

# 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 during  
30 the postglacial sea level rise and the progressive isolation of Favignana from mainland Sicily.  
31 We detected an intensification of marine resource exploitation between ~9.6 ka and ~7.8 ka  
32 BP, which corresponds with the isolation of Favignana Island and, later on, with the  
33 introduction of early agro-pastoral economy in this region. We suggest that a higher  
34 investment in marine resource exploitation by late foragers and early farmers in NW Sicily  
35 was also supported by an increase in marine productivity in the south Tyrrhenian Sea in the  
36 Middle Holocene.

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## 38 **Keywords**

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

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## 1. Introduction

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

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

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

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

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## 91 **2. Archaeological setting**

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### 93 **2.1. *Grotta d’Oriente***

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95 The island of Favignana, the largest (~20 km<sup>2</sup>) 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 were  
100 conducted in the small chamber in 1972 (Mannino, 1972; 2002; Mannino et al., 2012; 2014),  
101 and it was excavated again in 2005 as part of an interdisciplinary project carried out by the  
102 University of Florence and Museo Fiorentino di Preistoria. The results presented in this study  
103 are part of this multidisciplinary research programme and details of the stratigraphy, material  
104 culture and burial practice can be found in Lo Vetro and Martini (2006) and Martini et al.  
105 (2012).

106

107 The excavations in 2005 shed light on an archaeological deposit (~1.5 m thick) spanning from  
108 the Late Pleistocene to the Middle Holocene. The coherent stratigraphic distribution of the  
109 <sup>14</sup>C 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 to  
113 the late Upper Palaeolithic (layer 7; ~14.2 cal ka BP), Early Mesolithic (layer 6; ~9.7 and 9.6 cal  
114 ka BP), and Late Mesolithic or Early Neolithic (layers 5; ~7.8 cal ka BP). These cultural deposits  
115 were further divided into sublayers, each corresponding to different paleosurfaces which are  
116 often characterized by hearths (more or less structured) and pits.

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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 typical

121 Late Epigravettian assemblages, layer 6 (sublayers 6A-6D) is characterized by a Sauveterrian-  
122 like technocomplex, while layer 5 instead presents a stone assemblage marked by the  
123 presence of blades and trapezes, and by the appearance of the pressure blade technique (Lo  
124 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 Mesolithic  
137 or the Early Neolithic (Lo Vetro and Martini, 2016). The only <sup>14</sup>C date available for layer 5,  
138 obtained from the top of the deposit (sublayer 5A), is contemporaneous with the Early  
139 Neolithic of Grotta dell'Uzzo (NW Sicily) (Collina, 2016). No pottery remains were recovered,  
140 however domestic faunal remains (*Ovis vel Capra*) and obsidian flakes, although rare, were  
141 found in sublayers 5A and 5C. The scant stone tool assemblage (Martini et al. 2012; Lo Vetro  
142 and Martini 2016) might be comparable both to the Castelnovian and the Early Neolithic  
143 industries found at Grotta dell'Uzzo (Collina, 2016). Sublayers 5A - 5C are thus associated to  
144 the Late Mesolithic (Castelnovian) or the Early Neolithic (hereafter referred to as Late  
145 Mesolithic/Early Neolithic) as it is impossible to exclude either of the two cultural attributions  
146 based on the related archaeological record. Although the chronology and paucity of domestic  
147 faunal remains and obsidian could suggest an Early Neolithic occupation, the occurrence of  
148 these items could also attest to contact between the latest Mesolithic groups and the earliest  
149 Neolithic communities which could have cohabited in NW Sicily at that time (Lo Vetro and  
150 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 assemblages  
167 attributed to Late Epigravettian. Moreover the deposit underneath (sublayer 7E) provided a  
168 radiocarbon date comparable with sublayer 7D (Table 1). *Oriente C* had been partially  
169 disturbed when the initial excavations in 1972 intercepted the grave (Lo Vetro and Martini,  
170 2006). Two shells of *Pirenella conica* from Layer 7E were dated to the Early Holocene (shell  
171 7E1: 9,715±35 BP, CNA822 and shell 7E2: 9,130±35 BP, CNA823), confirming some  
172 stratigraphic disturbance. Other human burials were recovered in 1972 (*Oriente A* and *Oriente*  
173 *B*), together with at least 40 human remains retrieved outside burial contexts (Mannino, 1972,  
174 2002; D'Amore et al., 2010; Mannino et al., 2012). While the chronological attribution of  
175 *Oriente A* (adult male) remains a matter of debate, the Early Mesolithic origin of *Oriente B*  
176 (adult female) is supported by a direct <sup>14</sup>C date of ~10.6 ka cal BP (D'Amore et al., 2010;  
177 Mannino et al., 2012). The ulna of a possible fourth individual (*Oriente X*) retrieved in 1972  
178 has been recently <sup>14</sup>C dated to ~9.6 ka cal BP (Mannino et al., 2012), roughly corresponding  
179 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., 1993;  
186 Antonioli et al., 2002). According to postglacial sea level curves from NW Sicily and the Italian  
187 Peninsula (Antonioli et al., 2002; Lambeck et al., 2004), the cave must have been located ~3  
188 to ~4 km inland during the Upper Palaeolithic occupation (layer 7), when the relative sea level  
189 was ~90 m lower than present day and Favignana was part of Sicily (see also Mannino et al.,  
190 2014). During the Early Mesolithic (layer 6) the sea level was ~40 to ~50 m below that of  
191 present day and the cave was located ~1 km from the coast. Abrupt changes in coastal areas  
192 must have occurred with the submersion of the coastal plain and the isolation of Favignana  
193 when the cave was visited by Late Mesolithic/Early Neolithic groups (layer 5). At that time the  
194 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 of  
203 Florence, La Specola Museum, and the Civic Natural History Museum of Verona. Taxonomic  
204 identification and quantification was supported by specialised literature (Monod, 1968;  
205 Kusaka, 1974; Wilkens, 1986; Wheeler and Jones, 1989; Stewart, 1991; Watt et al., 1997;  
206 Albertini and Tagliacozzo, 2000; Doneddu and Trainito, 2005; Campbell 2008; Zohar et al.,  
207 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](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 reliably  
214 distinguished using shell morphology (Mauro et al., 2003; Petraccioli et al., 2010; Sanna et al.,  
215 2012). Thus shells with characteristics typically associated to these species (e.g., Doneddu and  
216 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 for  
220 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 vertebral  
225 elements for fish. Fish remains were measured according to established protocols (Wilkens,  
226 1986; Wheeler and Jones, 1989; Zohar et al., 2001; Orchard, 2005; Thieren et al., 2012) and  
227 compared with reference collections. Moray remains were measured using approaches  
228 described for eel in Thieren et al. (2012), due to the high variability in size-class and vertebral  
229 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 ( $m^3$ ) 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 matrix,  
235 preservation conditions through the succession (Jerardino, 1995; 2016) and the non-  
236 contiguous distribution of the remains when the sedimentary deposits include structures such  
237 as hearths and pits. Due to the limited number of radiocarbon dates, the deposition rate could  
238 be estimated only between sublayers 6B and 6D (2.06 m/ka). However, the average volume  
239 of sediment per unit area at 9.6 cal ka BP (0.13  $m^3$ , sublayers 6B and 6C) and 14.2 ka cal BP  
240 (0.11  $m^3$ , sublayers 7D and 7E) suggest comparable depositional rates in most parts of the

241 deposit. The nature of the sedimentary matrix has not been studied in detail, however  
242 according to field observations there were few differences between layers 5 and 6, which  
243 were mainly composed of silts and sand typically found in active karst settings (Woodward  
244 and Goldberg, 2001). In contrast, layer 7 showed an increase in clay and considerably lower  
245 anthropogenic deposits (for faunal remains see below). Finally, the presence of fish and small  
246 fragile shell remains (e.g. freshwater) is clear evidence of good overall preservation (see  
247 below). Shell fragmentation is minor and prevalently related to food processing (in the case  
248 of *P. turbinatus*) as well as *post-mortem* taphonomic processes prior to shell transport into  
249 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 breakdown  
265 of proteins which is affected by time, temperature, and a range of environmental factors (e.g.  
266 Demarchi and Collins, 2014). Racemization involves the interconversion of L-amino acids to  
267 their D- counterpart, resulting in D/L values which vary between 0 (when an organism is alive)  
268 and 1 (when the reaction has achieved equilibrium, over geological timescales).  
269 Developments in the AAR method during the last decade (e.g. Penkman et al., 2008) revealed  
270 that in some biominerals, including the aragonitic shell of *Phorcus* sp. (Bosch et al., 2015a), a  
271 fraction of intra-crystalline proteins can be isolated by strong oxidation; these approximate a  
272 closed-system with regard to diagenesis, and therefore complicating environmental factors  
273 (other than temperature) can be assumed to be unimportant. A further advantage of the  
274 method is that, by analysing two fractions of amino acids from each shell sample (i.e. the free  
275 and total hydrolysable amino acids (FAA and THAA)), it is possible to recognise samples which  
276 have been compromised during their burial history. This “open-system behaviour” is  
277 highlighted by non-covariance of FAA and THAA D/L values, and might result from the  
278 introduction of exogenous amino acids, e.g. bacterial or, in general, peptides that are not part  
279 of the original biomineral-specific proteins enclosed in the crystals (Bosch et al., 2015a). This  
280 typically occurs during recrystallization of the mineral phase from aragonite to the more

281 stable calcite, which can variably affect the endogenous isotopic composition. FAA vs THAA  
282 co-variance plots can therefore be used to detect whether the isotopic composition values  
283 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 and  
290 then prepared for the analysis of the FAA and THAA fractions (Penkman et al., 2008; Demarchi  
291 et al., 2013). Each was analysed twice for chiral amino acids using Kaufman and Manley's  
292 (Kaufman and Manley, 1998) method for liquid chromatography (RP-HPLC). The D- and L-  
293 enantiomers of Asx (aspartic acid/asparagine), Glx (glutamic acid/glutamine), Ser (serine), Ala  
294 (alanine), Val (valine) are reported.

295

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

301

302 Oxygen isotope analysis on mollusc shells is a well-established approach for investigating the  
303 seasonality of mollusc exploitation. Shell  $\delta^{18}\text{O}$  values are a function of the oxygen isotopic  
304 composition of the ambient water and temperature (Epstein et al., 1953). *P. turbinatus* lives  
305 in Mediterranean coastal areas with marine salinity (Menzies et al., 1992), therefore seasonal  
306 changes in shell  $\delta^{18}\text{O}$  values are primarily related to temperature (Mannino et al., 2008;  
307 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 these  
311 previous results to include 20 additional shells from sublayer 5B (n = 10) and sublayer 6B (n =  
312 10). Specimens with width and height ranging from 23.3 to 17 mm and from 21 to 14.3 mm  
313 were selected in order to ensure a high sampling resolution per growth rate (Fig. 2A).

314

315 After rinsing and air-drying, shells were partially embedded in an epoxy resin (Araldite rapid  
316 epoxy) and sectioned perpendicularly to the growth lines at the aperture, using a Buehler  
317 Isomet 1000 Precision Saw. Four samples were taken from the inner nacreous aragonite layer,  
318 starting from the shell aperture toward the apex, with an interval of  $\sim 1$  mm using a manual  
319 microdrill with a 0.4 mm drill bit following the method described in Mannino et al. (2007) and  
320 Colonese et al. (2009). In short, samples taken at the shell aperture were milled in order to



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

326

327 The samples were analysed at the stable isotope facility of the British Geological Survey  
328 (Nottingham, UK). Powdered samples were reacted with 100%  $\text{H}_3\text{PO}_4$  at 90 °C overnight, and  
329 the evolved  $\text{CO}_2$  was analysed with an IsoPrime IRMS plus multiprep. The precision was  
330 <0.05‰ for  $\delta^{18}\text{O}$  values.

331

## 332 4. Results

333

### 334 4.1. Shellfish remains

335

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

347

348 Upper Palaeolithic deposits (sublayers 7B to 7E; Fig. 3) contained the least number of mollusc  
349 remains of the entire sequence (MNI = 1306; MNI/m<sup>3</sup> = 1711) and a relatively high taxonomic  
350 variability (average Shannon index = 1.54). These were dominated by small-sized species  
351 typically found in lagoons, estuaries, large shallow inlets and bays such as *Pirenella conica*  
352 (52%) and *Bittium* spp. (23%). Their shells were fragmented and abraded due to exposure to  
353 near-shore waves or currents (Bosch et al., 2015b), and were likely transported incidentally  
354 into the cave, thus they are hereafter considered non-food taxa (Jerardino, 1993; Stiner,  
355 1999). Taxa possibly exploited as food (17%) included *Cerithium vulgatum*, *Porchus*  
356 *turbinatus*, *Phorcus articulatus*, *P. caerulea/ulyssiponensis*, collected in large shallow inlets,  
357 bays and lagoons, and intertidal reefs. Few shells of *P. turbinatus* (8.8%) were fractured or  
358 had their apex sectioned for removing the animal flesh as observed in other Upper  
359 Palaeolithic and Mesolithic sites in Sicily (Compagnoni 1991; Mannino et al., 2011).  
360 Crustaceans (MNI = 78) and echinoderms (MNI = 127) were similarly retrieved from these

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

365

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

376

377 The Late Mesolithic/Early Neolithic deposits (sublayers 5A to 5C) marked a turning point in  
378 the exploitation of intertidal resources as food at ORT. While the absolute number of shell  
379 remains (MNI = 3696) was comparable with the previous Early Mesolithic occupations, there  
380 was a considerable increase in the overall density value (MNI/m<sup>3</sup> = 4421), where food taxa  
381 (>95%) dominated over non-food taxa with ratios (food/non-food taxa) ranging from 51  
382 (sublayer 5C) to 163 (sublayer 5A). The taxonomic diversity was the lowest of the entire  
383 sequence (average Shannon index = 0.97), due to an overwhelming presence of *P.*  
384 *caerulea/ulyssiponensis* and *P. turbinatus*, the latter with the majority of their shells fractured  
385 for the extraction of the animal's flesh (63% to 83%). Echinoderms and crustaceans showed  
386 similar density values to the previous Mesolithic phase (Fig. 4).

387

#### 388 4.2. Fish remains

389

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

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

410

411 Fish density (MNI/m<sup>3</sup>) was positively correlated with the estimated relative sea level ( $R^2 =$   
412 0.66) from the Upper Palaeolithic to Mesolithic/Early Neolithic layers, indicating again an  
413 increase in procurement and consumption with decreasing distance from the coast.  
414 Specifically, the Upper Palaeolithic deposits (sublayers 7B to 7E) provided the lowest amount  
415 of remains (NISP = 15; MNI = 8; MNI/m<sup>3</sup> = 10) and the lowest taxonomic diversity (average  
416 Shannon index = 0.31). They were mainly represented by postcranial elements of mullets, sea  
417 breams and Mediterranean morays (Fig. 5).

418

419 In the Early Mesolithic (sublayers 6A to 6D) fish remains (NISP = 182; MNI = 53; MNI/m<sup>3</sup> = 31)  
420 and taxonomic variability (average Shannon index = 1.25) increased. These included taxa  
421 already present in the Upper Palaeolithic, such as mullets, sea breams, white seabream  
422 (*Diplodus sargus*), gilthead seabream (*Sparus auratus*), salema (*Sarpa salpa*), and  
423 Mediterranean morays, but also new types such as brown wrasse (*Labrus merula*) and  
424 groupers (*Epinephelus* sp.).

425

426 Finally, a remarkable change occurred during the Late Mesolithic/Early Neolithic (sublayers  
427 5A to 5C), essentially following the aforementioned trend observed in marine molluscs. Fish  
428 remains doubled in number compared to the Early Mesolithic (NISP = 421; MNI = 130),  
429 showing a much higher density (MNI/m<sup>3</sup> = 136) and taxonomic diversity (average Shannon  
430 index = 1.75). The assemblage was dominated by sea breams (including large-eye dentex  
431 (*Dentex macrophthalmus*) and *Dentex* sp.), mullets and morays, followed by combers,  
432 wrasses and gobids. It is worth noting that combers were definitely more abundant, possibly  
433 represented by painted combers (*Serranus* cf. *scriba*) and groupers, the latter with specimens  
434 of up to 90 cm.

435

436 4.3. *Shell AAR and stable isotopes of Phorcus turbinatus: diagenetic integrity of the*  
437 *shells and seasonality of exploitation*

438

439 Diagenetic indices measured on the FAA and THAA fractions from all the 13 shells show very  
440 good covariation (Fig. 6; Supplementary table 4). FAA and THAA values fall on a definite

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

453

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

473

## 474 5. Discussion

475

### 476 5.1. Upper Palaeolithic (Late Pleistocene)

477

478 Shellfish and fish were seldom processed/consumed as food at ORT during the Upper  
479 Palaeolithic at ~14.2 ka cal BP, presumably due to a combination of the distance of the cave  
480 from the coast and the intermittent nature of its occupation, likely used in the context of

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

486

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

499

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

521 (Mannino et al., 2011a). Small abraded gastropod shells were also found in Upper Palaeolithic  
522 deposits at Grotta della Serratura (Colonese and Wilkens, 2005) and Riparo Mochi in the  
523 Italian Peninsula (Stiner, 1999).

524

### 525 5.2. Early Mesolithic (Early Holocene)

526

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

545

### 546 5.3. Late Mesolithic/Early Neolithic (Late Holocene)

547

548 It is during the Late Mesolithic/Early Neolithic occupation that food procurement at ORT had  
549 an unprecedented focus on fish and shellfish, presumably coinciding with the isolation of  
550 Favignana from mainland Sicily. This phase is marked by the prevailing exploitation of reef  
551 species, presumably reflecting the establishment of rockshore environments in the area and  
552 the retraction of coastal lagoons. *P. caerulea/ulyssiponensis* gradually replace *Phorcus* spp. in  
553 abundance and ultimately become the dominant taxa at ORT, as observed in several Late  
554 Mesolithic and Early Neolithic sites along the Tyrrhenian coast of the southern Italian  
555 Peninsula and in Sicily (Durante and Settepassi, 1972; Wilkens, 1993; Colonese and Tozzi,  
556 2010). It is at this time that a significant decrease in the size of *P. caerulea/ulyssiponensis* is  
557 observed at ORT (but not of *P. turbinatus*), but whether this was caused by environmental  
558 changes, human pressure or both is a matter of debate (Colonese et al., 2014). We note that  
559 *Patella* spp. is the more profitable in terms of meat yield (Dupont and Gruet 2002) and thus  
560 even in a context of environmental change *Patella* spp. may still have offered larger energetic

561 returns compared to *P. turbinatus*. The size decrease of *P. caerulea/ulyssiponensis* could thus  
562 represent the combined effect of environmental change and intensification of exploitation.

563

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

573

574 Considering the environmental and biological impact of the isolation of Favignana between  
575 ~9.6 ka and ~7.8 ka BP, increasing fishing and shellfish collection at ORT could be interpreted  
576 as a response to reduced mammalian game on the island. While this strategy might be  
577 expected for foragers, it is less envisioned for farmers who possessed livestock and  
578 domesticated crops to mitigate natural resource fluctuations. Interestingly, the increased  
579 focus on fish and shellfish at ORT, or its relative intensification compared to the previous  
580 phases, roughly mimics a similar trend detected at Grotta dell'Uzzo, where an unprecedented  
581 focus on coastal and marine resources took place during Late Mesolithic and Early Neolithic  
582 (Tagliacozzo, 1993; 1994; Mannino et al., 2015). Conversely to ORT, however, the  $\delta^{18}\text{O}$  data  
583 of *P. turbinatus* shells and fish sclerochronology revealed that shellfish and fish were exploited  
584 in different seasons at Grotta dell'Uzzo, possibly due to a more residential or ritual use of the  
585 cave (Tagliacozzo, 1993; Mannino et al., 2007). Moreover, the steep bathymetry at Uzzo  
586 suggests that the cave was never very far from the coast and therefore intensification of  
587 marine resources had little to do with the sea level rise (Tagliacozzo, 1993). Despite the  
588 contrasting settlement pattern and environmental conditions between ORT and Grotta  
589 d'Uzzo during the Late Mesolithic, we suspect that intensification of marine resources at both  
590 sites responded to common processes operating at the regional scale. Mannino and Thomas  
591 (2009) suggested that population growth since the Early Holocene had a negative impact on  
592 terrestrial faunal turnover in Sicily, consequently increasing competition for resources and  
593 territoriality around profitable resource patches by Late Mesolithic groups. Cultural  
594 transmission among hunter-gatherers, including technology and information on resource  
595 distribution and productivity, is crucial during resource shortfalls and facilitated in areas  
596 under greater population density (Fitzhugh et al., 2011; Eerkens et al., 2014). Under these  
597 conditions coastal areas of NW Sicily may have offered idea contexts for social interaction,  
598 and as such for transferring collective information on marine resource acquisition. The Late  
599 Mesolithic and Early Neolithic at ORT and Grotta dell'Uzzo could be expressions of this  
600 scenario.

601

602 Palaeoceanographic records indicate that there may have been suitable environmental  
603 conditions at this time for supporting an intensification of marine resources. A distinctive  
604 increase in primary productivity, the highest coccolith absolute abundance over the last 25.0  
605 ky, is visible in the Alboran Sea roughly between about 9.5 and 6.0 ka cal BP (Colmenero-  
606 Hidalgo et al., 2004; Ausín et al., 2015). The primary productivity increase was likely triggered  
607 by the post-glacial sea-level rise, at its maximum rate during the meltwater pulse 1B just after  
608 the Younger Dryas (Lambeck et al., 2014), that promoted the maximum water exchange at  
609 the Gibraltar Strait (Myers et al., 1998). Enhanced Atlantic surface water inflow, which is  
610 nutrient-enriched compared to Mediterranean water, may have fuelled phytoplankton  
611 blooming (Ausín et al., 2015). This mechanism is potentially suitable to increase productivity  
612 in a large sector of the western-central Mediterranean Sea, because the response of nutrient  
613 dynamics to late Quaternary climatic variations seems to be similar in the Sicily Channel and  
614 Alboran, southern Tyrrhenian and Balearic Seas (Incarbona et al., 2013; Di Stefano et al.,  
615 2015). This is especially true for the Egadi Archipelago region, where long time series  
616 estimates of chlorophyll concentration by satellite imagery demonstrate that approximately  
617 80% of the variance is explained by the advection of chlorophyll- and nutrient-enriched  
618 Atlantic Water (Rinaldi et al., 2014).

619

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

630

631 An abrupt increase in marine productivity also involved the eastern Mediterranean Sea  
632 between about 10.5 and 6 ka cal BP, during the deposition of the most recent organic-rich  
633 layer, the so-called sapropel S1 (Casford et al., 2002; Rohling et al., 2015). Peaks of biogenic  
634 barite and concordant indication of a deep chlorophyll maximum in micropaleontological  
635 studies (Rohling and Gieskes, 1989; Castradori, 1993; Kemp et al., 1999; Meier et al., 2004)  
636 testify to a dramatic ecological change in this part of the Mediterranean Sea, which is today  
637 one of the poorest trophic areas in the world. This may have again supported the larger  
638 economic focus on marine resources in this region (Rose, 1995; Mylona, 2003; Rainsford et  
639 al., 2014), including the development of early fishing villages (Galili et al., 2003; 2004), adding  
640 to the complex, multidimensional nature of coastal exploitation in the Mediterranean.



641

642 **6. Conclusions**

643

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

659

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674

675 **Contributions**

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

679

680 **Figure captions**

681

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

684

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

688

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

697

698 **Figure 4.** Absolute abundance of echinoderm and crustacean remains from Upper  
699 Palaeolithic, Mesolithic and Late Mesolithic/Early Neolithic deposits. Their density for the  
700 volume of sediment (MNI/m<sup>3</sup>) is also reported.

701

702 **Figure 5.** Relative abundance (%NISP) of fish remains from Upper Palaeolithic, Mesolithic and  
703 Late Mesolithic/Early Neolithic deposits, including their density for the volume of sediment  
704 (MNI/m<sup>3</sup>), species diversity and the environmental gradient represented by first axis of the  
705 correspondence analysis. The ecological attributions refer to the Habitat type of the European  
706 Union Habitats Directive  
707 ([http://ec.europa.eu/environment/nature/natura2000/marine/index\\_en.htm](http://ec.europa.eu/environment/nature/natura2000/marine/index_en.htm)); 1120:  
708 Posidonia beds (*Posidonia oceanica*); 1130: Estuaries; 1150: Coastal lagoons; 1160: Large  
709 shallow inlets and bays; 1170: reefs.

710

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

714

715 **Figure 7.** Oxygen isotope composition of *Phorcus turbinatus* shell. A) sequential  $\delta^{18}\text{O}$  values  
716 of shells from sublayer 5B and 6B; B) the distribution of  $\delta^{18}\text{O}$  values (0.5‰ bins) of shells from  
717 sublayer 5B and 6B indicate low temperature when compared with the range of  $\delta^{18}\text{O}$  values  
718 from sequential shells (dark and grey bands and dotted lines); C) Jitter plot of  $\delta^{18}\text{O}$  values of  
719 *Phorcus turbinatus* from Grotta d’Oriente for Early Mesolithic and Late Mesolithic/Early  
720 Neolithic deposits. The interpretation is based on the comparison between shell aperture

721  $\delta^{18}\text{O}$  values (filled black circles) against the sequential  $\delta^{18}\text{O}$  values (grey circles and boxplot).  
722 Data from 5A and 6C were taken from Colonese et al. (2009). Data from trenches were taken  
723 from Mannino et al. (2014).

724

## 725 **Table captions**

726

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

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732

## 733 **Supplementary information (Figures)**

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

735

## 736 **Supplementary information (Table)**

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

740

741 **Supplementary table 2.** Freshwater molluscs recovered in Upper Palaeolithic and Early  
742 Mesolithic deposits.

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

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

749 **Supplementary table 5.** Oxygen isotope values obtained on shells of *Phorcus turbinatus* from  
750 Mesolithic (layer 6B) and Late Mesolithic/Early Neolithic (layer 5B) deposits.

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