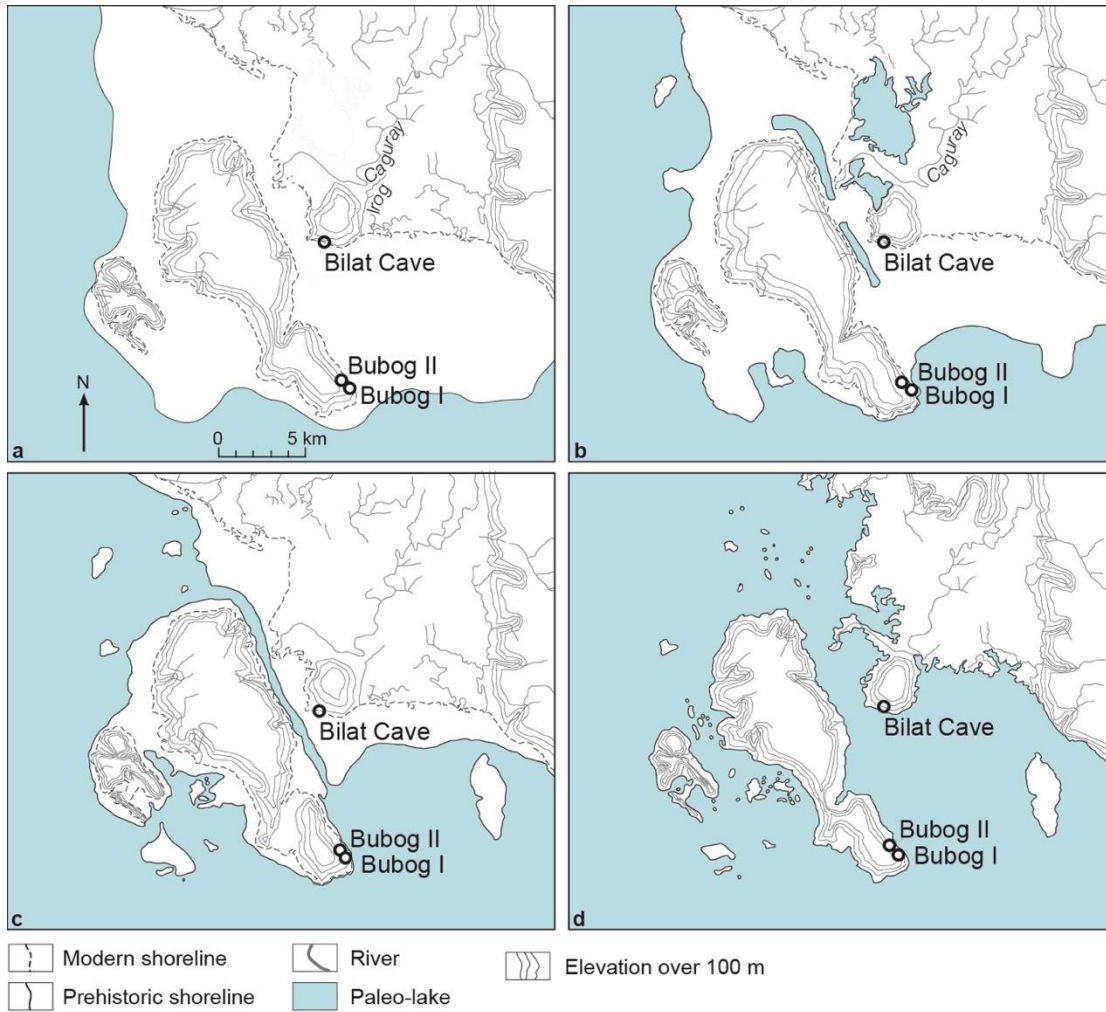


1015  
 1016 Figure 3. Average rarefaction curves built on NISP counts per taxa for each cultural layer of  
 1017 each site. Plain lines are the interpolated predicted curves. Dashed lines are the extrapolated  
 1018 rarefied curves.



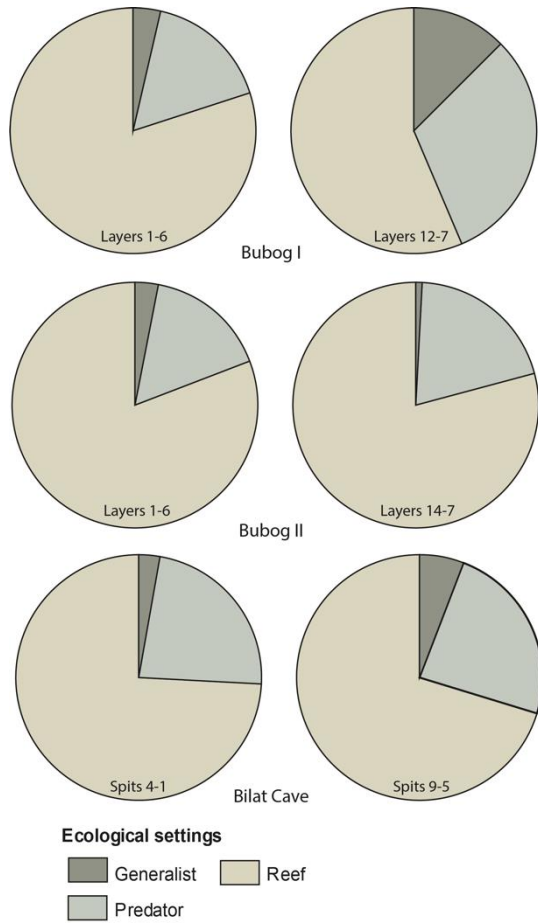
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Figure 4. a.1. Dorsal spine of Scombrinae recovered from Layer 10 at Bubog I. a.2. Left hyomandibular (external view) of *Lethrinus* sp. (Lethrinidae) recovered from Layer 5 at Bubog I. b.1. Left dentary (external view) of *Lutjanus* sp. (Lutjanidae) recovered from Layer 2 at Bubog II. b.2. Left premaxilla (external view) of *Chlorurus* sp. (Scaridae) recovered from Layer 4 at Bubog II. c.1. Right articular (external view) of *Cetoscarus ocellatus* (Scaridae) recovered from Spit 7 at Bilat Cave. c.2. Premaxilla (ventral view) of *Diodon hystrix* recovered from Spit 2 at Bilat Cave.



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Figure 5. Sea level and landscape reconstructions of the Ilin Island and the southwestern Mindoro region. a. ca. 32-13 kya; b. ca. 10 kya; c. ca. 7.6 kya; d. since ca. 6 kya., modified from (Pawlik et al., 2014).



1033  
 1034 Figure 6. Proportions of NISP per taxa ecological settings and chronological phase (Tab. 5) at  
 1035 Bubog I, Bubog II and Bilat. Here, ‘reef’ refers to fishes that are found only in the coral reef,  
 1036 ‘generalist’ refers to fishes that can be found on the reef but also in mangrove swamps and  
 1037 coastal and estuarine areas, while ‘predators’ refers to carnivorous fishes, some of them being  
 1038 categorized as pelagic but often found in the reef for hunting.

1039 **Tables and captions**

1040

1041 Table 1. Number of identified specimens (NISP) and minimum number of individuals (MNI)  
1042 at Bubog I.

1043

1044 Table 2. Number of identified specimens (NISP) and minimum number of individuals (MNI)  
1045 at Bubog II.

1046

1047 Table 3. Number of identified specimens (NISP) and minimum number of individuals (MNI)  
1048 at Bilat Cave.

1049

1050 Table 4. Number and percentage of cultural and taphonomic disturbances on fish remains at  
1051 Bubog I, Bubog II and Bilat Cave.

1052

1053 Table 5. Taxon richness and evenness at Bubog I, Bubog II and Bilat Cave.

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1057 **Supplemental material**

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1062 Figure A4. Perforated vertebra of Carcharhinidae (requiem shark) using digital microscopy  
1063 (Hirox) with a magnification of  $\times 35$  on the surface of the centrum in order to highlight use-  
1064 wear traces.

1065

1066

1067 Table A1. Minimum Number of Elements (MNE) at Bubog I.  
1068  
1069 Table A2. Minimum Number of Elements (MNE) at Bubog II.  
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1071 Table A3. Minimum Number of Elements (MNE) at Bilat Cave.  
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