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1 **INSHORE OR OFFSHORE? THE NEOLITHIC FISHERMEN OF RA'S AL-HAMRA (RH-6, RH-5,**
2 **MUSCAT, SULTANATE OF OMAN)**

3 Anaïs MARRAST¹, Philippe BÉAREZ¹, Emilie BADEL², Lapo Gianni MARCUCCI³.
4

5 **ABSTRACT**

6 Ra's al-Hamra 6 (RH-6) and Ra's al-Hamra 5 (RH-5) are two of the most important Neolithic
7 coastal sites in the Sultanate of Oman. Located in the capital Muscat, they have supplied an
8 important corpus of fish bones and revealed a high taxonomic richness in the different
9 assemblages. The results provided information on fishing practices that held an important role
10 in the subsistence strategies of the inhabitants during the two millennia of occupation (6th–4th
11 millennia BC). Pelagic species (jacks and kawakawa/tunas) were largely dominant throughout
12 both occupations, calling into question the interpretation of inshore or offshore fishing; these
13 fish could have been caught with a hook-and-line or by setting nets at a reasonable distance
14 from the coast. However, the inhabitants also had to supplement this subsistence by catching
15 demersal fish and small fish, caught from the cliff, in the estuary or the mangrove. At both sites,
16 the inhabitants clearly exploited the different nearby inshore environments: coastal open water,
17 reefs, estuary and mangrove. Moreover, the high fish richness (69 genera at RH-6; 35 genera at
18 RH-5) indicates that both sites could have been occupied on a year-round basis.
19

20 **INTRODUCTION**

21 Many shell middens have been identified in South Eastern Arabia for the Middle Holocene
22 (7th–4th millennia), and the important economic role of aquatic resources is well established
23 (e.g., Beech 2004; Biagi 1994, 2006). Fishing does appear to have been important to these
24 populations, described as fisher-hunter-gatherer communities (Charpentier 2008; Cleuziou and
25 Tosi 2007; Cleuziou 2005), yet surprisingly, fish remains from only a few sites in Oman have

26 been analysed and published (Cartwright 2004; Uerpmann and Uerpmann 2003; Wilkens
27 2005).

28 The ancient shell midden of Ra's al-Hamra 6 (RH-6) and the more recent one of Ra's al-
29 Hamra 5 (RH-5) are two of the most important Neolithic sites in the Gulf of Oman (Figure 1).
30 The total area of each of the two sites is estimated at approximately 3500 m² for RH-6 and 3000
31 m² for RH-5. Several successive campaigns have highlighted a deep stratigraphy of almost 2 m
32 with numerous finds, including animal remains, fishing gear, and burials (Biagi 1987, 1999;
33 Biagi and Maggi 1987; Biagi and Nisbet 1992; Biagi and Salvatori 1986; Coppa et al. 1985;
34 Marcucci et al. 2011, 2014; Salvatori 2007). The first fish bone analyses at Ra's al-Hamra were
35 carried out by Biagi and Travers (1985), followed by more recent studies by Uerpmann and
36 Uerpmann (2003) and Wilkens (2005); however, their results did not take into account the
37 chronology of the site.

38
39 *Figure 1. (A) Location, altitudinal and bathymetric mapping of the Qurum mangrove and*
40 *the Ra's al-Hamra's cape, with location of the archaeological sites; (B) Map of the excavated*
41 *sectors of RH-6 (Marcucci et al., 2014, fig. 1.A.); and (C) Map of the excavated sectors of*
42 *RH-5 (Marcucci et al., 2011, fig. 2.)*

43
44 The latest investigations on the Arabian Sea coastal fringe include new fish bone studies
45 from two Neolithic sites: Suwayh 1 (SWY-1) and Ruways 1 (RWY-1), which provide
46 information on specific subsistence strategies. At these sites, ancient fishermen specialized in
47 lagoon environment exploitation, although with very different patterns of fishing: primarily
48 sharks at SWY-1 (Marrast, Béarez, and Charpentier 2020), and sardines, mullets, and juvenile
49 fish at RWY-1 (Berger et al. 2020).

50 Based on recent excavations at RH-6 and RH-5 (Marcucci et al. 2011, 2014; Marcucci,
51 Badel, and Genchi 2021), this paper presents the results from new fish bone analyses (Marrast
52 2020) and sheds light on Neolithic fishing practices in the capital area of Muscat (southern coast
53 of the Gulf of Oman).

54

55 *Environmental setting*

56 The study area is located at the southeastern end of the sandy beaches in the Al Batinah
57 Region, where the Qurum mangrove swamp stands, and where the rocky shores of Muscat
58 begin. The settlements of Ra's al-Hamra are located on the eastern edge of the Qurum Natural
59 Reserve in the district of Qurum (Figure 1A). In this area, twelve settlements have been reported
60 and four have been excavated (Durante & Tosi 1977; Uerpmann and Uerpmann 2003). Today,
61 RH-6 is about 600 m away from the sea, and RH-5 is on top of the rocky headland overhanging
62 the Gulf of Oman. But, it is important to note that at the end of the fifth millennium BC, which
63 corresponds to the end of RH-6 and the beginning of RH-5 occupations, a higher sea level (+
64 1m) than today has been identified in the northern coast of Batinah (Vita-Finzi 1982; Berger et
65 al. 2005, 56). The sites are surrounded by a multifaceted natural setting which allowed Neolithic
66 communities quick access to the Qurum mangrove, the shallow sea, the estuary, the sandy
67 beach, and even the rocky shoreline along the cliffs. In these distinct environments, ancient
68 fishermen had access to various animal resources, such as seashells, crabs, and, of course, fish
69 (Biagi 1987; Biagi and Maggi 1987; Biagi and Travers 1985; Tosi 1975). Within the Gulf of
70 Oman, the Omani Coast is influenced by monsoonal winds; it is also indirectly affected by the
71 Arabian Sea upwellings, which bring nutrient rich cold waters to the surface (Al-Azri et al.
72 2014).

73

74 Both sites offer insight into the continuous occupation of this area from the middle of the
75 sixth millennium to the end of the fourth millennium BC. This occupation took place during the
76 Holocene Humid Period, which had a stronger summer monsoon than today, illustrating a
77 climatic optimum induced by a higher latitude position of the Intertropical Convergence Zone
78 (ITCZ) (Fleitmann et al. 2007; Lézine et al. 2017; McClure 1976). This situation was probably
79 favorable for the extension of mangrove and lagoon ecosystems, as confirmed by the numerous
80 *Terebralia palustris* shells and *Avicennia* sp. charcoal fragments radiocarbon dated from this
81 period (Berger et al. 2013; Tengberg 2005).

82 83 *Archaeological setting*

84 The occupation of RH-6 ranges from the sixth millennium to the middle of the fifth
85 millennium BC, but the graveyard is currently dated to the beginning of the fourth millennium
86 BC (Biagi 2006; Zazzo et al. 2016). Dating of the settlement makes RH-6 the oldest site in the
87 archaeological sequence of Qurum. Recent excavations identified several sectors (Marcucci et
88 al. 2014): Sector A (eastern edge of the midden); B (post-occupation burials of RH-6 that were
89 contemporaneous with the occupation of RH-5); C/TT-Z (eastern edge of the midden); and
90 Trench North (northern edge of the midden) (Figure 1B). Several post holes and hearths,
91 indicating the presence of huts and living structures, were uncovered. Sector C/TT-Z, a trench
92 with a maximum depth of about 1.75 m, was selected for bioarchaeological sampling. This
93 trench provided a lot of organic material: seeds and charcoal fragments, seashells, and remains
94 of terrestrial and marine mammals, sea turtles (Frazier et al. 2018), and fish. Each stratigraphic
95 unit (SU) was sieved using 3 mm and 1 mm mesh. Thirty-two samples of charcoal fragments,
96 shells, and human bones were selected for ¹⁴C dating (Zazzo et al. 2016). The same protocol
97 was then applied to the Trench North excavation. Six periods were defined in Sector C/TT-Z
98 and four in Trench North (Marcucci et al. 2014).

100 The occupation of RH-5 ranges from the end of the fifth to the end of the fourth millennium
101 BC (Biagi 1994; Biagi and Nisbet 2006; Zazzo, Munoz, and Saliège 2014). During recent
102 excavations, the study area was divided into six sectors (Figure 1.C). Sector B2, which is the
103 subject of this study, dates from 3910-3640 cal BC (LTL12826A: 4943±45 BP, IntCal05)
104 (Marcucci 2015) and covers an area of 25 m², under an archaeological deposit 10–20 cm deep;
105 here, 200 post holes were detected related to six living structures and associated with six
106 probable waste pits. Four phases were defined in this sector with multiple remains of non-
107 permanent living structures in connection with hearths, storage, and dump pits, and the many
108 intersections of these structures, which suggest intensive and prolonged occupation of the site.
109 Each SU was sieved using a 1 mm mesh (Marcucci et al. 2011; Marcucci, Badel, and Genchi
110 2021).

112 *Previous ichthyological studies*

113 Several studies have been conducted on the fish bones recovered during the excavations of
114 the 1980s and 1990s, while three have been carried out using the RH-6 material. Biagi and
115 Travers (1985) undertook an exploratory study on material taken from the first excavation
116 (1981). The *in situ* occurrence of small pelagic species, such as sardines (Clupeidae) and
117 anchovies (Engraulidae), was noted, as was the presence of large pelagic species, such as tunas
118 (*Thunnus* spp., Scombridae) and numerous coastal fishes from rocky or sandy-mud bottoms,
119 and many marine catfishes (Ariidae). Another study by Uerpmann and Uerpmann (2003, table
120 9.7) (51 NISP) questioned some of the previous identifications (Table 1). They obtained only
121 one marine catfish specimen but 22 identified specimens belonging to jacks and trevallies
122 (Carangidae), and 23 identified specimens from tunas. A complementary study was
123 subsequently carried out by Wilkens (2005) on Sector A (570 NISP) that highlighted the

124 presence of different pelagic fish, such as several scombrids and numerous benthic-demersal
125 fish taxa. In all these studies, the main taxa identified were similar (i.e., Scombridae,
126 Carangidae, Sparidae, Serranidae, Lethrinidae).

127
128 *Table 1. Table synthesizing the main results from previous studies on the fish bone remains*
129 *from RH-6 and RH-5 (for Uerpmann and Uerpmann 2003, NISP have been calculated from*
130 *identified Actinopterygii and Chondrichthyes), and modern data of artisanal fishing from the*
131 *governorate of Muscat for 2009-2018 (M.A.F. 2018)*

132
133 The RH-5 material studied by Uerpmann and Uerpmann (2003, table 9.3) came from across
134 the whole site, without precise context (Table 1). Based on an NISP of 12,891, the authors
135 indicated that fishing activities were oriented mainly toward the exploitation of medium-sized
136 tunas (NISP = 7596), and jacks/trevallies (NISP = 4065). The exploitation of demersal taxa,
137 such as breams (Sparidae), emperors (Lethrinidae), or parrotfishes (Scaridae), was secondary.
138 However, they noted the occurrence of a large grouper (*Epinephelus* sp.), estimated at a
139 minimum of 150 cm, and a shark represented by a vertebra of 40 mm in diameter, which is very
140 large. In contrast, they also indicated the presence of a high number of small fish in the 1 mm
141 samples (NISP = 402 of 3920 remains counted).

142 143 MATERIAL AND METHODS

144 The material studied here came from Sector C/TT-Z and Trench North for RH-6, and from
145 Sector B2 for RH-5 (Figure 1B-C). For the RH-6 material, each stratigraphic unit was sieved
146 using 3 mm and 1 mm mesh. For the RH-5 material, each SU was sieved using 1 mm mesh.
147 Cut marks were absent, and all burning marks were reported. However, due to the high
148 fragmentation and the number of remains, we did not record the fragmentation pattern. To

149 facilitate the reader's understanding, the results are presented by period; more detailed results
150 are available in Marrast (2020).

151 For the identification of the fish remains, we used the fish skeletons reference collection of
152 the National Museum of Natural History of Paris, which contains for ca. 900 specimens
153 representing ca. 500 species of Indo-Pacific fishes. Fish remains were identified at the most
154 precise taxonomic level (species), but due to the high fragmentation of the remains, the
155 identification was done mainly to genus or family level. Occasionally, we used higher taxa,
156 such as the superfamily Sparoidea, which here includes all species of the families Sparidae,
157 Lethrinidae, and Nemipteridae, as they have very similar vertebrae or teeth which were
158 numerous in the small material and difficult to differentiate.

159 Grouping of fish skeletal elements is adapted from Wheeler and Jones (1989): cranial bones
160 (neurocranium and branchiocranium elements); vertebrae; and others (fin elements, scales, and
161 scutes). Fish systematic nomenclature follows Fricke, Eschmeyer, and Van der Laan (2021).

162 As for fish habitat and ecology, we followed the information from Randall (1995), and
163 FishBase (Froese and Pauly 2021). To simplify our interpretations, the fishes have been
164 classified into two main categories: pelagic fish, which include all species living in the water
165 column (whether coastal or open sea, up to 200 m deep), and demersal fish, which are associated
166 with coastal substrates. To discuss the seasonality of fishing activities and site occupation, we
167 used information from the Ministry of Agriculture and Fisheries (M.A.F.) of the Sultanate of
168 Oman, which provides data on monthly artisanal fisheries landings for the governorate of
169 Muscat (M.A.F. 2013, 2015, 2016, 2018).

170
171 We mainly use the term NISP (Number of Identified Specimens), which corresponds to the
172 number of fish remains identified to at least superorder level for Chondrichthyes (Batoidea for
173 rays, Selachimorpha for sharks), and order level for Actinopterygii (e.g., Clupeiformes,

174 Siluriformes, Tetraodontiformes). We also use the term WISP (Weight of Identified Specimens)
175 for the weight of the identified bone remains.

176 We used the classical approach of comparative anatomy and chose to estimate the live weight
177 of the fish, rather than its size, because this seems to be a better indicator of the amount of flesh
178 the fish can provide. The live weights we provide are weight visual estimates, made by direct
179 comparison with specimens from the fish reference collection of known live weight and length
180 data, not reconstructions using osteometric models. The estimate of the MNI (Minimum
181 Number of Individuals) was performed on the main taxa (species or genus level) despite the
182 high number of vertebrae, which sometimes made it very difficult. MNI was estimated by
183 counting the most frequent anatomical element of a given species after considering laterality
184 and size (i.e., MNI of combination; Poplin, 1976). Several species of jacks and trevallies present
185 in the study area have characteristic swollen bones (hyperostosis) on the occipital crest or
186 cleithrum, which, due to their good preservation, were often found and used for the estimation
187 of the MNI.

188 In order to compare results from different chronological periods, chi square tests were
189 performed on the corresponding NISP to detect the dependency between two faunal
190 assemblages, and therefore the associated fishing patterns (Chenorkian, 1996). Tests were
191 performed on each pair of assemblages from two successive periods (H_0 : The two relative
192 proportions do not differ significantly). To respect the test conditions ($n > 5$) for each test, only
193 the most important fish families (between 5 or 7, depending on the assemblages) were tested.

195 RESULTS

196 *The RH-6 site*

197 Since Trench North is more representative of the beginning of the occupation and Sector
198 C/TT-Z is more representative of the end, we will present the results in this order. The

199 equivalence between the periods in the two sectors is adapted from Marcucci (2015: table
200 A2.13). For ease of presentation, we discuss the results for the main families and mostly at the
201 genus level, except for Thunnini. All the species identifications can be found in supplemental
202 files 1–3.

204 Trench North – 3 mm

205 For Trench North, located at the northern edge of the shell midden, vertebrae were the most
206 abundant (66.5% of the material anatomically identified), followed by cranial elements
207 (26.5%), and other post-cranial elements (7%). The dentary was the most represented cranial
208 bone (NISP = 528), followed by the premaxilla (NISP = 353) (Table 2). These jaw bones are
209 among the strongest bones in most teleosteans (bony fish) and consequently have a very good
210 conservation rate (Wheeler and Jones 1989, 90). Still, there is a major imbalance between the
211 remains of the skull and the spine because the vertebrae are thicker than the skull bones and
212 therefore better preserved.

213
214 *Table 2. Element distribution on the two sites according to the sector studied and the*
215 *sieving mesh size (Chondr. = Chondrichthyes)*

216
217 A total of 9116 fish bones (NISP) were identified. Most of this material corresponded to the
218 beginning of the occupation of RH-6, i.e., periods 1–4 of Sector C/TT-Z. In Trench North, four
219 periods were defined. However, as periods 3 and 4 were poor in fish (NISP = 9) these results
220 were not included in the discussion. Period 1 is taxonomically rich (32 families, 51 genera),
221 associated with a high NISP (4908). Period 2, with a lower NISP (4208), is less taxonomically
222 rich (23 families, 38 genera) (Figure 2A).

224 *Figure 2. Taxonomic richness at family and genus levels for different sectors and time*
225 *periods*

226
227 Chi square tests were performed between the assemblages but did not reveal any significant
228 differences (χ^2 : 6.6397, $p > 0.1$, df: 4) (Figure 3A; Table 3). Pelagic fish represent more than
229 91% of the assemblage NISP for the two periods, with trevallies (*Carangoides* spp.) as the main
230 taxon (20%). Kawakawa (*Euthynnus affinis*) and jacks (*Caranx* spp.) were of similar
231 importance throughout the site's occupation (15.5% and 12%), as was the golden trevally
232 (*Gnathanodon speciosus*) (3.6%), while tunas seem to be the least important of the pelagic
233 fishes; the two species accounting for just 5–6%. The contribution of demersal fish, mainly
234 represented by different seabreams, emperors, and groupers (Serranidae), was very low (9%)
235 (Table 3).

236
237 *Figure 3. Illustration of the main taxa distribution (NISP).*

238 *(A) RH-6, Trench North, 3 mm; (B) RH-6, Sector C/TT-Z, 3 mm. Made with ACACIA*
239 *(Nourissier, Nocus, and Dufraisie, 2010)*

240
241 *Table 3. Zooarchaeological fish remains from RH-6, Trench North, 3 mm, according to*
242 *periods in NISP, % of NISP and WISP (g). Other pelagic = 12 families (Supplemental file 1);*
243 *Other demersal = 19 families (Supplemental file 1).*

244
245 The mean weight of the caught fish varied between periods. Indeed, while the tuna mean
246 weight for period 1 is 7 kg, it falls to 4.5 kg, and has a greater distribution, in period 2 (Figure
247 4A). In contrast, jacks are larger in period 2 (2.5 kg versus 1 kg in period 1), while kawakawas,
248 and trevallies weigh in at 3 to 3.5 kg for both periods (Figure 4B-D). However, the NISP of

249 kawakawa and jacks must be considered against the MNI (Table 4). Most of the kawakawa
250 bones are vertebrae, which have high conservation rates because of their extremely robust
251 constitution. On the other hand, many cranial elements of jacks were found, increasing their
252 MNI. The difference in proportions between kawakawa and tunas is less when measured by
253 MNI than by NISP.

254
255 *Figure 4. Illustration of the estimated weight of each main pelagic taxa from the richest*
256 *RH-6 periods (P: Period), both sectors (TN: Trench North, C-TTZ: Sector C TT-Z). Min:*
257 *Minimum, Max: Maximum, Q: Quartile. (A) Thunnus spp; (B) Euthynnus affinis; (C)*
258 *Carangoides spp.; (D) Caranx spp.*

259
260 *Table 4. MNI estimates of the main pelagic taxa at RH-6, 3 mm, according to periods and*
261 *comparison with the NISP*

262
263 *Sector C/TT-Z – 3 mm*

264 For Sector C/TT-Z, vertebrae were also the most abundant element (62% of the material
265 anatomically identified), followed by cranial elements (30%), and other post-cranial elements
266 (8%). Jaw bones, with 508 premaxillae and 496 dentaries, were the most frequently represented
267 cranial bones (Table 2).

268 A total NISP of 8489 have been determined, but abundance of fish bones was very disparate
269 from one period to another. Fish bones were much less abundant in the four oldest periods than
270 in the two most recent ones (Figure 3B). Taxonomic richness has increased over time (Figure
271 2B), in a trend that appears to be roughly independent of the NISP. Richness peaked in period
272 6 (26 families, 52 genera), while its NISP (3464) was lower than in period 5 (4109).

274 In this sector, pelagic fish taxa were also dominant (Figure 3B, Table 5). Jacks were the main
275 taxa (18% of the total assemblage), followed by trevallies (11.5%), and kawakawas (10%). Chi
276 square tests were performed between all pairwise assemblages, with the exception of period 2
277 due to its small sample size but did not reveal any significant differences between periods 3 and
278 4 (Figure 3B) (χ^2 : 12.93, $p > 0.01$, df: 4). On the contrary, periods 4 and 5 exhibited a strong
279 statistical difference in faunal composition, supporting a genuine increase in the proportions of
280 the two main pelagic families (from 64 % to 82%) and a decrease in demersal fish (from 34%
281 to 16%) (χ^2 : 82.39, $p < 0.001$, df: 4). For the end of the occupation, between periods 5 and 6, a
282 chi square test indicated the opposite effect (χ^2 : 35.01, $p < 0.001$, df: 4), with an increase of
283 demersal fish (from 16% to 20.5%) and a decrease of pelagic fish, driven by the decrease of
284 scombrids (from 25% to 21%).

285
286 *Table 5. Zooarchaeological fish remains from RH-6, Sector C/TT-Z, 3 mm, according to*
287 *periods in NISP, % of NISP and WISP (g). Other pelagic = 5 families (Supplemental file 1);*
288 *Other demersal = 24 families (Supplemental file 1)*

289
290 In Sector C/TT-Z, an increase in MNI is associated with the end of occupation. Indeed,
291 periods 5 and 6 were represented by 386 and 294 main pelagic fishes, much more than in
292 previous periods (Table 4).

293
294 Mean fish weights were estimated for the two most recent periods (Figure 4), periods 5 and
295 6, because their sample sizes were large enough to allow comparison with the Trench North
296 periods. For kawakawa and tunas, specimens were bigger in period 6 with a mean weight
297 reaching 4 kg (versus 3.1 kg) and 5 kg (versus 3.5 kg), respectively (Figure 4A-B). Conversely,
298 for jacks and trevallies, there was a decrease in the mean weight at the end of RH-6 occupation,

299 with the mean weight of jacks decreasing from 2 kg to 700 g, and that of trevallies decreasing
300 slightly from 3 kg to 2.6 kg (Figure 4C-D).

301
302 Sector C/TT-Z – 1 mm sampling

303 Here, the results are presented only for periods 2 to 6 of Sector C/TT-Z. Two samples were
304 taken for each period (Table 6). A significant disparity was observed between the numbers of
305 vertebrae (95%), cranial elements (4.5%), and other elements (0.5%) (Table 2).

306
307 *Table 6. Zooarchaeological fish remains from RH-6, Sector C/TT-Z, 1 mm in NISP and % of*
308 *NISP by period. Other pelagic = 9 families (Supplemental file 1); Other demersal = 13*
309 *families (Supplemental file 1)*

310
311 A total of 9388 fish bones (NISP) were identified within 22 families and 16 genera (Figure
312 2C), reflecting the potential information added with fine mesh sieving. As sieving was not
313 uniform, we chose not to perform chi square testing; however, a major change through time can
314 still be observed. Sardines (Clupeidae) take on greater importance in the faunal assemblage
315 until period 5 (Figure 5). Although the species could not be identified, it was probably mainly
316 the Indian oil sardine (*Sardinella longiceps*), along with some goldstripe sardinella (*Sardinella*
317 *gibbosa*), as is reported today among the traditional fishery in Oman (Strømme 1986). Different
318 scads (Carangidae) were noteworthy, with bigeye scads (*Selar crumenophthalmus*)
319 representing more than 90% of NISP. Their proportional abundance nevertheless declines from
320 29.6% in period 2 to 12% in period 6. The occurrence of silversides (Atherinidae) was
321 noticeable, as was the presence of mullets and juvenile breams/emperors (Sparoidea).

322
323 *Figure 5. Illustration of the main taxa distribution (NISP).*

RH-6, Sector C/TT-Z, 1 mm (Periods 2, 3, 4, 5, 6) – RH-5, Sector B2, 1mm (Phases 2, 3,
4). Made with ACACIA (Nourissier, Nocus, and Dufraisse, 2010)

The RH-5 site

In Sector B2, all zooarchaeological material was recovered by sieving with a 1 mm mesh. There was a discrepancy in the anatomical distribution of vertebrae (95%), cranial elements (4.5%), and other elements (0.5%) (Table 2). A total of 8406 specimens were identified, weighing 92 g (Table 7). Assemblage abundance was variable over time and due to low specimen numbers in phase 1, these data are excluded from the interpretation of the results.

Table 7. Zooarchaeological fish remains from RH-5, Sector B2, 1 mm, according to periods in NISP, % of NISP and WISP (g). Other pelagic = 7 families (Supplemental file 1); Other demersal = 20 families (Supplemental file 1)

Since the beginning of occupation, richness was relatively high. For phase 1, despite a very low NISP (32), high richness was noted (7 families, 7 genera). It reached a peak in phase 3 (27 families, 33 genera), with the highest NISP (6640) counted. During phase 4 (15 families, 17 genera), there was a decrease in NISP (1492) (Figure 2D).

Chi square tests were performed between the assemblages and revealed significant proportional differences in faunal composition between phases 2 and 3 (χ^2 : 55.84, $p < 0.001$, df: 4). These changes are driven by the observed increases or decreases in several taxa. In phase 2, carangids, including bigeye scads, were the most abundant taxon, representing 44.5% of identified specimens (Table 7, Figure 5). They decreased to 36% in phase 3, replaced by sardines (55% in phase 3). For the phases 3 and 4, Chi square tests did not reveal significant

349 proportional difference in faunal composition (χ^2 : 6.68, $p < 0.001$, df: 5). Indeed, the sardines
350 contributed a similar proportion to the assemblage in phase 4. Other pelagic (mulletts,
351 barracudas) and demersal (Sparoidea) taxa declined in abundance over time.

352 The assemblages were composed mainly of small vertebrae, which complicated the MNI
353 calculation. Estimating precise live weight from small bones is challenging, but most of the
354 RH-5 fish (scads, sardines, mullets, Indian mackerel) belonged to the 150 g weight category.
355 No fish larger than 5 kg were recorded from our study at RH-5.

357 DISCUSSION

358 Several trends clearly emerged concerning different aspects of the fishing economy across
359 the Ra's al-Hamra sites, although the materials analyzed came from distinctly separate sectors.

360 *Taphonomic remarks*

361 The NISP of kawakawa and jacks must be considered alongside the MNI (Table 4). Most of
362 the kawakawa bones are vertebrae, which have high conservation rates because of their
363 extremely robust constitution. On the other hand, many cranial and hyperostotic elements of
364 jacks and trevallies were found, which increases their MNI. The difference in proportions
365 between kawakawa and jacks, therefore, no longer appears to be as great with the MNI as with
366 the NISP.
367

368
369 As the cranial elements were highly represented in each SU and no traces of butchery were
370 found, fish were probably complete and fresh when brought to the site. Apart from gutting, they
371 were probably not processed before consumption. As for the burn marks on the bones, very few
372 were noticed on both sites and no burning pattern could be discerned. The bones could be

373 completely burnt, indicating that they had probably simply been thrown into the fire after the
374 fish had been consumed.

375

376 *Fishing patterns*

377 Our results indicate slight changes through time between the two sites. The RH-6 fishermen
378 concentrated their efforts on catching medium-sized pelagic fish, comparable with previous
379 RH-5 results. At both sites, pelagic fish accounted for more than 80 % over time (Tables 1, 3,
380 5), illustrating a subsistence strategy probably adapted to a marine environment rich in pelagic
381 fish. However, when considering the proportions of the two main families of pelagic fish, the
382 fishing pattern of the late RH-6 occupation (Period 6) and that of RH-5 (Table 1; Uerpmann
383 and Uerpmann, 2003) appeared to be highly different (χ^2 : 2934.68, $p < 0.001$, df: 6). The
384 inhabitants of RH-5 seem to have concentrated their efforts on catching different scombrids.
385 This change may represent different cultural choices in fishing strategies.

386 The results from the 1 mm mesh fraction highlighted the importance of small fish, with a
387 high number of remains counted at both sites (Tables 6, 7). It is particularly important to note
388 here the very high proportion of vertebrae (95%) in the 1 mm fraction material at both sites.
389 The preservation of vertebrae is often better than that of cranial bones, but this is even more
390 true in the case of small fish. Based on the study of this material, fishing patterns appear to be
391 very specific to each site (RH-6-P6 and RH-5-Ph3, χ^2 : 1400.76, $p < 0.001$, df: 6). Sardines
392 constituted 45% of the fish remains at the beginning of RH-6 occupation, but by the end
393 constituted 70% of the faunal assemblage. At RH-5, scads are abundant at the beginning of
394 occupation (36% in phase 2, while sardines occupied 35%), but this pattern is reversed at the
395 end of the occupation (sardines 58% and scads 32%). For RH-5, however, consideration of
396 WISP provides a more nuanced understanding of the results. Indeed, if sardines, scads, and
397 mackerel are dominant based on NISP, kawakawas, barracudas, and jacks/trevallies are the best

398 represented according to the WISP, especially jacks (*Caranx* spp.). Demersal fish were rare at
399 RH-5, and it is interesting to note that most of the fish in Sector B2 were represented by
400 specimens weighing less than 150 g.

401

402 Nowadays, artisanal fishing, by line, troll, or net, provides landings composed mainly of
403 large pelagic species, such as longtail tuna (*Thunnus tonggol*), yellowfin tuna (*Thunnus*
404 *albacares*), kawakawa (*Euthynnus affinis*), large jacks/trevallies (*Caranx* spp. and *Carangoides*
405 spp.), and Talang queenfish (*Scomberoides commersonianus*). An important part of the
406 fishery, however, consists of small pelagic fish, such as sardines (Clupeidae), Indian mackerel
407 (*Rastrelliger kanagurta*), and mullets (Mugilidae) (Table 1, M.A.F. 2018). However, while the
408 species fished today were already present on the two archaeological sites, two pelagic species,
409 the Talang queenfish and the Narrow-barred Spanish mackerel (*Scomberomorus commerson*),
410 are absent or only very occasionally present in the mid-Holocene catch (see Supplemental file
411 1). Moreover, the proportions are very different today, with pelagic fish representing more than
412 80% of the catch at RH-6 and RH-5, compared to 70% in the modern catch.

413

414 *Inshore or offshore?*

415 Despite the occurrence of medium-sized pelagic fish in several sites throughout the Persian
416 Gulf and Gulf of Oman for the Neolithic period, such as Delma (Lidour and Beech 2019), Akab
417 (Lidour et al. 2020), Dosariyah (Uerpmann and Uerpmann 2018), and Khor Milkh (Uerpmann
418 and Uerpmann 2003), the sites of Ra's al-Hamra appear to be distinctive given the high
419 proportion of these fish in their faunal material.

420 The abundance of tuna and other pelagic fish raises questions about the existence of offshore
421 fishing in the Neolithic sites of the Gulf of Oman. Since the first studies, interpretations have
422 leaned towards offshore fishing, with the use of boats suggested for catching tunas/kawakawas

423 and jacks/trevallies (Biagi et al. 1984; Biagi and Nisbet 1992; Uerpmann and Uerpmann 2003:
424 198). The terminology of fishing areas was clarified by Pickard and Bonsall (2004) and adjusted
425 by Béarez et al. (2016) who added water depth as an important parameter. We follow the latter
426 to denote an inshore fishery as one that is conducted in the inshore and nearshore zone (down
427 to 30 m depth), an offshore fishery as one that is conducted in deeper waters but within sight of
428 land (< 5 km), and an open sea (deep-sea) fishery as one that is conducted out of sight of land.

429
430 Although jacks, trevallies, tunas and kawakawa are pelagic, these species can approach
431 relatively close to the coast (Anderson 2013; Collette 2001). Tunas and other scombrids are
432 pelagic fish known to form large, sometimes multi-species schools of thousands of individuals
433 (Collette and Nauen 1983), a behavior which is also observed at a lesser scale in many carangids
434 (scads and young to small adult trevallies and jacks). These open water schools can be observed
435 by fishermen from the coast, especially when sea birds fly over them (Cartwright 2004; Lidour
436 et al. 2020, fig. 7.A). Until recently, fishermen used small rafts or boats, such as *shasha*, to join
437 a school of tunas, once sighted, and then deployed hook-and-lines or nets to catch them. These
438 small boats are mainly made of date leaves and date palm fibers, which provide buoyancy (Al-
439 Marshudi and Kotamaga 2006; Goddard 1985; Johnson 2016; Uerpmann and Uerpmann, 2003,
440 198-199). Similar, frail embarcations could have been made during the Middle Holocene with
441 materials collected in the vicinity of the Ra's al-Hamra sites, such as Mazari palm (*Nannorrhops*
442 *ritchiana*), common reed (*Phragmites australis*), or cattail (*Typha* spp.) (Biagi et al. 1984;
443 Biagi and Nisbet 1999; M. Tengberg, pers. comm.). Stronger and sewn vessels are only attested
444 for the third millennium (Cleuziou 2003; Vosmer 2019). As for the ropes of the lines and nets,
445 they may also have been made from Mazari palm; indeed, ropes found at the Shahi Tump site
446 (Iran, fourth millennium BC) were made from this species (Thomas et al. 2012). In addition,
447 fishing cordage has traditionally been made from this species along the Omani Coast

448 (Richardson and Dorr 2003); it is favored by fishermen because its strength is increased when
449 wet. Finally, on both RH-6 and RH-5 sites, different shell-hooks and sinkers have been
450 recovered (Biagi, 1987; Marcucci et al., 2011, 2014).

451

452 Unfortunately, the difficulty in separating the two species of tuna, yellowfin and longtail,
453 based on their osteology may explain the high rate of identifications at the genus level (*Thunnus*
454 spp.) in our studies and those of Uerpmann and Uerpmann (2003), which limits the robustness
455 of the interpretations. Normally, yellowfin tuna can reach larger sizes than the longtail tuna.
456 However, at both archaeological sites, yellowfin tunas appear to be smaller than longtail tuna.
457 Small schools of small tunas probably approached the coast on their own, while larger
458 individuals remained offshore. In addition, kawakawa is the main scombrid found at both sites.
459 It is known that among the schools of kawakawa targeted by fishermen, small tuna specimens
460 may also have been present (Uerpmann and Uerpmann 2003, 199), so the mixed scombrids
461 fishery may well have been inshore. Fishermen would only need a glittering hook, such as a
462 mother-of-pearl hook, to catch voracious scombrids (Uerpmann and Uerpmann 2003, 198). The
463 casting of nets from boats is suggested by the presence of large net sinkers, but this practice
464 was probably difficult due to the vulnerability of their frail boats; also, this fishing technique
465 may have been particularly dangerous (Lidour et al. 2020; Uerpmann and Uerpmann 2003,
466 199). Furthermore, it is possible to fish tuna from shore; indeed, this practice is conducted today
467 for sport (Karachle, Dimarchopoulou, and Tsikliras 2020).

468

469 Large individuals of carangids can currently be found living solitary or in small groups along
470 the coast (Grandcourt 2012; Grandcourt et al. 2004). In the Ra's al-Hamra material, three genera
471 are important: *Carangoides*, *Caranx*, and *Gnathanodon*. The golden trevally (*G. speciosus*) is
472 often associated with deep reefs and deep lagoons (Grandcourt et al. 2004). As they represent

473 the main family at RH-6, their presence could be connected with the numerous small line
474 sinkers or the many complete or fragmented hooks found at RH-6 in different stages of
475 manufacture (Biagi 1999). This could indicate a specialization in hook-and-line fishing.
476 However, the large size of some sinkers (Durante and Tosi 1977) may suggest the use of big
477 nets in open water, or fish traps (*gargour* in Arabic) (Uerpmann and Uerpmann 2003).

478

479 While offshore navigation is attested for the Neolithic of the Arabian Peninsula in the Persian
480 Gulf, with the occupation of islands 10 km from the coast and the presence of bitumen (Beech
481 2004; Beech et al. 2016; Carter and Crawford 2010; Lidour et al. 2020), and in Oman with the
482 occupation of Masirah Island (Charpentier et al. 2013), it is not clear whether the fish
483 assemblage reflects offshore fishery. Indeed, previous studies have shown that the presence of
484 scombrids is not necessarily a sign of this activity (Anderson 2013; Béarez, Gay, Lunniss 2012).
485 As most of the species identified at RH-6 and RH-5 are found close to the coast (< 5 km), and
486 there is an absence of large pelagic species such as Indo-Pacific sailfish (*Istiophorus*
487 *platypterus*) or large tunas (> 10 kg), this might suggest inshore fishery. The presence of
488 dolphins and whales at both sites could be an indication of offshore fishing, but their presence
489 is too sporadic (NISP: 46 small dolphin, 34 big dolphin, and 31 small whale remains at RH-5)
490 to indicate systematic fishing activity; however, scavenging of beached carcasses cannot be
491 ruled out (Uerpmann and Uerpmann 2003).

492

493 *Estuary and mangrove exploitation*

494 In the underwater environment of Ra's al-Hamra, many demersal species could be fished,
495 such as emperors, groupers, snappers, seabreams, and even parrotfish and porcupinefish, all of
496 which have been found at both sites (Supplemental files 2–3). The main taxa from this category
497 (seabreams, emperors, and groupers) appear to be able to be caught using the same fishing

498 techniques. These fish can be caught by net, trap, or hook-and-line, and are to be found all year-
499 round, so they may have been used for daily subsistence.

500
501 Another environment exploited for fishing by the inhabitants of both sites was the mangrove.
502 Indeed, using the 1 mm mesh size on both excavations allowed new information to come to
503 light about this specific fishing ground, which is used as a nursery by many species, especially
504 fish (Abu El-Regal and Ibrahim 2014; Laegdsgaard and Johnson 2001; Nagelkerken et al. 2002;
505 Robertson and Duke 1987). The mangrove edges and shores can be considered excellent spots
506 for positioning a fishing camp. These brackish-water ecosystems are normally characterized by
507 their high biomass, with the presence of numerous mullets and sardines (Kulbicki 1997).
508 Although Uerpmann and Uerpmann (2003, 198-199) have already noted the presence of many
509 small fish at Ra's al-Hamra, they minimized their inclusion in the diet of ancient populations by
510 suggesting that they could be tuna stomach contents. Our study, however, places greater
511 importance on these fish as they correspond to an environment highlighted by previous
512 environmental studies showing the most extensive development of mangrove at the end of the
513 fifth millennium/beginning of the fourth millennium BC (Berger et al. 2013; Berger et al. 2005;
514 Biagi and Nisbet 1992; Tengberg 2005). The many hooks found in situ do not coincide with
515 this type of mangrove fishing, however, and the size of the fish suggests the use of small-mesh
516 nets or beach seine. This accords with the small-sized sinkers (Biagi 1999, fig. 14: 1-7), possibly
517 used for cast nets (Marrast 2020; Marrast, Béarez, and Charpentier 2020), or maybe the
518 construction of a fish weir in the mangrove swamp.

519 520 *Seasonality of fishing activities*

521 Our results question the seasonality of site occupation. Today, the pelagic species observed
522 in Ra's al-Hamra's faunal assemblage represent an important part of the fishery landings in the

523 Sultanate of Oman, especially in Muscat. Unfortunately, the data provided by the Ministry of
524 Agriculture and Fisheries (M.A.F. 2013, 2015, 2016, 2018) are not precise enough, with many
525 species (e.g., large jacks, emperors, seabreams) mixed into a single category, which does not
526 allow for a detailed comparison of the data. However, it is clear that some species are caught
527 all year round, while others are available in abundance on a seasonal basis (Figures 6–7).

528
529 *Figure 6. Compiled data (in metric tons) for 4 years (2013, 2015, 2016, 2018) of artisanal*
530 *fisheries in Muscat governorate for Thunnus tonggol, Thunnus albacares, Euthynnus affinis,*
531 *and large jacks (Carangidae) (M.A.F. 2013, 2015, 2016, 2018). The thick line represents the*
532 *mean. The filled area is the standard deviation of the mean*

533
534 *Figure 7. Ecological distribution of the main taxa found at both sites according to Froese*
535 *and Pauly (2021), Randall (1995) and personal observations. Vector objects are from*
536 *Vecteezy.com (Graphics RF)*

537
538 Jacks and trevallies are regularly caught throughout the year, but this is not the case for tunas
539 and kawakawas (Figure 6A-B, D). In the Muscat landings, kawakawas appear to be
540 continuously caught, but between October and November catches peak (Figure 6C). For longtail
541 tuna, the major peak is between May and June, but abundance is high until October (Figure
542 6A). Yellowfin tuna is mostly present between September and November (Figure 6B). The
543 occurrence of scombrids in the summer months on the shores of the Gulf of Oman could be
544 linked to the Southwest monsoon (June - September), which brings moist air masses. At the
545 same time, an upwelling phenomenon occurs along the southern coast of Oman, which also
546 affects the Gulf of Oman (Al-Azri et al. 2010; Elliot and Savidge 1990; Watanabe et al. 2017).
547 Upwelling brings nutrient-rich waters to the surface, allowing an important trophic network to

548 develop, including schools of small pelagics, much sought after by scombrids and other pelagic
549 species (Lee et al. 2000). As for sardines, even if they are available all year round, they are
550 particularly important during the cooler season (Northeast monsoon), between November to
551 March (Al-Jufaili and Al-Jahwari 2011). However, this could be partly due to the fact that
552 weather (strong winds) and sea conditions (big waves) affect the sardine beach seine fishery
553 during the summer. It is likely that coastal communities have been highly dependent on the
554 summer upwelling phenomenon linked to the Southwest monsoon (Biagi and Salvatori 1986;
555 Cavulli and Scaruffi 2013).

556 Since jacks were important at both sites, we can conclude that the fishery for coastal pelagic
557 species could have been all year round, with tuna fishing most active in the autumn and winter.
558 Though it should be noted that pelagic fishing is also associated with significant demersal
559 fishing and a high exploitation of the mangrove and estuarine environment.

560
561 As previously mentioned, mangroves are used as a nursery by many species. In this region
562 of the world, seabreams (*Acanthopagrus* spp. and *Rhabdosargus* spp.), scads (*Trachurus*
563 *indicus*, *S. crumenophthalmus*), some jacks, trevallies, mojarras (Gerreidae), and goatfishes
564 (Mullidae) spawn in the spring, suggesting that juveniles may be found in the mangrove in
565 summer–autumn. In addition to these juveniles, which are characteristic of this environment,
566 many adult fish are also found in the mangrove: jacks and trevallies, mojarras, and goatfishes
567 all frequent the mangrove in autumn; sardines are spotted between winter and spring; and
568 groupers, parrotfishes, and goatfishes in summer. In general, a peak in mangrove frequentation
569 in this part of the world seems to be marked between winter and spring (Abu El-Regal 2013;
570 Abu El-Regal and Ibrahim 2014; Laroche, Baran, and Rasoanandrasana 1997). Barracudas
571 (Sphyraenidae) and small sharks can also be found throughout the year (Marrast, Béarez, and
572 Charpentier 2020). All studies suggest that juveniles can be found in the mangrove at any time,

573 with a peak occurrence between spring and summer, suggesting that this was the best time for
574 the exploitation of this marine resource in this ecosystem (Abu El-Regal 2013; Abu El-Regal
575 and Ibrahim 2014; Lidour, Béarez, and Méry 2020; Robertson and Duke 1987).

577 *Seasonality of site occupation*

578 The exploitation of diverse resources during the 2,000 year occupation at Ra's al-Hamra
579 implies that the communities had an excellent knowledge of the marine coastline, wildlife
580 ecology, and climatic and environmental features (monsoon and upwelling). This fits well with
581 fisher-hunter-gatherer patterns whose subsistence strategies are based on the acquisition of wild
582 resources, implying a long familiarity with biotopes and wildlife ecology (Acheson 1981; Collet
583 1991). This multifaceted environment allows diversification in the resources consumed,
584 enabling fluctuations in seasonal resources and any possible shortages to be offset (Biagi et al.
585 1984; Yesner et al. 1980).

586 Hunter-gatherers vary in their degree of mobility and may occupy different camps
587 throughout the year. According to Yesner et al. (1980), this makes adaptation to resources
588 possible, allowing the exploitation of several ecological niches (Figure 7). However, as hunters
589 do not adapt to a single environment for their subsistence strategy, the long-term use of space
590 can vary over the year. Fishing activities involve the making and handling of fishing gear, as
591 well as fish preparation and storage activities, and require a high degree of social cooperation
592 to manage the capture and arrival of large quantities of fish (Camelin 1995; Collet 1991). Such
593 cooperation, therefore, fits better with a more sedentary lifestyle.

594
595 Until recently, traditional Bedouins on the coast of the Gulf of Oman had to move several
596 times a year because none of the resources they exploited was permanent (Lancaster and
597 Lancaster 1995; Miles 1910). Early ethnographic comparisons have established that shell

598 middens indicate winter camps and that Bedouin communities moved onto the piedmont in the
599 primeval period and then into the mountain valleys in small, scattered groups (Cleuziou 2005;
600 Cordes and Scholz 1980; Lancaster and Lancaster 1995). Within archaeological communities,
601 some authors even talk of large-scale transhumance between coastal sites and inland pastures
602 (al-Buhais 18, BHS-18) during the arid periods of the fourth millennium BC (Kutterer and
603 Uerpmann 2017). Even if it is reasonable to consider the idea of small scale nomadism along
604 the wadis between the coast and the foothills, due to the high temperatures recorded on the coast
605 in summer, and because of the perishable character of the habitat structures that suggests
606 structures were temporary (Cavulli and Scaruffi 2013), our data do not confirm such a scenario.
607 This illustrates the complexity surrounding the seasonal occupation of Neolithic sites in the
608 southeast Arabian Peninsula.

609
610 At RH-5, the community seems to be permanently settled (Munoz 2014; Salvatori 2007),
611 observable in the high density of habitat structures (Marcucci et al. 2011) and no phases of
612 abandonment (Béguier and Marcucci 2018; Marcucci et al. 2011; Marcucci, Badel, and Genchi
613 2021). Moreover, anthropological studies have established a certain genetic isolation (reduced
614 tooth size) and increasing population density, suggesting the sedentary or semi-sedentary
615 lifestyle of the RH-5 inhabitants (Macchiarelli 1989). This hypothesis is reinforced by
616 geochemical analyses on human skeletons, which indicate a strong dependence on marine
617 resources (Zazzo, Munoz, and Saliège 2014; Zazzo et al. 2016). This is consistent with the
618 multi-niche ecological arguments and the slaughter pattern observed in the domestic animals
619 present in the graves. Sometimes the remains indicated more than one and sometimes up to six
620 animals; “*such slaughtering events require stable animal populations*” (Uerpmann 2003, 79).

621

622

CONCLUSION

623 At both sites, our results show that all the fish could have been caught in the vicinity of the
624 site. The residents of RH-6 and RH-5 intensively exploited pelagic fish, either by hook-and-
625 line or by setting nets at a reasonable distance from the coast. However, they also had to
626 supplement this subsistence by setting nets in the mangrove, which provided the opportunity to
627 catch many small fish.

628

629 For RH-6, our study is the first to provide results based on such a large corpus of remains,
630 highlighting a predominance of jacks over Thunnini during the entire period of occupation.
631 Fishing activities were mainly oriented toward the exploitation of medium-sized pelagic fish,
632 especially different Thunnini and jacks, which had approximately the same importance. While
633 these pelagic species dominate throughout the occupation, a gradual decrease in pelagic fish is
634 observed over time.

635 The results of our analysis show the fishing activities practiced during part of the first
636 occupation of the RH-5 site (3910-3640 cal BC), following the end of the RH-6 occupation.
637 The fishery during phases 1 and 2 mainly exploited small pelagic species, such as sardines or
638 bigeye scads. Their frequency is even greater during phases 3 and 4, where they constitute more
639 than 90% of the assemblage. This indicates fishing with small-meshed gillnets or beach seines,
640 as the hooks found at the site are too large to catch such small species.

641 However, a few medium-sized fish were also present, corresponding mainly to individuals
642 of pelagic species, such as tunas or various jacks. These taxa are easy to catch using hook-and-
643 lines thrown from a small boat or even from rocky points, such as those found at the foot of the
644 Ra's al-Hamra cliff. Our study also showed the importance of sieving with a small mesh, which
645 in this case revealed the diversity of the environments exploited and the diversity of fishing
646 techniques implemented at a fishing station in the Neolithic period. These results are extremely
647 promising for redefining the role of fish in the diet and daily life of Neolithic populations.

648 Indeed, although the importance of marine resources has always been considered by
649 researchers, quantitative and detailed results are still scarce.

650

651 In contrast to many contemporary sites in the Persian Gulf (Beech 2004; Lidour, Béarez, and
652 Méry 2020; Lidour and Beech 2019) and in the Arabian Sea, such as SWY-1 and RWY-1
653 (Berger et al. 2020; Marrast, Béarez, and Charpentier 2020) where lagoons have been mainly
654 exploited, the Neolithic inhabitants of the capital area of Muscat appear to have specialized in
655 the exploitation of coastal pelagic species. This kind of exploitation has already been
656 highlighted at a few sites in the Persian Gulf, particularly at Akab, where carangids and
657 scombrids represented 50% of the material (Lidour et al. 2020), and at Khor Milkh 1 (KM-1)
658 (Uerpmann and Uerpmann 2003, 194), just south of Ra's al-Hamra. However, the specialization
659 of this type of fishing (more than 80% at RH-6 and RH-5) in the Gulf of Oman is, for the
660 moment, unique in this region. New ichthyoarchaeological studies in the region and their
661 publication, especially from more recent sites (Bronze Age) or from areas that are still poorly
662 known, will make it possible to complete the picture of ancient fisheries in this part of the world
663 and, in particular, to better understand the reasons that led the coastal inhabitants to turn to
664 pelagic resources. Similarly, the integration of analyses of other marine resources (crustaceans
665 and crabs, sea turtles, cetaceans, etc.) would provide an accurate picture of the dietary habits
666 during the Middle Holocene and improve our understanding of the role of the sea for the coastal
667 populations of southeast Arabia.

668

669

SUPPLEMENTAL FILES

670

671

672

Supplemental file 1. List and NISP of taxa recovered at RH-6 and RH-5, arranged in taxonomic order. B: benthic; D: demersal; EP: epipelagic; P: pelagic. For fish behaviour, we followed the information from Randall (1995) and FishBase (Froese and Pauly 2021)

673

674 *Supplemental file 2. Illustration of different bones from main taxa at both sites and*
675 *possible fishing environment. Pelagic fishes: (A) Thunnus albacares, precaudal vertebra*
676 *(ventral view); (B) Thunnus tonggol, caudal vertebra (lateral view); (C) Euthynnus affinis,*
677 *precaudal vertebra (ventral view); (D) Caranx sexfasciatus, right cleithrum (lateral view); (E)*
678 *Carangoides chrysophrys, supraoccipital hyperostosis (lateral view); (F) Gnathanodon*
679 *speciosus, precaudal vertebra (ventral view). Demersal fishes: (G) Sufflamen fraenatum, left*
680 *premaxilla (lateral view); (H): Scarus sp., left dentary (lateral view); (I) Epinephelus sp.,*
681 *right premaxilla (lateral view); (J) estuary view; (K) open sea view from the shore*

682

683 *Supplemental file 3. Illustration of different bones from main taxa at both sites and*
684 *possible fishing environment. Small pelagic fishes: (A) Selar crumenophthalmus, precaudal*
685 *vertebra (ventral view); (B) Clupeidae (cf. Sardinella longiceps), precaudal vertebra (ventral*
686 *view); (C) Alepes djedaba, first vertebra (ventral view); (D) Rastrelliger kanagurta, caudal*
687 *vertebra (lateral view); (E) Mugilidae, precaudal vertebra (ventral view). Juvenile demersal*
688 *fishes: (F) Pomadasys sp., first vertebra (ventral view); (G) Sparoidea, teeth; (H-I) Qurum*
689 *mangrove views*

690

691

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704
705 **DECLARATION OF INTEREST STATEMENT**

706 The authors declare that they have no conflict of interest.
707

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1024 *Journal of Physical Anthropology* 153 (3): 353–364. doi:10.1002/ajpa.22434.

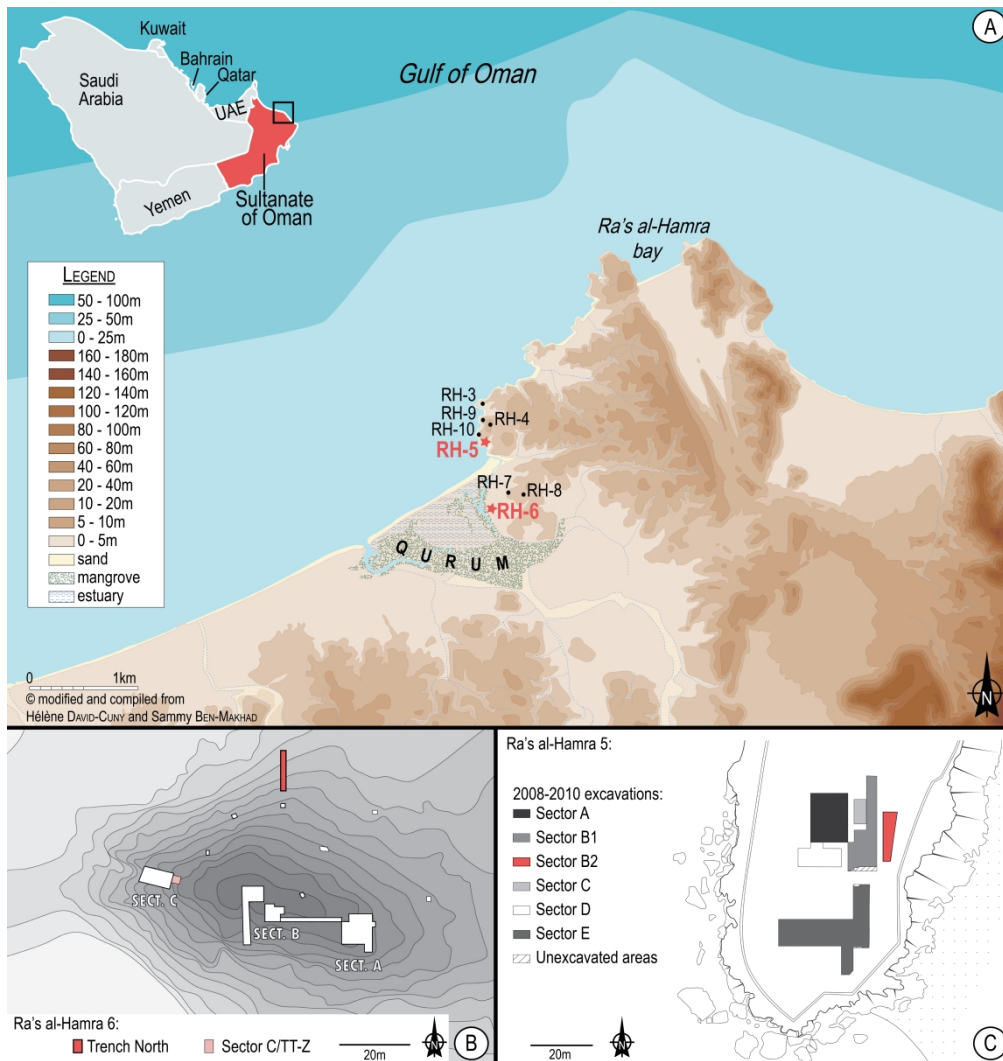


Figure 1. (A) Location, altitudinal and bathymetric mapping of the Qurum mangrove and the Ra's al-Hamra's cape, with location of the archaeological sites; (B) Map of the excavated sectors of RH-6 (Marcucci et al., 2014, fig. 1.A.); and (C) Map of the excavated sectors of RH-5 (Marcucci et al., 2011, fig. 2.)

923x973mm (150 x 150 DPI)

Main taxa	RH-6 (Uerpmann and Uerpmann)		RH-6 (Wilkens 2005)		RH-5 (Uerpmann and Uerpmann 2003)			M.A.F. (2018)		
	NISP	WISP	NISP	WISP	NISP	NISP %	WISP	Catches (tons)	%	% (without small pelagic)
Scombridae	23	9.1	311	-	7596	58.9	6527.4	49466	28.1	44.0
Carangidae	22	15.8	74	-	4065	31.5	5934.7	10572	6.0	9.4
Other pelagic fish	2	0.1	17	-	209	1.6	100.5	18203	10.3	16.2
Mugilidae	1	0.2	3	-	11	0.1	5.3	821	0.5	
Small pelagic fish	-	-	-	-	-	-	-	62897	35.7	
Sparidae	2	0.1	47	-	662	5.1	295.4	2533	1.4	2.3
Lethrinidae	-	-	19	-	150	1.2	117.4	5356	3.0	4.8
Serranidae	-	-	56	-	36	0.3	76.6	3359	1.9	3.0
Other demersal fish	1*	0.3	36	-	150	1.2	171.8	15243	8.6	13.5
Sharks/Rays	-	-	7	-	12	0.1	20.2	7777	4.4	6.9
Total NISP	51	25.6	570	0	12891	100	13249.3	176227	100	100

Table 1. Table synthesizing the main results from previous studies on the fish bone remains from RH-6 and RH-5 (for Uerpmann and Uerpmann 2003, NISP have been calculated from identified Actinopterygii and Chondrichthyes), and modern data of artisanal fishing from the governorate of Muscat for 2009-2018 (M.A.F. 2018). *Ariidae

Anatomical element		Total RH-6			Total RH-5
		Trench North (3 mm)	Sector C/TT-Z (3 mm)	Sector C/TT-Z (1 mm)	
Cranium	Dentary	528	496	6	23
	Premaxilla	353	508	10	31
	Maxilla	248	206	1	5
	Quadrate	179	263	4	12
	Opercle	187	209	6	7
	Anguloarticular	166	209	1	4
	Cleithrum	232	114	-	7
	Vomer	133	113	2	2
	Scapula	26	100	1	4
	Pharyngeal bone	49	63	-	1
	Tooth	41	50	406	215
	Hyomandibula	19	61	1	1
	Palatine	17	31	-	4
	Basioccipital/ Parasphenoid	66	50	13	50
	Otolith	-	1	21	2
	Other	248	289	-	44
	Vertebral column	First vertebra	284	127	707
Precaudal vertebra		2069	2103	4065	4349
Caudal vertebra		3211	3242	5257	2926
Other		712	231	1	14
Others	Pterygiophore	493	704	17	44
	Scale	-	-	41	-
	Scute	188	1	-	4
Chondr.	Tooth	2	-	2	2
	Vertebra	4	3	-	-
	Other	-	-	1	-
Unidentified remains		113325	46275	472	8559
Total		122780	55449	11035	17727

Table 2. Element distribution on the two sites according to the sector studied and the sieving mesh size (Chondr. = Chondrichthyes).

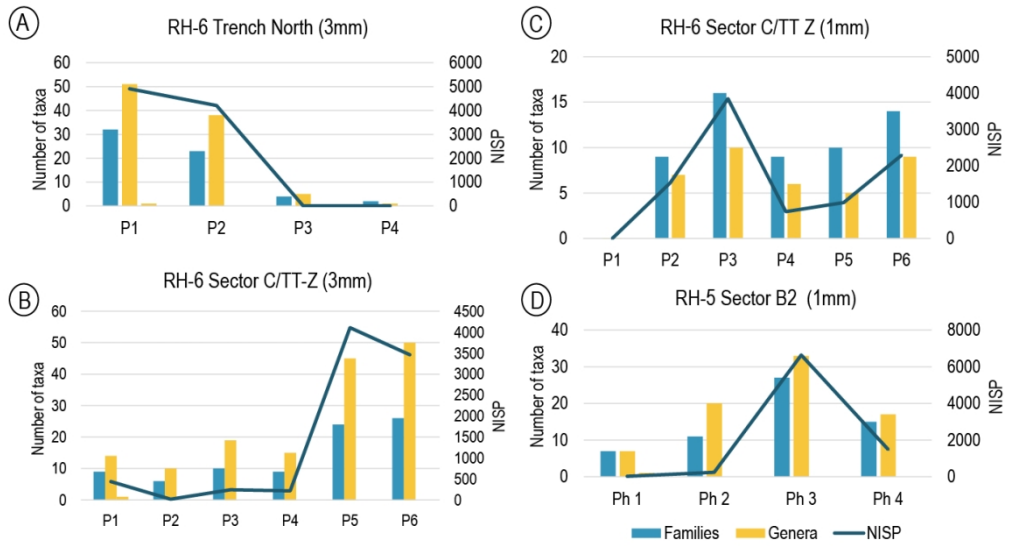


Figure 2. Taxonomic richness at family and genus levels for different sectors and time periods

233x127mm (150 x 150 DPI)

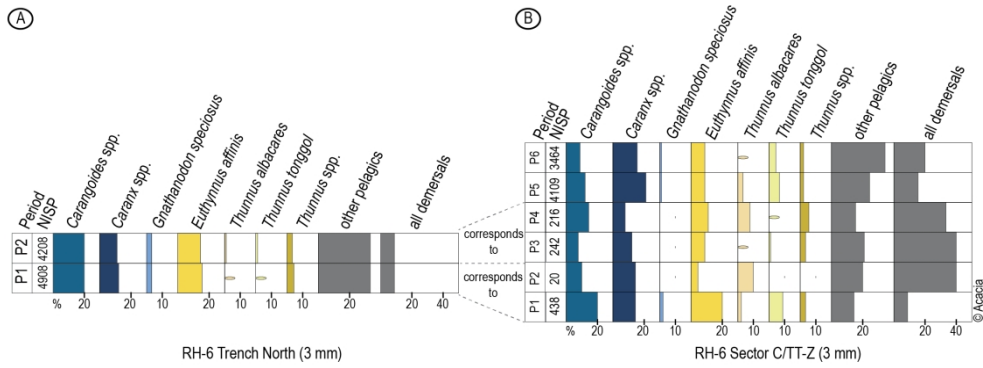


Figure 3. Illustration of the main taxa distribution (NISP).

(A) RH-6, Trench North, 3 mm; (B) RH-6, Sector C/TT-Z, 3 mm. Made with ACACIA (Nourissier, Nocus, and Dufraisse, 2010)

214x79mm (300 x 300 DPI)

Main taxa		Total Period 1			Total Period 2			Total		
		NISP	%	WISP	NISP	%	WISP	NISP	%	WISP
Carangidae	<i>Carangoides</i> spp.	986	20.09	786.21	852	20.2	618.3	1838	20.2	1404.51
	<i>Caranx</i> spp.	602	12.27	413.07	489	11.6	677.97	1091	12	1091.04
	<i>Gnathanodon speciosus</i>	180	3.67	111.44	147	3.5	154.23	327	3.6	2,65.67
	Other Carangidae	1278	26.04	398.45	1079	25.6	409.43	2357	25.9	807.89
Scombridae	<i>Euthynnus affinis</i>	775	15.79	506.04	609	14.5	377.02	1384	15.2	883.06
	<i>Thunnus albacares</i>	21	0.43	14.07	73	1.7	47.05	94	1	61.13
	<i>Thunnus tonggol</i>	4	0.08	2.48	47	1.1	24.01	51	0.6	26.48
	<i>Thunnus</i> spp.	239	4.87	133.52	146	3.5	82.37	385	4.2	215.89
	Other Scombridae	280	5.7	90.31	319	7.6	106.41	599	6.6	196.72
Other pelagic		98	2	16.23	51	1.2	12.1	149	1.6	28.33
Sparidae	<i>Acanthopagrus</i> spp.	58	1.18	13.84	34	0.8	114.25	92	1	128.09
	<i>Rhabdosargus</i> spp.	20	0.41	5.74	8	0.2	8.28	28	0.3	14.01
	Other Sparidae	44	0.9	16.53	94	2.2	45.51	138	1.5	62.03
Lethrinidae	<i>Lethrinus</i> spp.	80	1.63	19.18	110	2.6	23.75	190	2.1	42.93
	Other Lethrinidae				1	0	0.84	1	0	0.84
Serranidae	<i>Cephalopholis</i> spp.	39	0.79	4.61	21	0.5	7.15	60	0.7	11.76
	<i>Epinephelus</i> spp.	23	0.47	13.75	26	0.6	300.96	49	0.5	314.71
	Serranidae	27	0.55	7.03	20	0.5	28.07	47	0.5	35.09
Other demersal		154	3.14	36.57	82	1.9	27.9	236	2.6	64.47
Total pelagic		4463		2471.81	3812		2508.9	8275		4980.71
Total demersal		445		117.24	396		556.69	841		673.94
Unidentified fish		80701		13144.07	32906		5685.25	113607		18829.32
TOTAL NISP		4908	100	2589.05	4208	100	3065.59	9116	100	5654.64

Table 3. Zooarchaeological fish remains from RH-6, Trench North, 3 mm, according to periods in NISP, % of NISP and WISP (g) - Other pelagic (12 families; see Appendix), Other demersal (19 families; see Appendix)

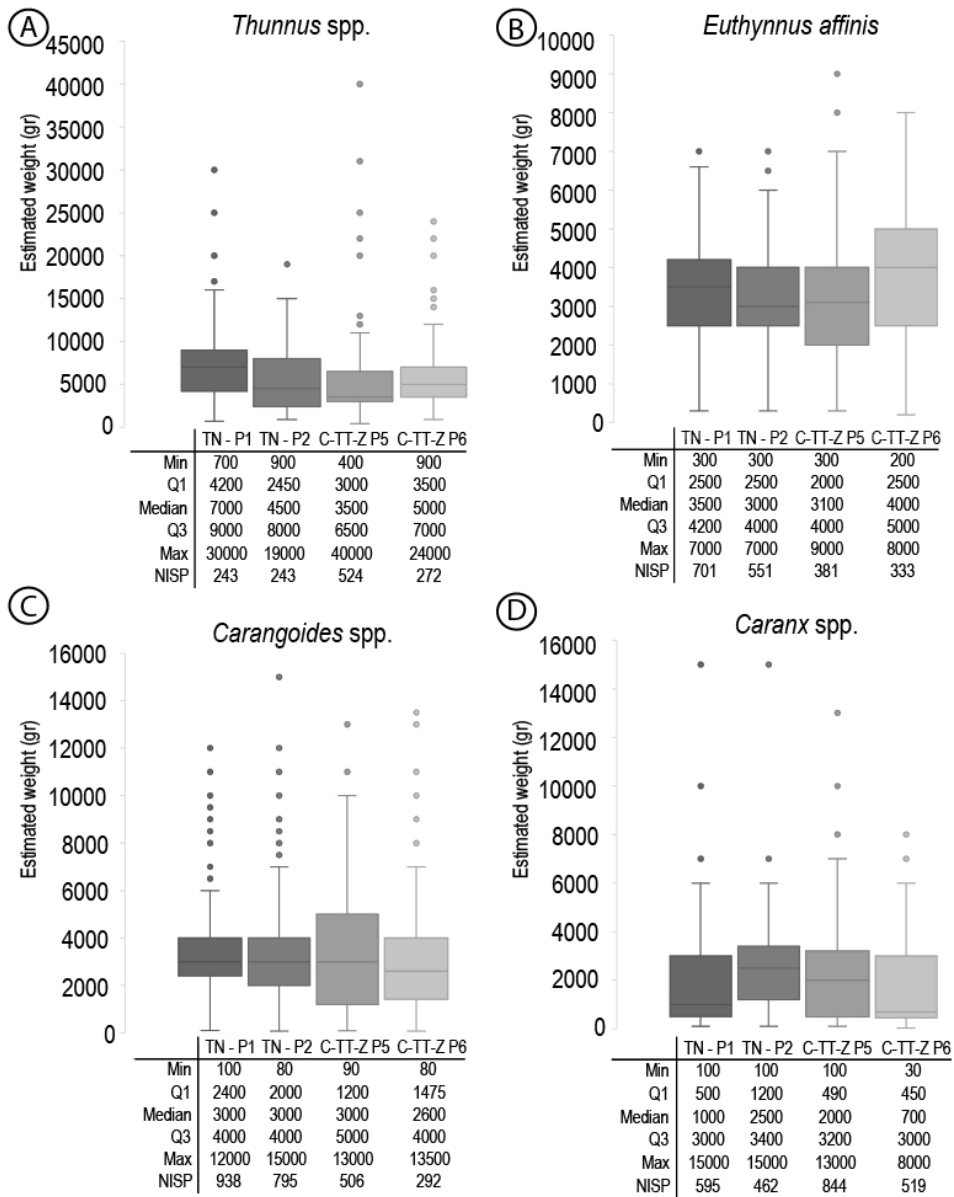


Figure 4. Illustration of the estimated weight of each main pelagic taxa from the richest RH-6 periods (P: Period), both sectors (TN: Trench North, C-TTZ: Sector C TT-Z). Min: Minimum, Max: Maximum, Q: Quartile. (A) *Thunnus* spp.; (B) *Euthynnus affinis*; (C) *Carangoides* spp.; (D) *Caranx* spp.

130x165mm (150 x 150 DPI)

Main taxa	Trench North				Sector C/TT-Z											
	P1		P2		P1		P2		P3		P4		P5		P6	
	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP
<i>Carangoides</i> spp.	180	986	168	852	39	92	1	2	9	19	14	32	109	527	68	308
<i>Caranx</i> spp.	110	602	133	489	23	67	2	3	14	31	14	18	128	876	99	542
<i>Gnathanodon speciosus</i>	35	180	35	147	9	13	-	-	-	-	-	-	22	62	18	50
<i>Euthynnus affinis</i>	72	775	58	609	14	89	1	1	6	24	6	24	53	388	58	342
<i>Thunnus albacares</i>	7	21	23	73	7	12	1	1	1	2	7	19	33	146	18	34
<i>Thunnus tonggol</i>	1	4	8	47	12	43	-	-	3	4	1	1	34	312	28	168
<i>Thunnus</i> spp.	34	239	23	146	2	15	-	-	5	10	5	12	7	111	5	92
Total	439	2807	448	2363	106	331	5	7	38	90	47	106	386	2422	294	1536

Table 4. MNI estimates of the main pelagic taxa at RH-6, 3 mm, according to periods and comparison with the NISP.

For Peer Review Only

Main taxa		Period 1			Period 2			Period 3			Period 4			Period 5			Period 6			Total		
		NISP	%	WISP	NISP	%	WISP	NISP	%	WISP	NISP	%	WISP	NISP	%	WISP	NISP	%	WISP	NISP	%	WISP
Carangidae	<i>Carangoides</i> spp.	92	21	65.12	2	10	0.59	19	7.9	6.49	32	14.8	38.77	527	12.8	316.49	308	8.9	1060.29	980	11.5	1487.75
	<i>Caranx</i> spp.	67	15.3	69.84	3	15	1.29	31	12.8	5.67	18	8.3	9.85	876	21.3	487.14	542	15.6	239.08	1537	18.1	812.87
	<i>Gnathanodon speciosus</i>	13	3	13.93										62	1.5	49.16	50	1.4	41.32	125	1.5	104.41
	Other Carangidae	62	14.2	33.87	3	15	2.53	21	8.7	5.28	22	10.2	6.08	870	21.2	200.76	1086	31.4	682.25	2064	24.3	930.77
Scombridae	<i>Euthynnus affinis</i>	89	20.3	58.56	1	5	0.24	24	9.9	8.38	24	11.1	7.37	388	9.4	252.34	342	9.9	271.25	868	10.2	598.13
	<i>Thunnus albacares</i>	12	2.7	6.82	2	10	1.62	2	0.8	0.4	19	8.8	9.92	146	3.6	73.67	34	1	18.62	215	2.5	111.05
	<i>Thunnus tonggol</i>	43	9.8	20.83				4	1.7	2.07	1	0.5	0.73	312	7.6	134.48	168	4.8	103.21	528	6.2	261.33
	<i>Thunnus</i> spp.	15	3.4	9.58				10	4.1	3.61	12	5.6	3.89	111	2.7	341.48	92	2.7	49.39	240	2.8	407.94
	Other Scombridae	2	0.5	0.48				9	3.7	1.56	11	5.1	2.07	79	1.9	30.92	99	2.9	17.71	200	2.4	52.73
	Other pelagic	4	0.9	1.96	1	5	0.03	23	9.5	2.04	3	1.4	1.56	89	2.2	11.13	30	0.9	10.72	150	1.8	27.45
Sparidae	<i>Acanthopagrus</i> spp.	6	1.4	6.47	1	5	0.26	30	12.4	5.13	8	3.7	1.29	127	3.1	25.99	136	3.9	13.46	308	3.6	52.6
	<i>Rhabdosargus</i> spp.	3	0.7	1.06	2	10	0.54	19	7.9	6.4	13	6	5.36	23	0.6	10.87	14	0.4	6.73	74	0.9	30.97
	Other Sparidae	2	0.5	0.75	3	15	0.31	8	3.3	1.76	8	3.7	0.53	41	1	14.23	53	1.5	10.01	115	1.4	27.6
Let.	<i>Lethrinus</i> spp.	16	3.7	5.36	1	5	0.05	20	8.3	2.32	16	7.4	3.38	218	5.3	41.79	208	6	27.23	479	5.6	80.13
Serranidae	<i>Cephalopholis</i> spp.	3	0.7	0.73				5	2.1	1.32	13	6	2.17	42	1	6.95	66	1.9	17.85	129	1.5	29.01
	<i>Epinephelus</i> spp.	4	0.9	1.88	1	5.0	0.21	7	2.9	0.9	1	0.5	0.12	62	1.5	11.59	61	1.8	16.23	136	1.6	30.94
	Other Serranidae	2	0.5	0.81				3	1.2	0.18	6	2.8	0.66	14	0.3	2.22	32	0.9	6.2	57	0.7	10.06
	Other demersal	3	0.7	1.53				7	2.9	1.03	9	4.2	6.49	122	3	34.19	143	4.1	22.12	284	3.3	65.36
	Total pelagic	399		280.97	12		6.31	143		35.5	142		80.24	3460		1897.57	2751		2493.83	6907		4794.42
	Total demersal	39		18.6	8		1.37	99		19.05	74		19.99	649		147.84	713		119.83	1582		326.66
	Unidentified fish				942		51.7	1336		96.17	1120		103.96	18337		2831.27	25225		3262.15	46960		6345.25
	TOTAL NISP	438	100	299.569	20	100	7.65	242	100	54.549	216	100	100.22	4109	100	2045.4	3464	100	2613.67	8489	100	5121.09

Table 5. Zooarchaeological fish remains from RH-6, Sector C/TT-Z, 3 mm, according to periods in NISP, % of NISP and WISP (g) - Other pelagic (5 families; see Appendix), Other demersal (24 families; see Appendix)

Main taxa	Period 2		Period 3		Period 4		Period 5		Period 6		Total	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Clupeidae	691	45.2	2486	64.7	539	72.8	825	83.4	1600	69.9	6141	65.4
Carangidae	452	29.6	822	21.4	85	11.5	90	9.1	274	12.0	1723	18.4
Atherinidae	212	13.9	155	4.0	34	4.6	9	0.9	237	10.4	647	6.9
Mugilidae	98	6.4	158	4.1	17	2.3	3	0.3	31	1.4	307	3.3
Other pelagic	1	0.1	6	0.2	44	5.9	22	2.2	35	1.5	108	1.2
Sparoidea	67	4.4	194	5.0	13	1.8	36	3.6	97	4.2	406	4.3
Other demersal	8	0.5	21	0.5	8	1.1	4	0.4	15	0.7	56	0.6
Total pelagic	1454		3627		719		949		2177		8926	
Total demersal	75		215		21		40		112		462	
Unidentified fish	224		417		399		139		468		1647	
Total NISP	1529	100	3842	100	740	100	989	100	2289	100	9388	100

Table 6. Zooarchaeological fish remains from RH-6, Sector C/TT-Z, 1 mm, according periods in NISP and % of NISP. Other pelagic (9 families; see Appendix), Other demersal (13 families; see Appendix)

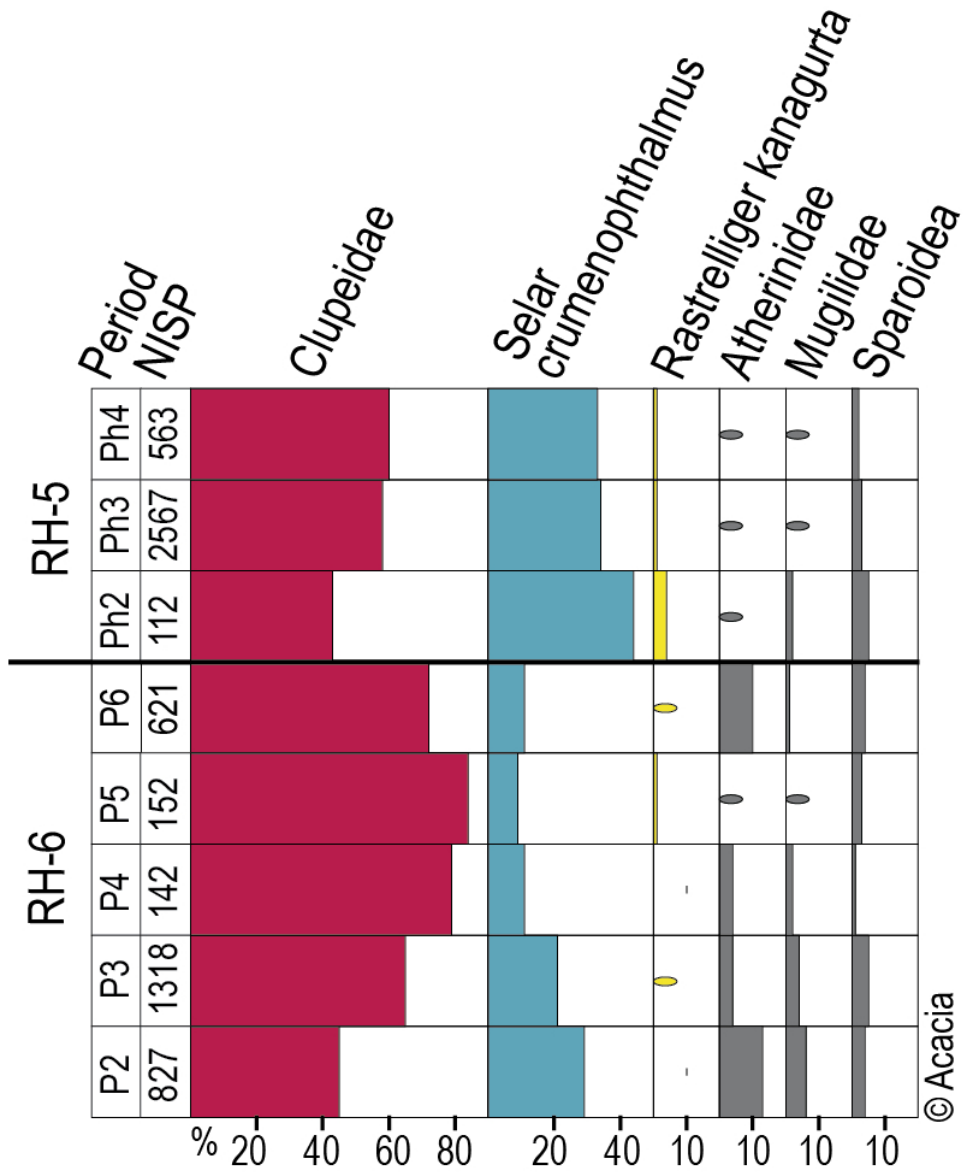


Figure 5. Illustration of the main taxa distribution (NISP).
 RH-6, Sector C/TT-Z, 1 mm (Periods 2, 3, 4, 5, 6) – RH-5, Sector B2, 1mm (Phases 2, 3, 4). Made with ACACIA (Nourissier, Nocus, and Dufraisse, 2010)

68x84mm (300 x 300 DPI)

Taxa		Phase 1			Phase 2			Phase 3			Phase 4			Total		
		NISP	%	WISP	NISP	%	WISP	NISP	%	WISP	NISP	%	WISP	NISP	%	WISP
Clupeidae		3	9.4	0.00	85	35.1	0.18	3668	55.2	9.92	863	57.8	2	4619	54.9	12.10
Carangidae	<i>Carangoides</i> spp.				2	0.8	1.49	8	0.1	2.55	1	0.1	0.01	11	0.1	4.13
	<i>Caranx</i> spp.	1	3.1	7.47	4	1.7	0.43	31	0.5	11.61	0	0.0	0	36	0.4	19.52
	<i>Selar crumenophthalmus</i>	8	25.0	0.06	88	36.4	0.43	2175	32.8	10.66	484	32.4	1.99	2755	32.8	13.14
	<i>Trachurus indicus</i>				5	2.1	0.05	61	0.9	0.31	17	1.1	0.08	83	1.0	0.44
	Other Carangidae	5	15.6	0.45	9	3.7	0.95	97	1.5	7.1	14	0.9	1.56	125	1.5	10.06
Scombridae	<i>Auxis thazard</i>	2	6.3	0.1				12	0.2	1.03	3	0.2	0.07	17	0.2	1.20
	<i>Euthynnus affinis</i>				8	3.3	2.31	34	0.5	6.66	3	0.2	0.98	45	0.5	9.95
	<i>Rastrelliger kanagurta</i>	3	9.4	0.06	8	3.3	0.15	109	1.6	2.06	24	1.6	0.18	144	1.7	2.45
	Other Scombridae				3	1.2	0.63	10	0.2	3.1	1	0.1	0.26	14	0.2	3.99
Mugilidae		1	3.1	0.03	5	2.1	0.1	45	0.7	0.51	13	0.9	0.11	64	0.8	0.75
Atherinidae					1	0.4	0	13	0.2	0.01	4	0.3	0	18	0.2	0.01
Sphyraenidae					3	1.2	0.52	43	0.6	0.69	7	0.5	0.08	53	0.6	1.29
Other pelagic							0	13	0.2	0.31		0.0		13	0.2	0.31
Sparoidea		8	25.0	0.47	10	4.1	0.57	225	3.4	5.91	38	2.5	1.37	281	3.3	8.32
Other demersal		1	3.1	0.04	11	4.5	0.51	96	1.4	4.15	20	1.3	0.18	128	1.5	4.89
Total pelagic		23		8.17	221		7.24	6319		56.52	1434		7.32	7997		79.34
Total demersal		9		0.51	21		1.08	321		10.06	58		1.55	409		13.21
Unidentified fish		91		4.90	608		26.78	7251		192.53	1371		31.80	9321		256.00
Total NISP		32	100	8.68	242	100	8.32	6640	100	66.58	1492	100	8.87	8406	100	92.55

Table 7. Zooarchaeological fish remains from RH-5, Sector B2, 1 mm, according to periods in NISP, % of NISP and WISP (g) - Other pelagic (7 families; see Appendix), Other demersal (20 families; see Appendix)

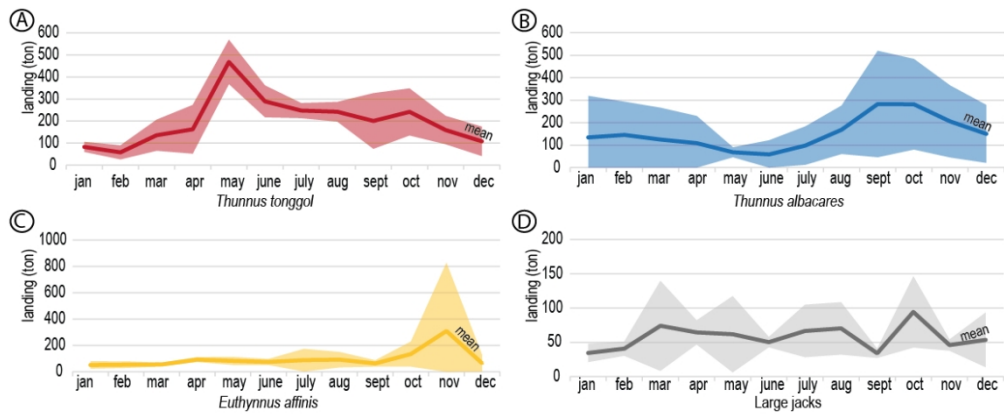


Figure 6. Compiled data (in metric tons) for 4 years (2013, 2015, 2016, 2018) of artisanal fisheries in Muscat governorate for *Thunnus tonggol*, *Thunnus albacares*, *Euthynnus affinis*, and large jacks (Carangidae) (M.A.F. 2013, 2015, 2016, 2018). The thick line represents the mean. The filled area is the standard deviation of the mean

199x81mm (150 x 150 DPI)

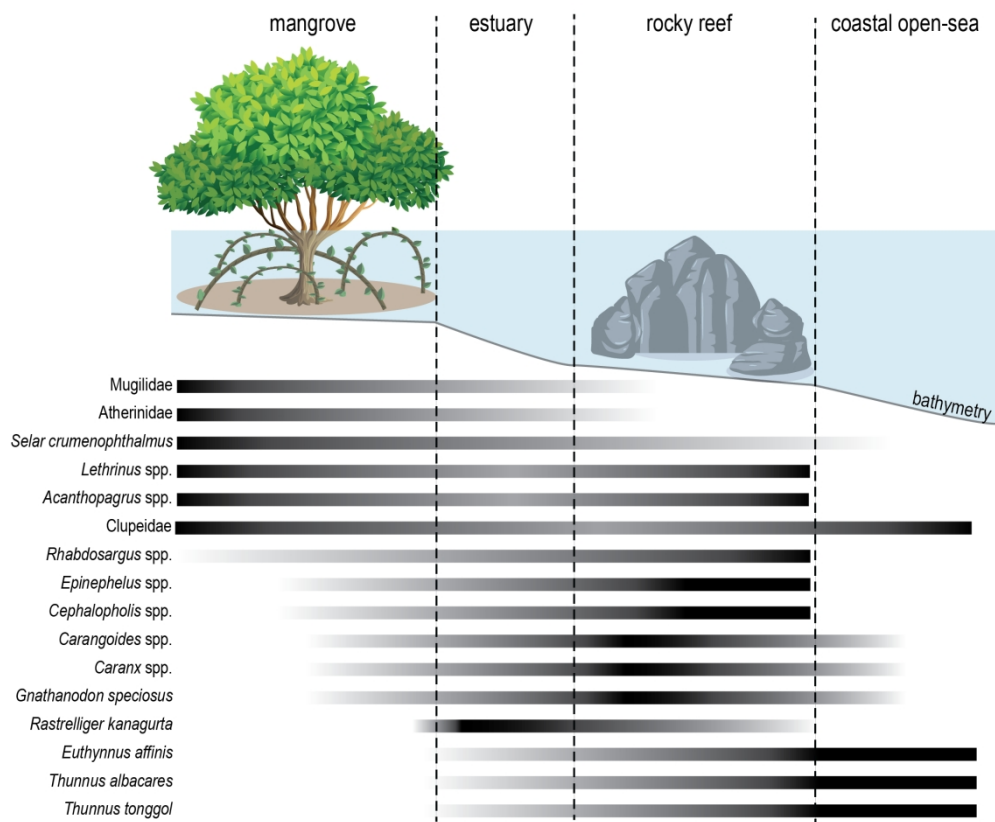


Figure 7. Ecological distribution of the main taxa found at both sites according to Froese and Pauly (2021), Randall (1995) and personal observations. Vector objects are from Vecteezy.com (Graphics RF)

178x147mm (300 x 300 DPI)

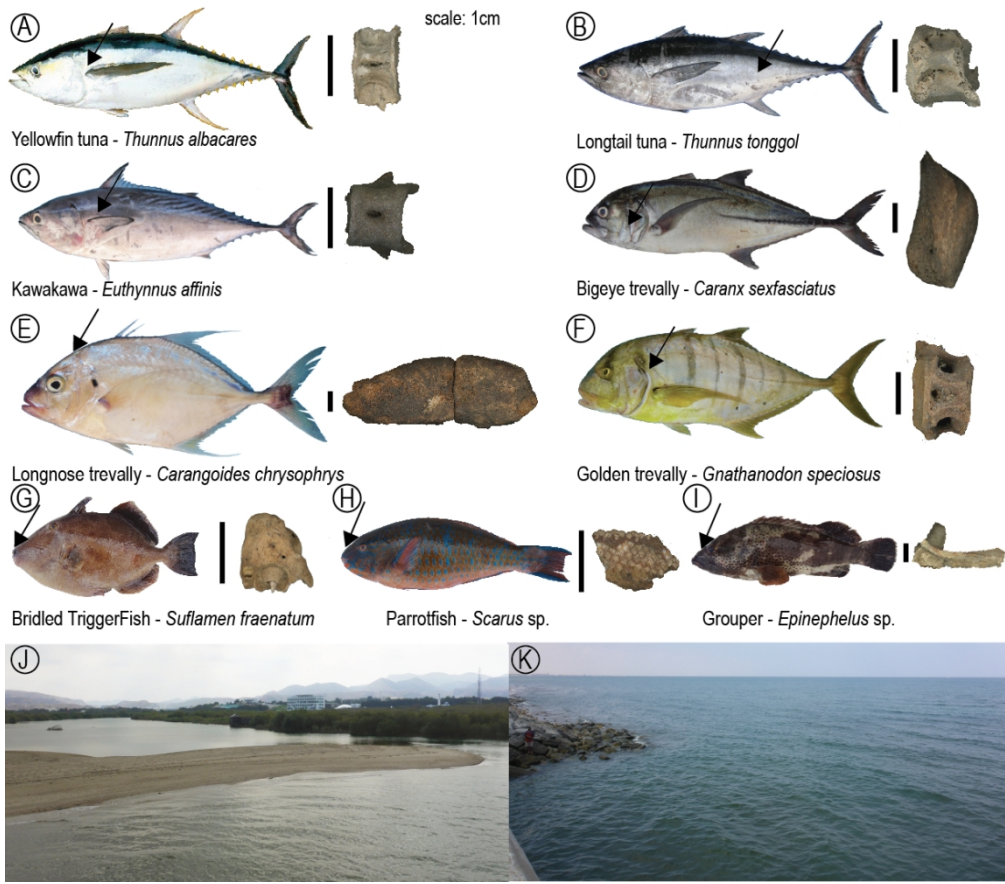
Higher taxa	Genus/Species	RH-6 Trench North	RH-6 Sector C/TT-Z	RH-6 Sector C/TT-Z - 1mm	RH-5 Sector B2	Habitat - Behavior
Selachimorpha					2	P
Carcharhinidae		5		1		P
Batoidea			1	2		D
Dasyatidae		1	2			D
Albulidae	<i>Albula</i> sp.		2			D
Muraenidae		3				B
	<i>Gymnothorax</i> spp.	5	5			B
Ophichthidae		2			1	B
Clupeidae		5		6141	4619	EP
Engraulidae				49		P
Chirocentridae	<i>Chirocentrus nudus</i>	2	4	1		P
Pristigasteridae	<i>Ilisha compressa</i>			31	1	P
Silluriformes				1		B
Plotosidae				11		B
Ariidae		13	3		3	D
	<i>Netuma bilineata</i>		3		1	D
	<i>Netuma</i> spp.	10	5			D
	<i>Plicofolis</i> spp.	2			1	D
Holocentridae	<i>Sargocentron</i> sp.		4			D
Stromateidae	<i>Pampus argenteus</i>	1				EP
Pomatomidae	<i>Pomatomus saltatrix</i>	1				P
Scombridae		435	118		8	P
	<i>Auxis thazard</i>	53	14		17	P
	<i>Euthynnus affinis</i>	1384	868		45	P
	<i>Katsuwonus pelamis</i>	82	42			P
	<i>Rastrelliger kanagurta</i>	27	17	22	144	P
	<i>Sarda orientalis</i>	1	2		2	P
	<i>Scomber australasicus</i>		4			P
	<i>Scomberomorus commerson</i>	1	3			P
	<i>Thunnus albacares</i>	94	215			P
	<i>Thunnus tonggol</i>	51	528			P
	<i>Thunnus</i> spp.	385	240		4	P
Trichiuridae	<i>Trichiurus</i> sp.	1				P
Sphyraenidae	<i>Sphyraena acutipinnis</i>		3			P
	<i>Sphyraena jello</i>		10			P
	<i>Sphyraena putnamae</i>	3	4			P
	<i>Sphyraena qenie</i>	1				P
	<i>Sphyraena</i> spp.	81	97	2	53	P
Polynemidae	<i>Eleutheronema tetradactylum</i>				1	D
Paralichthyidae	<i>Pseudorhombus</i> sp.	1				P

Carangidae		2248	1797	27	82	P
	<i>Alectis indica</i>		7			P
	<i>Alepes djedaba</i>	27	2	8	3	P
	<i>Alepes vari</i>		1		1	P
	<i>Alepes</i> spp.	9	9		1	P
	<i>Carangoides bajad</i>		106			P
	<i>Carangoides chrysophrys</i>	14	79			P
	<i>Carangoides equula</i>	2				P
	<i>Carangoides ferdau</i>	10			1	P
	<i>Carangoides fulvoguttatus</i>	4	248			P
	<i>Carangoides gymnosthetus</i>	10				P
	<i>Carangoides</i> spp.	1800	547		10	P
	<i>Caranx heberi</i>	1	180			P
	<i>Caranx ignobilis</i>		185			P
	<i>Caranx sexfasciatus</i>	107	386		8	P
	<i>Caranx</i> spp.	981	786	1	28	P
	<i>Decapterus macarellus</i>	2	1		1	P
	<i>Elagatis bipinnulata</i>	2	4		2	P
	<i>Gnathanodon speciosus</i>	327	125		1	P
	<i>Scomberoides commersonianus</i>		7			P
	<i>Scomberoides tol</i>		7		1	P
	<i>Scomberoides</i> spp.	13	13	2		P
	<i>Selar crumenophthalmus</i>	50	188	1677	2755	P
	<i>Selaroides leptolepis</i>				31	P
	<i>Seriola dumerili</i>	1	14			P
	<i>Seriolina nigrofasciata</i>		2			P
	<i>Trachinotus</i> spp.	4		8	2	P
	<i>Trachurus indicus</i>	1	12		83	P
Rachycentridae	<i>Rachycentron canadum</i>	9				P
Atherinidae				647	18	P
Belonidae		12	10	2	3	P
	<i>Albennes hians</i>	10				P
	<i>Tylosorus choram</i>				3	EP
	<i>Tylosurus crocodilus</i>				3	EP
	<i>Tylosurus</i> spp.	8	5		1	EP
Mugilidae		9	17	307	64	P
Drepaneidae	<i>Drepane</i> sp.		1			D
Chaetodontidae		1		4	5	D
Ephippidae			1			D
Siganidae	<i>Siganus</i> sp.	1	1	2	1	D
Acanthuridae		1				D
	<i>Acanthurus</i> spp.	3	2			D
	<i>Naso</i> spp.		4			D
Tetraodontiformes			2			D
Diodontidae		1				D
	<i>Diodon hystrix</i>		1			D

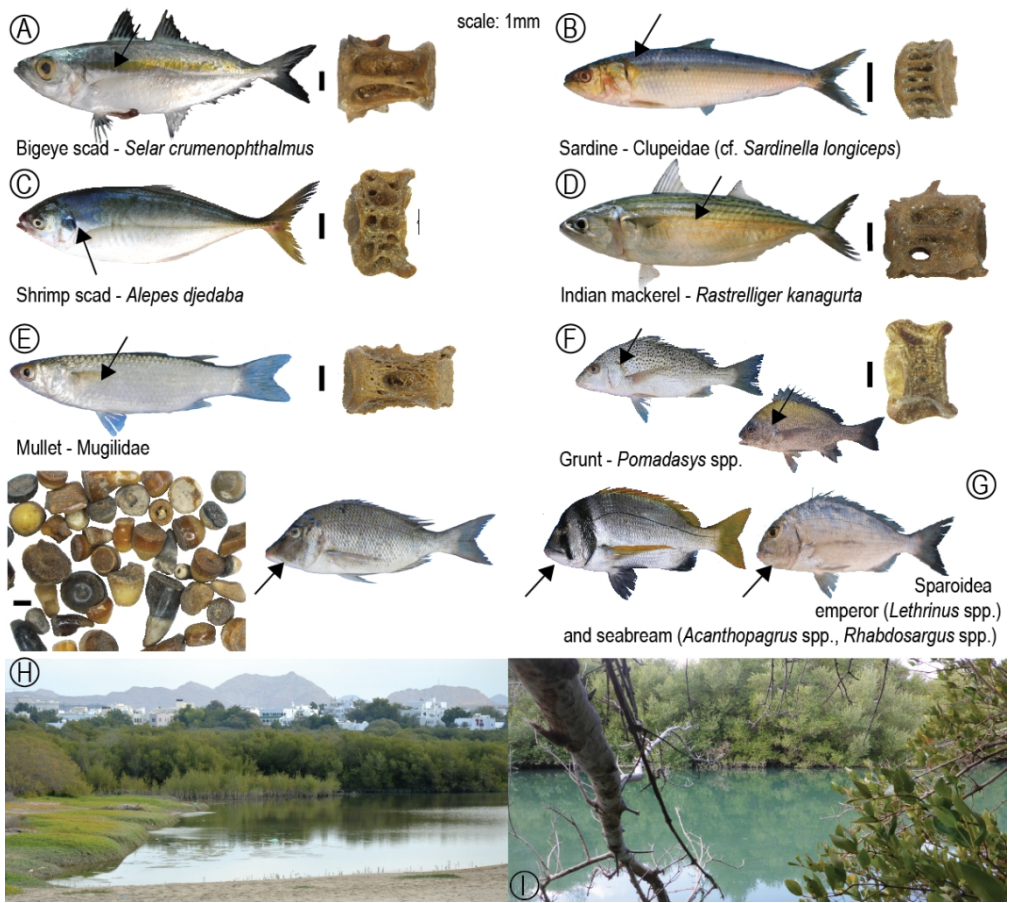
Tertraodontidae			1			D
Balistidae		6	4		1	D
	<i>Abalistes stellatus</i>		1			D
	<i>Balistoides viridescens</i>	1	1			D
	<i>Canthidermis macrolepis</i>		1			D
	<i>Odonus niger</i>	1				D
	<i>Sufflamen fraenatum</i>	5	33			D
Terapontidae	<i>Terapon jarbua</i>	12	8	1	4	D
Ambassidae				15		D
Serranidae		47	56	7	8	D
	<i>Cephalopholis hemistiktos</i>	1	22			D
	<i>Cephalopholis sexmaculata</i>	2	23			D
	<i>Cephalopholis</i> spp.	57	84	1	5	D
	<i>Epinephelus coioides</i>		1			D
	<i>Epinephelus diacanthus</i>	1	2			D
	<i>Epinephelus radiatus</i>		3			D
	<i>Epinephelus stoliczkae</i>	4	6			D
	<i>Epinephelus</i> spp.	44	124		5	D
	<i>Plectropomus</i> sp.		1			D
Apogonidae	<i>Apogon</i> sp.	1				D
Sillaginidae	<i>Sillago</i> spp.	1		6	6	D
Lutjanidae	<i>Lutjanus coeruleolineatus</i>		6			D
	<i>Lutjanus ehrenbergii</i>		5			D
	<i>Lutjanus fulviflamma</i>		4			D
	<i>Lutjanus indicus</i>		2			D
	<i>Lutjanus</i> spp.	10	38	3	49	D
Caesionidae	<i>Caesio</i> sp.				1	D
Gerreidae	<i>Gerres</i> spp.	2		3	13	D
Haemulidae		10			4	D
	<i>Plectorhinchus gaterinus</i>		2			D
	<i>Plectorhinchus pictus</i>		3			D
	<i>Plectorhinchus schotaf</i>		2			D
	<i>Plectorhinchus</i> spp.	8	26		1	D
	<i>Pomadasys argenteus</i>		4			D
	<i>Pomadasys commersonnii</i>		1			D
	<i>Pomadasys</i> spp.	52	33		12	D
Sparoidea		23	43	265	179	D
Sparidae		80	94	130	37	D
	<i>Acanthopagrus bifasciatus</i>	1	6			D
	<i>Acanthopagrus</i> spp.	91	302		21	D
	<i>Argyrops spinifer</i>	20	14			D
	<i>Argyrops</i> spp.	35	2			D
	<i>Rhabdosargus haffara</i>		23			D
	<i>Rhabdosargus</i> spp.	28	51		1	D
	<i>Sparidentex hasta</i>	3	5			D
Lethrinidae	<i>Gnathodentex aureolineatus</i>	1				D

	<i>Lethrinus borbonicus</i>		4			D
	<i>Lethrinus lentjan</i>	2	26			D
	<i>Lethrinus mahsena</i>		1			D
	<i>Lethrinus microdon</i>	1	49			D
	<i>Lethrinus nebulosus</i>	3	29			D
	<i>Lethrinus</i> spp.	184	370	11	42	D
Nemipteridae			5		1	D
Sciaenidae		6	2			D
	<i>Argyrosomus</i> sp.		1			D
	<i>Umbrina</i> sp.	2				D
Mullidae			4			D
Pomacentridae					1	D
Labridae			3		4	D
	<i>Cheilinus</i> sp.	1				D
	<i>Choerodon robustus</i>		1			D
	<i>Coris</i> sp.		2			D
Scaridae		26	5		1	D
	<i>Chlorurus</i> sp.	4				D
	<i>Scarus ghobban</i>	3				D
	<i>Scarus</i> spp.	16	6			D
Platycephalidae		3				B
	Total NISP	9116	8489	9388	8406	

Supplemental file 1. List and NISP of taxa recovered at RH-6 and RH-5, arranged in taxonomic order. B: benthic; D: demersal; EP: epipelagic; P: pelagic. For fish behaviour, we followed the information from Randall (1995) and FishBase (Froese and Pauly 2021).



210x185mm (150 x 150 DPI)



204x184mm (150 x 150 DPI)