

1 **Late Pleistocene-Holocene coastal adaptation in central Mediterranean:**
2 **snapshots from Grotta d’Oriente (NW Sicily)**

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24
25 **Abstract**

26 Marine faunal remains from Grotta d’Oriente (Favignana Island, NW Sicily) offer invaluable
27 snapshots of human-coastal environment interaction in the central Mediterranean from the
28 Late Pleistocene to the Middle Holocene. The long-term shellfish and fish records reflect
29 human exploitation of coastal environments undergoing considerable reorganizations
30 during the postglacial sea level rise and the progressive isolation of Favignana from
31 mainland Sicily. We detected an intensification of marine resource exploitation between
32 ~9.6 ka and ~7.8 ka BP, which corresponds with the isolation of Favignana Island and, later
33 on, with the introduction of early agro-pastoral economy in this region. We suggest that a
34 higher investment in marine resource exploitation by late foragers and early farmers in NW
35 Sicily was also supported by an increase in marine productivity in the south Tyrrhenian Sea
36 in the Middle Holocene.

37
38 **Keywords**

39 Central Mediterranean, NW Sicily, Upper Palaeolithic to Early Neolithic, coastal adaptation,
40 environmental change

41

42 **1. Introduction**

43

44 Over the last decades human adaptation to coastal environments has gained increasing
45 consideration in debates around cultural variability and subsistence strategies among Late
46 Pleistocene and Holocene foraging societies in the Mediterranean. The nature of these
47 interactions varied from food provision to raw materials for symbolic/communication
48 systems (shell ornaments), and likely responded to interplaying cultural and natural factors
49 such as regional variability in marine productivity, environmental and climate changes and a
50 variety of cultural interactions across the basin over time (Tagliacozzo, 1994; Tortosa et al.,
51 2002; Stringer et al., 2008; d'Errico et al., 2009; Colonese et al., 2011; Cortés-Sánchez et al.,
52 2011; Lightfoot et al., 2011; Mannino et al., 2011b; 2012; 2015; Mylona, 2014; López de
53 Pablo et al., 2016; Perlès, 2016; Prendergast et al., 2016; Ramos-Muñoz et al., 2016;
54 Hoffmann et al., 2018).

55

56 From a dietary perspective it is likely that Late Pleistocene and Holocene foragers from this
57 region exploited marine resources as complementary sources of food within subsistence
58 strategies dominated by high-ranked and more profitable prey such as large terrestrial
59 mammals (Stiner and Kuhn, 2006). This is generally supported by stable isotope data
60 revealing that Palaeolithic and Mesolithic diets in Mediterranean coastal areas were
61 dominated by terrestrial resources (Francalacci, 1988; Vigne, 2004; Paine et al., 2009; Craig
62 et al., 2010; Lightfoot et al., 2011; Mannino et al., 2011a; 2011b; 2012; Goude et al., 2017).
63 Nevertheless there is considerable variability in this narrative as some stable isotope studies
64 also demonstrate that fish and sea mammals occasionally provided substantial dietary
65 proteins, particularly to Early and Middle Holocene foragers (Pouydebat, 1997; Bocherens,
66 1999; Costa et al., 2003; Garcia Guixé et al., 2006; Salazar-García et al., 2014; Mannino et al.,
67 2015; Cristiani et al., 2018), during a time interval punctuated by episodes of intense fishing
68 and shellfish exploitation around the basin (Galili et al., 2003; Aura et al., 2009; Colonese et
69 al., 2011; Hunt et al., 2011; Mylona, 2014; Rainsford et al., 2014; Perlès, 2016).

70

71 In the central Mediterranean, more precisely in Sicily, a remarkable increase in marine
72 exploitation has been observed during the Early and Middle Holocene possibly due to a
73 combination of population growth and increased territoriality, resource depletion on land,
74 abrupt climate change and introduction of new technologies with the maritime spread of
75 agro-pastoral economy (Tagliacozzo, 1993; Mannino and Thomas, 2009; Mannino et al.,
76 2011a; 2015). However, only a handful of archaeological sites in Sicily provide sufficient
77 contextual stratigraphic, chronological and qualitative information on fish and shellfish
78 remains to derive detailed snapshots of marine resource use through time. Here we provide
79 a novel contribution to these debates. Based on the most recent archaeological excavations
80 at Grotta d'Oriente on the island of Favignana (Sicily), we discuss the role of marine

81 resources in the central Mediterranean during the Upper Palaeolithic, Early Mesolithic and
82 Late Mesolithic/Early Neolithic. The study area was an extremely dynamic coastal
83 environment during the Late Pleistocene and Early Holocene, when Favignana was gradually
84 isolated from Sicily, becoming an island during the Middle Holocene. This time interval also
85 witnessed a remarkable increase in marine productivity and major cultural changes in NW
86 Sicily with the transition from foraging to farming. Marine faunal remains from Grotta
87 d’Oriente provide invaluable information on this long-term process, and offer new elements
88 for discussing the nature and development of human interaction with Mediterranean
89 coastal ecosystems in prehistoric times.

90

91 **2. Archaeological setting**

92

93 **2.1. *Grotta d’Oriente***

94

95 The island of Favignana, the largest (~20 km²) of a group of small islands forming the Egadi
96 Archipelago, is situated ~5 km from the NW coast of Sicily (Fig. 1A). There, Grotta d’Oriente
97 (ORT) opens on the north-eastern slope of Montagna Grossa, overlooking the sea at ~40 m
98 above sea level. The cave has two distinct areas, a small chamber to the left of the entrance
99 (south) and a large gallery to the right (north) (Martini et al., 2012). Previous excavations
100 were conducted in the small chamber in 1972 (Mannino, 1972; 2002; Mannino et al., 2012;
101 2014), and it was excavated again in 2005 as part of an interdisciplinary project carried out
102 by the University of Florence and Museo Fiorentino di Preistoria. The results presented in
103 this study are part of this multidisciplinary research programme and details of the
104 stratigraphy, material culture and burial practice can be found in Lo Vetro and Martini
105 (2006) and Martini et al. (2012).

106

107 The excavations in 2005 shed light on an archaeological deposit (~1.5 m thick) spanning
108 from the Late Pleistocene to the Middle Holocene. The coherent stratigraphic distribution of
109 the ¹⁴C dates on charcoal (Table 1) suggests that the existing sedimentary record retained its
110 general stratigraphic and cultural integrity. Despite this, several chronological hiatuses and
111 some stratigraphic disturbances were recorded between, as well as within, the Late
112 Pleistocene and Holocene deposits. Discrete archaeological layers were radiocarbon dated
113 to the late Upper Palaeolithic (layer 7; ~14.2 cal ka BP), Early Mesolithic (layer 6; ~9.7 and
114 9.6 cal ka BP), and Late Mesolithic or Early Neolithic (layers 5; ~7.8 cal ka BP). These cultural
115 deposits were further divided into sublayers, each corresponding to different paleosurfaces
116 which are often characterized by hearths (more or less structured) and pits.

117

118 Stone tool assemblages relate these archaeological layers and sublayers to different cultural
119 entities, each of which fits into the cultural framework known for the late Upper Palaeolithic
120 and Mesolithic of Sicily (Lo Vetro and Martini, 2012). Layer 7 (sublayers 7A-E) contains

121 typical Late Epigravettian assemblages, layer 6 (sublayers 6A-6D) is characterized by a
122 Sauveterrian-like technocomplex, while layer 5 instead presents a stone assemblage marked
123 by the presence of blades and trapezes, and by the appearance of the pressure blade
124 technique (Lo Vetro and Martini, 2016).

125

126 The archaeological sequence overlapped a deposit (layer 8) containing only rare Pleistocene
127 continental fauna remains with no evidence of human activity (Fig. 1C). The top of the late
128 Upper Palaeolithic deposit (sublayer 7A) presented evidence of a natural erosion (probably
129 due to water runoff) and intrusion of Mesolithic artefacts from subsequent occupations. The
130 Mesolithic disturbance was confirmed by a radiocarbon date obtained from charcoal (10145
131 - 9546 cal BP), therefore the archaeological materials from sublayer 7A have been excluded
132 from our analysis (see also Martini et al., 2012). Sediment mixing was evident along the cave
133 wall and the archaeological evidence resulting from these deposits was systematically
134 excluded from our analysis.

135

136 The cultural attribution of sublayers 5A - 5C could be associated either to the Late
137 Mesolithic or the Early Neolithic (Lo Vetro and Martini, 2016). The only ¹⁴C date available for
138 layer 5, obtained from the top of the deposit (sublayer 5A), is contemporaneous with the
139 Early Neolithic of Grotta dell'Uzzo (NW Sicily) (Collina, 2016). No pottery remains were
140 recovered, however domestic faunal remains (*Ovis vel Capra*) and obsidian flakes, although
141 rare, were found in sublayers 5A and 5C. The scant stone tool assemblage (Martini et al.
142 2012; Lo Vetro and Martini 2016) might be comparable both to the Castelnovian and the
143 Early Neolithic industries found at Grotta dell'Uzzo (Collina, 2016). Sublayers 5A - 5C are
144 thus associated to the Late Mesolithic (Castelnovian) or the Early Neolithic (hereafter
145 referred to as Late Mesolithic/Early Neolithic) as it is impossible to exclude either of the two
146 cultural attributions based on the related archaeological record. Although the chronology
147 and paucity of domestic faunal remains and obsidian could suggest an Early Neolithic
148 occupation, the occurrence of these items could also attest to contact between the latest
149 Mesolithic groups and the earliest Neolithic communities which could have cohabited in NW
150 Sicily at that time (Lo Vetro and Martini, 2016).

151

152 Several perforated marine shells, presumably used as ornaments, were also found at ORT.
153 Their taxonomic and technological composition provide further insights into the cultural
154 origin of the prehistoric deposits. Worth noting is the recovery from sublayer 5C of one
155 perforated shell of *Columbella rustica* with longitudinal incisions (Cilli et al., 2012; Martini et
156 al., 2012). Identical specimens have exclusively been found in Mesolithic deposits in NW and
157 E Sicily, including one shell from Isolidda (Lo Vetro et al., 2016), one from Grotta dell'Uzzo
158 (Tagliacozzo, 1993), and one from Perriere Sottano (Aranguren and Revedin, 1994). Taken
159 together, this evidence points toward a well-established shell ornament-symbolic tradition
160 shared by Mesolithic groups living across Sicily (Lo Vetro et al., 2016).

161

162 Upper Palaeolithic and Mesolithic human burials were also discovered at ORT. An adult
163 female (burial *Oriente C*) was found in layer 7 and has been chronologically attributed to the
164 late Upper Palaeolithic (Late Epigravettian) based on radiocarbon dating of charcoal from
165 sublayer 7D, where the funerary grave was opened (Lo Vetro and Martini, 2006; Martini et
166 al., 2012). Sublayer 7D was covered by sublayers 7A-C which provided stone tool
167 assemblages attributed to Late Epigravettian. Moreover the deposit underneath (sublayer
168 7E) provided a radiocarbon date comparable with sublayer 7D (Table 1). *Oriente C* had been
169 partially disturbed when the initial excavations in 1972 intercepted the grave (Lo Vetro and
170 Martini, 2006). Two shells of *Pirenella conica* from Layer 7E were dated to the Early
171 Holocene (shell 7E1: 9,715±35 BP, CNA822 and shell 7E2: 9,130±35 BP, CNA823), confirming
172 some stratigraphic disturbance. Other human burials were recovered in 1972 (*Oriente A* and
173 *Oriente B*), together with at least 40 human remains retrieved outside burial contexts
174 (Mannino, 1972, 2002; D'Amore et al., 2010; Mannino et al., 2012). While the chronological
175 attribution of *Oriente A* (adult male) remains a matter of debate, the Early Mesolithic origin
176 of *Oriente B* (adult female) is supported by a direct ¹⁴C date of ~10.6 ka cal BP (D'Amore et
177 al., 2010; Mannino et al., 2012). The ulna of a possible fourth individual (*Oriente X*) retrieved
178 in 1972 has been recently ¹⁴C dated to ~9.6 ka cal BP (Mannino et al., 2012), roughly
179 corresponding with the dates from the Mesolithic layer 6.

180

181 2.2. *Environmental setting*

182

183 Favignana underwent dramatic environmental changes from the Late Pleistocene to the
184 Middle Holocene, following the postglacial submersion of its continental shelf, which
185 culminated in its isolation from Sicily sometime between 8 and 7 ka cal BP (Agnesi et al.,
186 1993; Antonioli et al., 2002). According to postglacial sea level curves from NW Sicily and the
187 Italian Peninsula (Antonioli et al., 2002; Lambeck et al., 2004), the cave must have been
188 located ~3 to ~4 km inland during the Upper Palaeolithic occupation (layer 7), when the
189 relative sea level was ~90 m lower than present day and Favignana was part of Sicily (see
190 also Mannino et al., 2014). During the Early Mesolithic (layer 6) the sea level was ~40 to ~50
191 m below that of present day and the cave was located ~1 km from the coast. Abrupt
192 changes in coastal areas must have occurred with the submersion of the coastal plain and
193 the isolation of Favignana when the cave was visited by Late Mesolithic/Early Neolithic
194 groups (layer 5). At that time the sea level was ~15 m below the present day.

195

196 3. **Materials and methods**

197

198 3.1. *Faunal remains*

199

200 Mollusc, crustacean, echinoderm and fish remains were retrieved from the bulk sediments

201 through wet sieving using a 1 mm mesh. The remains were identified using reference
202 collections located in several Italian institutions, including the University of Pisa, University
203 of Florence, La Specola Museum, and the Civic Natural History Museum of Verona.
204 Taxonomic identification and quantification was supported by specialised literature (Monod,
205 1968; Kusaka, 1974; Wilkens, 1986; Wheeler and Jones, 1989; Stewart, 1991; Watt et al.,
206 1997; Albertini and Tagliacozzo, 2000; Doneddu and Trainito, 2005; Campbell 2008; Zohar et
207 al., 2008; Peres, 2010). The nomenclature follows the World Register of Marine Species
208 (<http://www.marinespecies.org/index.php>; last access May 2017) while the ecological
209 attributions refer to the European Union Habitats Directive
210 (http://ec.europa.eu/environment/nature/natura2000/marine/index_en.htm) and FishBase
211 (<http://www.fishbase.org/>).

212
213 Recent studies have shown that *Patella caerulea* and *Patella ulyssiponensis* cannot be
214 reliably distinguished using shell morphology (Mauro et al., 2003; Petraccioli et al., 2010;
215 Sanna et al., 2012). Thus shells with characteristics typically associated to these species
216 (e.g., Doneddu and Trainito, 2005) were considered as *P. caerulea/ulyssiponensis*.

217
218 Crustacean, echinoderm and fish remains were quantified to the number of identified
219 specimens (NISP) and the minimum number of individuals (MNI) using approaches specific
220 for each type of remain. Mollusc remains were quantified for the MNI only. The MNI was
221 estimated using the highest number of left or right chelipeds for crustaceans, the highest
222 number of anatomical plates for echinoderms (e.g. genital, buccal, ambulacral and
223 interambulacral), the number of apices for gastropods, the highest number of whole valves
224 (left or right) and fragments with umbo for bivalves, and the left or right cranial and
225 vertebral elements for fish. Fish remains were measured according to established protocols
226 (Wilkens, 1986; Wheeler and Jones, 1989; Zohar et al., 2001; Orchard, 2005; Thieren et al.,
227 2012) and compared with reference collections. Moray remains were measured using
228 approaches described for eel in Thieren et al. (2012), due to the high variability in size-class
229 and vertebral elements.

230
231 In order to explore diachronic variations within each faunal category we standardised the
232 faunal indicators (NISP, MNI) for the total volume of sediment (m³) for each archaeological
233 sublayer (e.g. Zangrando, 2009; Jerardino, 2016; Perlès, 2016). This approach inherently
234 assumes constant deposition rates, in addition to minimal differences in sedimentary
235 matrix, preservation conditions through the succession (Jerardino, 1995; 2016) and the non-
236 contiguous distribution of the remains when the sedimentary deposits include structures
237 such as hearths and pits. Due to the limited number of radiocarbon dates, the deposition
238 rate could be estimated only between sublayers 6B and 6D (2.06 m/ka). However, the
239 average volume of sediment per unit area at 9.6 cal ka BP (0.13 m³, sublayers 6B and 6C)
240 and 14.2 ka cal BP (0.11 m³, sublayers 7D and 7E) suggest comparable depositional rates in

241 most parts of the deposit. The nature of the sedimentary matrix has not been studied in
242 detail, however according to field observations there were few differences between layers 5
243 and 6, which were mainly composed of silts and sand typically found in active karst settings
244 (Woodward and Goldberg, 2001). In contrast, layer 7 showed an increase in clay and
245 considerably lower anthropogenic deposits (for faunal remains see below). Finally, the
246 presence of fish and small fragile shell remains (e.g. freshwater) is clear evidence of good
247 overall preservation (see below). Shell fragmentation is minor and prevalently related to
248 food processing (in the case of *P. turbinatus*) as well as *post-mortem* taphonomic processes
249 prior to shell transport into the cave for non-food taxa (see below).

250

251 Statistical analyses were performed using PAST 3.06 (Hammer et al., 2001). Correspondence
252 Analysis (CA) was used to derive environmental information from taxonomic composition,
253 abundance and frequency of mollusc and fish remains through the stratigraphy. Taxonomic
254 diversity was explored using the Shannon diversity index (H), which takes into account the
255 abundance and evenness of species (but also genera and families) within and between
256 sublayers.

257

258 3.2. *Intra-crystalline protein diagenesis and stable isotopes of Phorcus turbinatus* 259 *shells.*

260

261 Chiral amino acid analysis (or amino acid racemization, AAR) was applied to shells of *Phorcus*
262 *turbinatus* with the aim of assessing the integrity of calcium carbonate for stable isotope
263 analysis (Bosch et al., 2015a) and whether the data could be used to build an independent
264 relative chronology for the shell remains. AAR dating is based on the post-mortem
265 breakdown of proteins which is affected by time, temperature, and a range of
266 environmental factors (e.g. Demarchi and Collins, 2014). Racemization involves the
267 interconversion of L-amino acids to their D- counterpart, resulting in D/L values which vary
268 between 0 (when an organism is alive) and 1 (when the reaction has achieved equilibrium,
269 over geological timescales). Developments in the AAR method during the last decade (e.g.
270 Penkman et al., 2008) revealed that in some biominerals, including the aragonitic shell of
271 *Phorcus* sp. (Bosch et al., 2015a), a fraction of intra-crystalline proteins can be isolated by
272 strong oxidation; these approximate a closed-system with regard to diagenesis, and
273 therefore complicating environmental factors (other than temperature) can be assumed to
274 be unimportant. A further advantage of the method is that, by analysing two fractions of
275 amino acids from each shell sample (i.e. the free and total hydrolysable amino acids (FAA
276 and THAA)), it is possible to recognise samples which have been compromised during their
277 burial history. This “open-system behaviour” is highlighted by non-covariance of FAA and
278 THAA D/L values, and might result from the introduction of exogenous amino acids, e.g.
279 bacterial or, in general, peptides that are not part of the original biomineral-specific proteins
280 enclosed in the crystals (Bosch et al., 2015a). This typically occurs during recrystallization of

281 the mineral phase from aragonite to the more stable calcite, which can variably affect the
282 endogenous isotopic composition. FAA vs THAA co-variance plots can therefore be used to
283 detect whether the isotopic composition values might have been skewed by diagenesis.

284
285 A total of 13 individual shells were analysed at the NEaar laboratory, University of York (UK);
286 these came from sublayer 5A (n = 4), sublayer 6B (n = 6) and sublayer 7D (n = 3). Each shell
287 was sampled on the rim, cleaned by drilling the outer surface and by sonication in ultrapure
288 water. Dry fragments were powdered and immersed in NaOCl (12 % w/v) for 48 hours to
289 isolate the intra-crystalline proteins. Two subsamples were taken from each rim fragment
290 and then prepared for the analysis of the FAA and THAA fractions (Penkman et al., 2008;
291 Demarchi et al., 2013). Each was analysed twice for chiral amino acids using Kaufman and
292 Manley's (Kaufman and Manley, 1998) method for liquid chromatography (RP-HPLC). The D-
293 and L-enantiomers of Asx (aspartic acid/asparagine), Glx (glutamic acid/glutamine), Ser
294 (serine), Ala (alanine), Val (valine) are reported.

295
296 Further to AAR analysis, shells were also randomly selected for X-ray diffraction (XRD) in
297 order to assess the integrity of mineral composition used for stable isotope analysis.
298 Powdered samples from the inner shell layer of 6 specimens were analysed using an Oxford
299 Diffraction SuperNova X-ray diffractometer using the copper X-ray source (λ 1.54184 Å) at
300 the Department of Chemistry, University of York (UK).

301
302 Oxygen isotope analysis on mollusc shells is a well-established approach for investigating
303 the seasonality of mollusc exploitation. Shell $\delta^{18}\text{O}$ values are a function of the oxygen
304 isotopic composition of the ambient water and temperature (Epstein et al., 1953). *P.*
305 *turbinatus* lives in Mediterranean coastal areas with marine salinity (Menzies et al., 1992),
306 therefore seasonal changes in shell $\delta^{18}\text{O}$ values are primarily related to temperature
307 (Mannino et al., 2008; Colonese et al., 2009; Prendergast et al., 2013).

308
309 Oxygen isotope analyses have been previously performed on *P. turbinatus* shells from
310 Holocene deposits of ORT (Colonese et al., 2009; Mannino et al., 2014). Here we extend
311 these previous results to include 20 additional shells from sublayer 5B (n = 10) and sublayer
312 6B (n = 10). Specimens with width and height ranging from 23.3 to 17 mm and from 21 to
313 14.3 mm were selected in order to ensure a high sampling resolution per growth rate (Fig.
314 2A).

315
316 After rinsing and air-drying, shells were partially embedded in an epoxy resin (Araldite rapid
317 epoxy) and sectioned perpendicularly to the growth lines at the aperture, using a Buehler
318 Isomet 1000 Precision Saw. Four samples were taken from the inner nacreous aragonite
319 layer, starting from the shell aperture toward the apex, with an interval of ~1 mm using a
320 manual microdrill with a 0.4 mm drill bit following the method described in Mannino et al.

321 (2007) and Colonese et al. (2009). In short, samples taken at the shell aperture were milled
322 in order to collect only the most recent shell deposits (Fig. 2A). The aperture $\delta^{18}\text{O}$ values are
323 used to interpret the season of collection. One shell per sublayer was selected for sequential
324 isotope analysis (~30 samples) using the sampling techniques described above (Fig. 2B). The
325 sequential $\delta^{18}\text{O}$ values provide the intra-annual range of temperature against which the
326 aperture $\delta^{18}\text{O}$ values can be compared.

327

328 The samples were analysed at the stable isotope facility of the British Geological Survey
329 (Nottingham, UK). Powdered samples were reacted with 100% H_3PO_4 at 90 °C overnight,
330 and the evolved CO_2 was analysed with an IsoPrime IRMS plus multiprep. The precision was
331 <0.05‰ for $\delta^{18}\text{O}$ values.

332

333 4. Results

334

335 4.1. Shellfish remains

336

337 Marine molluscs (MNI = 8977) were recovered from Upper Palaeolithic, Early Mesolithic and
338 Late Mesolithic/Early Neolithic layers (Fig. 3; Supplementary table 1). A remarkable
339 variability in the abundance and taxonomic composition was observed throughout the
340 stratigraphy. The density of shells (MNI/m^3) from layers 5, 6 and 7 show a positive linear
341 correlation ($R^2 = 0.82$) with the estimated relative sea level derived from NW Sicily
342 (Antonioli et al., 2002). This essentially reflects the increased processing/consumption of
343 marine molluscs at the cave with the approaching of the coastline. The mollusc assemblages
344 from layers 5, 6 and 7 are also clearly separated by the correspondence analysis
345 (Supplementary figure 1A), which shows in the first axis (65.5% of variance) the gradual
346 change from exploitations of coastal lagoons and marine reefs (Upper Palaeolithic and
347 Mesolithic) to marine reefs only (Late Mesolithic/Early Neolithic phase).

348

349 Upper Palaeolithic deposits (sublayers 7B to 7E; Fig. 3) contained the least number of
350 mollusc remains of the entire sequence ($\text{MNI} = 1306$; $\text{MNI}/\text{m}^3 = 1711$) and a relatively high
351 taxonomic variability (average Shannon index = 1.54). These were dominated by small-sized
352 species typically found in lagoons, estuaries, large shallow inlets and bays such as *Pirenella*
353 *conica* (52%) and *Bittium* spp. (23%). Their shells were fragmented and abraded due to
354 exposure to near-shore waves or currents (Bosch et al., 2015b), and were likely transported
355 incidentally into the cave, thus they are hereafter considered non-food taxa (Jerardino,
356 1993; Stiner, 1999). Taxa possibly exploited as food (17%) included *Cerithium vulgatum*,
357 *Porchus turbinatus*, *Phorcus articulatus*, *P. caerulea/ulyssiponensis*, collected in large
358 shallow inlets, bays and lagoons, and intertidal reefs. Few shells of *P. turbinatus* (8.8%) were
359 fractured or had their apex sectioned for removing the animal flesh as observed in other
360 Upper Palaeolithic and Mesolithic sites in Sicily (Compagnoni 1991; Mannino et al., 2011).

361 Crustaceans (MNI = 78) and echinoderms (MNI = 127) were similarly retrieved from these
362 deposits, and were represented by *Eriphia verrucosa* and *Paracentrotus lividus*, respectively
363 (Fig. 4). Freshwater molluscs were found in several Upper Palaeolithic layers and included
364 the genera *Stagnicola* (*Stagnicola* cf. *fuscus*) and *Lymnea* (*Lymnaea* (*Galba*) *truncatula*), very
365 likely transported incidentally to the cave (Supplementary table 2).

366

367 The Early Mesolithic deposits (sublayers 6A to 6D; Fig. 3) showed a remarkable change in
368 the abundance (MNI = 3975; MNI/m³ = 2657) and taxonomic diversity of mollusc remains
369 (average Shannon index = 1.83). The assemblages were dominated by food taxa (79.4%)
370 including *P. turbinatus*, *P. caerulea/ulyssiponensis*, *C. vulgatum* and *Hexaplex trunculus*. The
371 majority of the shells of *P. turbinatus* (66% to 87%) had their apex removed or were
372 fractured. Compared with the Upper Palaeolithic deposits, the number of *P. conica* and
373 *Bittium* spp. decreased dramatically (8.9% and 4.7% respectively), while freshwater species
374 practically disappeared (Supplementary table 2). Early Mesolithic deposits were also marked
375 by an increase in abundance of echinoderms (*P. lividus*) and crustaceans (in particular *E.*
376 *verrucosa*, and a few specimens of *Carcinus* sp.) (Fig. 4).

377

378 The Late Mesolithic/Early Neolithic deposits (sublayers 5A to 5C) marked a turning point in
379 the exploitation of intertidal resources as food at ORT. While the absolute number of shell
380 remains (MNI = 3696) was comparable with the previous Early Mesolithic occupations, there
381 was a considerable increase in the overall density value (MNI/m³ = 4421), where food taxa
382 (>95%) dominated over non-food taxa with ratios (food/non-food taxa) ranging from 51
383 (sublayer 5C) to 163 (sublayer 5A). The taxonomic diversity was the lowest of the entire
384 sequence (average Shannon index = 0.97), due to an overwhelming presence of *P.*
385 *caerulea/ulyssiponensis* and *P. turbinatus*, the latter with the majority of their shells
386 fractured for the extraction of the animal's flesh (63% to 83%). Echinoderms and
387 crustaceans showed similar density values to the previous Mesolithic phase (Fig. 4).

388

389 4.2. Fish remains

390

391 Fish remains (n = 2570) were retrieved from Upper Palaeolithic, Early Mesolithic and Late
392 Mesolithic/Early Neolithic deposits (Fig. 5; Supplementary table 3). The number of identified
393 specimens (NISP = 616) could only be established for 23.9% of the remains. Fish were mainly
394 represented by postcranial elements in all phases (~78%), followed by cranial elements
395 (16.5%) and undetermined fragments (5.3%). This pattern is suggestive of fish consumption
396 and refuse in place, instead of processing for consumption elsewhere (Stewart, 1991; Zohar
397 et al., 2001). Burn marks were also observed on ~41% of the remains, with this value
398 remaining fairly consistent throughout the stratigraphy. The taxonomic composition
399 includes sea breams (Sparidae; 35%), morays (Murenidae; 29%), grey mullets (Mugilidae;
400 20%), wrasses (Labridae; 8%), combers (Serranidae; 7.7%) and gobiids (Gobiidae; 0.2%). With

401 the exception of large-eye dentex (*Dentex macrophthalmus*), all these taxa could have been
402 captured from the shore, in shallow waters using a variety of tools, including nets, traps,
403 weirs, harpoons and hooks (Morales Muñiz, 2007). The number of remains and the
404 taxonomic diversity increased progressively from the Upper Palaeolithic to the Late
405 Mesolithic/Early Neolithic deposits. The distribution pattern observed in the CA provides
406 two main ordination axes that cumulatively explain more than 70% of the variability in
407 species composition among the sublayers (Supplementary figure 1B). However there is no
408 clear environmental gradient suggesting that fish were captured in a variety of coastal
409 environments through the sequence, although reef environments seem to be more
410 represented in Late Mesolithic/Early Neolithic deposits.

411

412 Fish density (MNI/m³) was positively correlated with the estimated relative sea level ($R^2 =$
413 0.66) from the Upper Palaeolithic to Mesolithic/Early Neolithic layers, indicating again an
414 increase in procurement and consumption with decreasing distance from the coast.
415 Specifically, the Upper Palaeolithic deposits (sublayers 7B to 7E) provided the lowest
416 amount of remains (NISP = 15; MNI = 8; MNI/m³ = 10) and the lowest taxonomic diversity
417 (average Shannon index = 0.31). They were mainly represented by postcranial elements of
418 mullets, sea breams and Mediterranean morays (Fig. 5).

419

420 In the Early Mesolithic (sublayers 6A to 6D) fish remains (NISP = 182; MNI = 53; MNI/m³ =
421 31) and taxonomic variability (average Shannon index = 1.25) increased. These included taxa
422 already present in the Upper Palaeolithic, such as mullets, sea breams, white seabream
423 (*Diplodus sargus*), gilthead seabream (*Sparus auratus*), salema (*Sarpa salpa*), and
424 Mediterranean morays, but also new types such as brown wrasse (*Labrus merula*) and
425 groupers (*Epinephelus* sp.).

426

427 Finally, a remarkable change occurred during the Late Mesolithic/Early Neolithic (sublayers
428 5A to 5C), essentially following the aforementioned trend observed in marine molluscs. Fish
429 remains doubled in number compared to the Early Mesolithic (NISP = 421; MNI = 130),
430 showing a much higher density (MNI/m³ = 136) and taxonomic diversity (average Shannon
431 index = 1.75). The assemblage was dominated by sea breams (including large-eye dentex
432 (*Dentex macrophthalmus*) and *Dentex* sp.), mullets and morays, followed by combers,
433 wrasses and gobids. It is worth noting that combers were definitely more abundant, possibly
434 represented by painted combers (*Serranus* cf. *scriba*) and groupers, the latter with
435 specimens of up to 90 cm.

436

437 4.3. *Shell AAR and stable isotopes of Phorcus turbinatus: diagenetic integrity of*
438 *the shells and seasonality of exploitation*

439

440 Diagenetic indices measured on the FAA and THAA fractions from all the 13 shells show very

441 good covariation (Fig. 6; Supplementary table 4). FAA and THAA values fall on a definite
442 diagenetic trajectory, thus displaying excellent closed-system behaviour. This indicates that
443 the inner nacreous aragonite sublayer was not compromised during the burial history
444 (Bosch et al., 2015a) and that it is likely that the original oxygen isotope composition is
445 retained. This was confirmed by XRD indicating that the inner shell deposit used for stable
446 isotope analysis was pure aragonite. Moreover, microscopic analysis did not reveal any
447 recrystallized or dissolved carbonate, and microgrowth increments were clearly visible on
448 the inner nacreous aragonite sublayer of the sectioned shells. We also note that Ala and Asx
449 D/Ls and [Ser/Ala] values offered the best resolution between sublayers 5A and 6B, and
450 show that shells from sublayer 5A are less degraded (and therefore younger) than those
451 from sublayer 6B and sublayer 7D. Despite the limited resolution of the method over these
452 timescales, this can be considered as independent evidence for supporting the radiocarbon
453 dates for the sublayers and the general integrity of the stratigraphic sequence.

454
455 Sequential shell $\delta^{18}\text{O}$ values of *P. turbinatus* reflect temperature oscillation during the life
456 span of the organism and can be used as a baseline for determining the seasonality of
457 collections (Mannino et al., 2007; Colonese et al., 2009). At ORT, sequential $\delta^{18}\text{O}$ values of
458 shells from sublayers 5B (shell B4.6) and 6B (shell B8.5) ranged from +2.1‰ to -0.8‰ ($\Delta^{18}\text{O}$
459 = 2.9‰) and from +3.3‰ to +0.2‰ respectively ($\Delta^{18}\text{O}$ = 3.1‰). The $\delta^{18}\text{O}$ values display a
460 quasi sinusoidal variation coherent with a period shorter than a one-year cycle (Fig. 7A).
461 Given that 1‰ changes in $\delta^{18}\text{O}$ values of biogenic aragonite correspond to a change in
462 temperature of ~ 4.3 °C (Grossman and Ku, 1986), the observed $\Delta^{18}\text{O}$ values are consistent
463 with annual temperature ranges of ~ 13 °C. Shell-aperture $\delta^{18}\text{O}$ values of specimens
464 retrieved from sublayers 5B (n = 10) and 6B (n = 10) were less variable than their relative
465 sequential $\delta^{18}\text{O}$ values, ranging from +2.1‰ to +1.2‰ ($\Delta^{18}\text{O}$ = 0.9‰) and from +2.5‰ to
466 +1.5‰ ($\Delta^{18}\text{O}$ = 1.0‰), respectively (Fig. 7B; Supplementary table 5). The high $\delta^{18}\text{O}$ values of
467 the shell-aperture and their low isotopic variability, corresponding to a temperature
468 variation of ~ 4.3 °C, indicate that collection occurred as short episodes during the colder
469 months of the year. Our results are consistent with previous studies on shells from sublayers
470 7C, 6C and 5A (Colonese et al., 2009) and from archaeological trenches of 1972's excavation
471 (Mannino et al., 2014), and support the view that Upper Palaeolithic, Early Mesolithic and
472 Late Mesolithic/Early Neolithic exploitation of *P. turbinatus* at ORT occurred prevalently
473 during the coldest months of the year and often as short-term episodes (Fig. 7C).

474

475 **5. Discussion**

476

477 **5.1. Upper Palaeolithic (Late Pleistocene)**

478

479 Shellfish and fish were seldom processed/consumed as food at ORT during the Upper
480 Palaeolithic at ~ 14.2 ka cal BP, presumably due to a combination of the distance of the cave

481 from the coast and the intermittent nature of its occupation, likely used in the context of
482 foraging trips (e.g. as a campsite or location *sensus* Binford, 1980). This is supported by the
483 dearth of terrestrial faunal remains (NISP = 125; Martini et al., 2012), as well as by oxygen
484 isotopic data from *P. turbinatus* shells (sublayer 7C) attesting to short episodes of collection
485 during the coldest months of the year, as also detected in other Upper Palaeolithic sites the
486 NW Sicily (Mannino et al., 2011a).

487
488 Nevertheless, the comparatively large numbers of *P. conica* and *B. cf. reticulatum* indicate
489 that Upper Palaeolithic people at ORT did exploited some coastal environments. The high
490 frequency of *P. conica*, for example, indirectly reveals the use of coastal lagoons and
491 estuaries, areas colonized by seagrass meadows (e.g. *Zostera* spp.; Plaziat, 1993; Kowalke,
492 2006; Smedile et al., 2012; Mosbahi et al., 2016). The transport of shell debris to the cave
493 suggests that such environments existed close to the site when the wide continental shelf of
494 Favignana was exposed. These environments must have been attractive to humans as
495 valuable sources of food as well as other resources that, by their nature, would not be
496 preserved in the cave deposits. Moreover the two freshwater species in Upper Palaeolithic
497 layers also suggest the presence of shallow, slow and fast-moving permanent and
498 temporary waters, such as ponds, lakes, streams and wet meadows (Ložek 1986; Trouve et
499 al., 2005). These environments may have existed in the coastal plain between Favignana and
500 Levanzo Island (Agnesi et al., 1993).

501
502 The use of seagrasses (both live and dead) could perhaps explain the incidental deposition
503 of non-food taxa at ORT. Seagrasses are natural traps of shell debris and sediments
504 (Boudouresque et al., 2016), and have been exploited by traditional coastal communities
505 worldwide for a variety of purposes, including the production of cordages, baskets, nets,
506 bedding, fuel, food and medicine (Milchakova et al., 2014). Early direct evidence of human
507 use of seagrasses is dated to the Early Holocene, where these were collected for producing
508 cordage and other artefacts (Connolly et al., 1995; Vellanoweth et al., 2003). The
509 unquestionable importance of aquatic plants to coastal communities therefore offers a
510 tentative framework for their interpretation. Intriguingly, the non-food taxa at ORT were
511 found in deposits containing Upper Palaeolithic and later, Early Mesolithic burials, but their
512 association remains unclear. The Upper Palaeolithic burial (*Oriente* C) had one shell of
513 *Cerithium* sp. used possibly as a grave good, but the Early Mesolithic burials unearthed in
514 1972 lacked detailed stratigraphic information for any interpretations to be made. At least
515 *P. conica* and *B. cf. reticulatum*, the most abundant shell remains in these deposits, were
516 not used as ornaments, which were confectioned with well-preserved shells of *C. rustica*,
517 *Cerithium* sp., *Nassarius (Hinia) incrassatus* (Cilli et al., 2012). However we cannot rule out
518 that non-food taxa may have been introduced along with shells collected for this purpose.
519 Indeed, seagrass debris deposited on the beach effectively constitutes a rich source of a
520 variety of shells. Similarly abraded and fragmented shells, including *Bittium* sp. and

521 *Cerithium* sp., were also found in Upper Palaeolithic deposits in Grotta delle Incisioni
522 all'Addaura (NW Sicily), but these were interpreted as possibly originating from raised beach
523 deposits rather than human use (Mannino et al., 2011a). Small abraded gastropod shells
524 were also found in Upper Palaeolithic deposits at Grotta della Serratura (Colonese and
525 Wilkens, 2005) and Riparo Mochi in the Italian Peninsula (Stiner, 1999).

526

527 5.2. Early Mesolithic (Early Holocene)

528

529 The picture changes with the Early Mesolithic occupation at ~9.6 ka cal. BP, when the rise of
530 the sea level and the submersion of the coastal plain possibly favoured the exploitation of
531 marine resources as the cave was much closer to the coastline. There was a noticeable
532 increase in fish and marine molluscs collected for food from a range of coastal environments
533 (lagoons and reefs), as well as remains of loggerhead sea turtle (*Caretta caretta*) (Martini et
534 al., 2012). These resources were possibly exploited during short visits to the coast in winter,
535 as suggested by the $\delta^{18}\text{O}$ values from *P. turbinatus* (Fig. 7C), in agreement with other
536 evidence of Mesolithic mollusc exploitation occurring prevalently in winter in Sicily
537 (Colonese et al., 2009; Mannino et al., 2011a; 2014). Land mammal remains are the least
538 represented of the whole sequence (NISP = 70; Martini et al., 2012), again suggesting
539 intermittent use of the cave. It is worth noting that a number of human burials were found
540 in the Mesolithic deposits, providing a tentative context for the consumption and/or
541 disposal of food, including marine resources, during funerary practices. As confirmed by
542 stable isotope analysis of human bone collagen, including individuals from ORT (Mannino et
543 al., 2011; 2012; 2015), marine resources made a minor contribution to dietary protein
544 during the Mesolithic in Sicily. Fish and shellfish consumed at seasonal bases as
545 complements to terrestrial resources, or occasionally in the context of specific social
546 activities, may be obscured by terrestrial proteins in bulk collagen stable carbon and
547 nitrogen isotope composition.

548

549 5.3. Late Mesolithic/Early Neolithic (Late Holocene)

550

551 It is during the Late Mesolithic/Early Neolithic occupation that food procurement at ORT had
552 an unprecedented focus on fish and shellfish, presumably coinciding with the isolation of
553 Favignana from mainland Sicily. This phase is marked by the prevailing exploitation of reef
554 species, presumably reflecting the establishment of rockshore environments in the area and
555 the retraction of coastal lagoons. *P. caerulea/ulyssiponensis* gradually replace *Phorcus* spp.
556 in abundance and ultimately become the dominant taxa at ORT, as observed in several Late
557 Mesolithic and Early Neolithic sites along the Tyrrhenian coast of the southern Italian
558 Peninsula and in Sicily (Durante and Settepassi, 1972; Wilkens, 1993; Colonese and Tozzi,
559 2010). It is at this time that a significant decrease in the size of *P. caerulea/ulyssiponensis* is
560 observed at ORT (but not of *P. turbinatus*), but whether this was caused by environmental

561 changes, human pressure or both is a matter of debate (Colonese et al., 2014). We note that
562 *Patella* spp. is the more profitable in terms of meat yield (Dupont and Gruet 2002) and thus
563 even in a context of environmental change *Patella* spp. may still have offered larger
564 energetic returns compared to *P. turbinatus*. The size decrease of *P. caerulea/ulyssiponensis*
565 could thus represent the combined effect of environmental change and intensification of
566 exploitation.

567
568 Fish included the Mediterranean moray, followed by an increase in sparidae and a slight
569 decrease in mullets, which were consumed in the cave. However, fish diversity expanded
570 compared to the previous Mesolithic phase to also include other elements such as grouper,
571 some of considerable size (90 cm) as recorded at this time at Grotta dell'Uzzo (Tagliacozzo,
572 1993). Increased fish diversity essentially reflects opportunistic captures. Land mammals
573 were also consumed at ORT at that time (NISP = 73; Martini et al., 2012) including some
574 livestock (i.e. sheep/goat, *Ovis vel Capra*). The relatively low amount of terrestrial faunal
575 remains suggests that ORT was used intermittently, as is also supported by the oxygen
576 isotope composition of *P. turbinatus* which continue to attest to very short-term winter
577 exploitation.

578
579 Considering the environmental and biological impact of the isolation of Favignana between
580 ~9.6 ka and ~7.8 ka BP, increasing fishing and shellfish collection at ORT could be
581 interpreted as a response to reduced mammalian game on the island. While this strategy
582 might be expected for foragers, it is less envisioned for farmers who possessed livestock and
583 domesticated crops to mitigate natural resource fluctuations. Interestingly, the increased
584 focus on fish and shellfish at ORT, or its relative intensification compared to the previous
585 phases, roughly mimics a similar trend detected at Grotta dell'Uzzo, where an
586 unprecedented focus on coastal and marine resources took place during Late Mesolithic and
587 Early Neolithic (Tagliacozzo, 1993; 1994; Mannino et al., 2015). Conversely to ORT, however,
588 the $\delta^{18}\text{O}$ data of *P. turbinatus* shells and fish sclerochronology revealed that shellfish and
589 fish were exploited in different seasons at Grotta dell'Uzzo, possibly due to a more
590 residential or ritual use of the cave (Tagliacozzo, 1993; Mannino et al., 2007). Moreover, the
591 steep bathymetry at Uzzo suggests that the cave was never very far from the coast and
592 therefore intensification of marine resources had little to do with the sea level rise
593 (Tagliacozzo, 1993). Despite the contrasting settlement pattern and environmental
594 conditions between ORT and Grotta d'Uzzo during the Late Mesolithic, we suspect that
595 intensification of marine resources at both sites responded to common processes operating
596 at the regional scale. Mannino and Thomas (2009) suggested that population growth since
597 the Early Holocene had a negative impact on terrestrial faunal turnover in Sicily,
598 consequently increasing competition for resources and territoriality around profitable
599 resource patches by Late Mesolithic groups. Cultural transmission among hunter-gatherers,
600 including technology and information on resource distribution and productivity, is crucial

601 during resource shortfalls and facilitated in areas under greater population density (Fitzhugh
602 et al., 2011; Eerkens et al., 2014). Under these conditions coastal areas of NW Sicily may
603 have offered idea contexts for social interaction, and as such for transferring collective
604 information on marine resource acquisition. The Late Mesolithic and Early Neolithic at ORT
605 and Grotta dell'Uzzo could be expressions of this scenario.

606

607 Palaeoceanographic records indicate that there may have been suitable environmental
608 conditions at this time for supporting an intensification of marine resources. A distinctive
609 increase in primary productivity, the highest coccolith absolute abundance over the last 25.0
610 ky, is visible in the Alboran Sea roughly between about 9.5 and 6.0 ka cal BP (Colmenero-
611 Hidalgo et al., 2004; Ausín et al., 2015). The primary productivity increase was likely
612 triggered by the post-glacial sea-level rise, at its maximum rate during the meltwater pulse
613 IB just after the Younger Dryas (Lambeck et al., 2014), that promoted the maximum water
614 exchange at the Gibraltar Strait (Myers et al., 1998). Enhanced Atlantic surface water inflow,
615 which is nutrient-enriched compared to Mediterranean water, may have fuelled
616 phytoplankton blooming (Ausín et al., 2015). This mechanism is potentially suitable to
617 increase productivity in a large sector of the western-central Mediterranean Sea, because
618 the response of nutrient dynamics to late Quaternary climatic variations seems to be similar
619 in the Sicily Channel and Alboran, southern Tyrrhenian and Balearic Seas (Incarbona et al.,
620 2013; Di Stefano et al., 2015). This is especially true for the Egadi Archipelago region, where
621 long time series estimates of chlorophyll concentration by satellite imagery demonstrate
622 that approximately 80% of the variance is explained by the advection of chlorophyll- and
623 nutrient-enriched Atlantic Water (Rinaldi et al., 2014).

624

625 Early Holocene increased productivity in the western Mediterranean Sea is expected to be
626 reflected in the marine food web (Macias et al., 2014; 2015), and would potentially facilitate
627 an increase in marine resource exploitation in NW Sicily. This time interval also corresponds
628 with the earliest evidence for Neolithic colonists in this region. The stable isotope analysis of
629 Neolithic human individuals from Grotta dell'Uzzo indicate some consumption of marine
630 protein by early farmers (Mannino et al., 2015) as this was the period of most intense
631 fishing at the cave (Tagliacozzo, 1993). The appearance of hooks made of bone or boar tusks
632 at Grotta dell'Uzzo during this time suggests the introduction of new technologies
633 (Tagliacozzo, 1993), which in turn may have allowed the Early Neolithic groups to capitalize
634 on this window of opportunity during their colonization efforts in NW Sicily.

635

636 An abrupt increase in marine productivity also involved the eastern Mediterranean Sea
637 between about 10.5 and 6 ka cal BP, during the deposition of the most recent organic-rich
638 layer, the so-called sapropel S1 (Casford et al., 2002; Rohling et al., 2015). Peaks of biogenic
639 barite and concordant indication of a deep chlorophyll maximum in micropaleontological
640 studies (Rohling and Gieskes, 1989; Castradori, 1993; Kemp et al., 1999; Meier et al., 2004)

641 testify to a dramatic ecological change in this part of the Mediterranean Sea, which is today
642 one of the poorest trophic areas in the world. This may have again supported the larger
643 economic focus on marine resources in this region (Rose, 1995; Mylona, 2003; Rainsford et
644 al., 2014), including the development of early fishing villages (Galili et al., 2003; 2004),
645 adding to the complex, multidimensional nature of coastal exploitation in the
646 Mediterranean.

647

648 **6. Conclusions**

649

650 Marine faunal remains in Late Pleistocene and Holocene archaeological deposits around the
651 Mediterranean basin are invaluable records of past human-environment interaction, and as
652 such can offer glimpses into past ecological conditions and the adaptive strategies of early
653 humans across the basin. An appreciation of the changing nature of these interactions is
654 imperative for distilling the cultural and socio-economic significance of coastal ecosystems
655 through time. In agreement with previous studies, the faunal record from ORT indicates that
656 fish and shellfish were exploited in NW Sicily at least since the Late Pleistocene, and
657 procurement strategies were influenced by local environmental conditions and site
658 occupation patterns. The shell record reflects a clear environmental gradient from coastal
659 transitional environments during the Late Pleistocene, when the sea level was considerably
660 lower and large areas of the continental shelf were exposed, to reefs during the middle
661 Holocene, when the area was isolated from mainland Sicily. An increased focus on marine
662 resources during the middle Holocene is chronologically synchronous with the isolation of
663 Favignana, as well as with major changes in marine productivity and the spread of the
664 Neolithic in the western Mediterranean.

665

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680

681 **Contributions**

682 ACC, WL, BD, CA, NH, ZG designed and performed the research; ACC, DLV, FM contributed
683 contextual information to aid interpretation; ACC, WL, BD, DLV, CA, NH, ACW analysed data;
684 ACC, BD, DLV, AI wrote the paper; all authors were involved in reviewing the manuscript.

685

686 **Figure captions**

687

688 **Figure 1.** A) Geographic location of Grotta d’Oriente (ORT); B) excavation areas; C)
689 stratigraphic deposit showing the layers and sublayers discussed in the paper.

690

691 **Figure 2.** A) Shell of *Phorcus turbinatus* used for oxygen isotope analysis. The grey shadow
692 area marks the sampling in the shell aperture; B) sectioned shell sampled for carbonate
693 (drilling) along the shell growth increments and along the aperture (milling).

694

695 **Figure 3.** Relative abundance (%MNI) of marine molluscs from Upper Palaeolithic,
696 Mesolithic and Late Mesolithic/Early Neolithic deposits, including their density for the
697 volume of sediment (MNI/m³), the ratio between food and non-food taxa, species diversity
698 and the environmental gradient represented by first axis of the correspondence analysis.
699 The ecological attributions refer to the Habitat type of the European Union Habitats
700 Directive (http://ec.europa.eu/environment/nature/natura2000/marine/index_en.htm);
701 1140: Sandbanks can be found in association with mudflats and sandflats not covered by
702 seawater at low tide; 1150: Coastal lagoons; 1160: Large shallow inlets and bays; 1170:
703 reefs.

704

705 **Figure 4.** Absolute abundance of echinoderm and crustacean remains from Upper
706 Palaeolithic, Mesolithic and Late Mesolithic/Early Neolithic deposits. Their density for the
707 volume of sediment (MNI/m³) is also reported.

708

709 **Figure 5.** Relative abundance (%NISP) of fish remains from Upper Palaeolithic, Mesolithic
710 and Late Mesolithic/Early Neolithic deposits, including their density for the volume of
711 sediment (MNI/m³), species diversity and the environmental gradient represented by first
712 axis of the correspondence analysis. The ecological attributions refer to the Habitat type of
713 the European Union Habitats Directive
714 (http://ec.europa.eu/environment/nature/natura2000/marine/index_en.htm); 1120:
715 Posidonia beds (*Posidonia oceanica*); 1130: Estuaries; 1150: Coastal lagoons; 1160: Large
716 shallow inlets and bays; 1170: reefs.

717

718 **Figure 6.** *Phorcus turbinatus* AAR data. A) Asx THAA vs FAA D/L; B) Ala THAA vs FAA D/L; C)
719 Ala vs Asx THAA D/L; D) Ser decomposition ([Ser]/[Ala] THAA vs FAA) – note that the axis
720 values have been plotted in reverse to ease interpretation.

721

722 **Figure 7.** Oxygen isotope composition of *Phorcus turbinatus* shell. A) sequential $\delta^{18}\text{O}$ values
723 of shells from sublayer 5B and 6B; B) the distribution of $\delta^{18}\text{O}$ values (0.5‰ bins) of shells
724 from sublayer 5B and 6B indicate low temperature when compared with the range of $\delta^{18}\text{O}$
725 values from sequential shells (dark and grey bands and dotted lines); C) Jitter plot of $\delta^{18}\text{O}$
726 values of *Phorcus turbinatus* from Grotta d’Oriente for Early Mesolithic and Late
727 Mesolithic/Early Neolithic deposits. The interpretation is based on the comparison between
728 shell aperture $\delta^{18}\text{O}$ values (filled black circles) against the sequential $\delta^{18}\text{O}$ values (grey
729 circles and boxplot). Data from 5A and 6C were taken from Colonese et al. (2009). Data from
730 trenches were taken from Mannino et al. (2014).

731

732 **Table captions**

733

734 **Table 1.** Radiocarbon age for the stratigraphic succession of Grotta d’Oriente. ^{14}C ages are
735 reported as conventional and calibrated years BP using IntCal13 (Reimer et al., 2013) in
736 OxCal v4.3. The radiocarbon dates were performed at the CEDAD, Lecce, Italy
737 (<http://www.cedad.unisalento.it/en/>).

738

739

740 **Supplementary information (Figures)**

741 **Supplementary figure 1.** Correspondence analysis of A) marine molluscs and B) fish remains.

742

743 **Supplementary information (Table)**

744 **Supplementary table 1.** Marine shell remains from Upper Palaeolithic to Meso/Neolithic
745 layers. Food (F) and non-food (NF) taxa, diversity of species (Shannon index) and first axis of
746 the CA are also reported.

747

748 **Supplementary table 2.** Freshwater molluscs recovered in Upper Palaeolithic and Early
749 Mesolithic deposits.

750 **Supplementary table 3.** Fish remains recovered from Upper Palaeolithic to Late
751 Mesolithic/early Neolithic layers. Diversity of species (Shannon index) and first axis of the CA
752 are also reported.

753 **Supplementary table 4.** AAR data (D/L values discussed in the text) from shells of *Phorcus*
754 *turbinatus* from Upper Palaeolithic (layer 7D), Mesolithic (6B) and Late Mesolithic/Early
755 Neolithic (layer 5A) deposits.

756 **Supplementary table 5.** Oxygen isotope values obtained on shells of *Phorcus turbinatus*

757 from Mesolithic (layer 6B) and Late Mesolithic/Early Neolithic (layer 5B) deposits.

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