Late Pleistocene-Holocene coastal adaptation in central Mediterranean: snapshots from Grotta d'Oriente (NW Sicily)

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Abstract

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

Keywords

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

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

2. Archaeological setting

2.1. Grotta d'Oriente

The island of Favignana, the largest (~20 km^2) of a group of small islands forming the Egadi Archipelago, is situated ~5 km from the NW coast of Sicily (Fig. 1A). There, Grotta d'Oriente (ORT) opens on the north-eastern slope of Montagna Grossa, overlooking the sea at ~40 m above sea level. The cave has two distinct areas, a small chamber to the left of the entrance (south) and a large gallery to the right (north) (Martini et al., 2012). Previous excavations were conducted in the small chamber in 1972 (Mannino, 1972; 2002; Mannino et al., 2012; 2014), and it was excavated again in 2005 as part of an interdisciplinary project carried out by the University of Florence and Museo Fiorentino di Preistoria. The results presented in this study are part of this multidisciplinary research programme and details of the stratigraphy, material culture and burial practice can be found in Lo Vetro and Martini (2006) and Martini et al. (2012).

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

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

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

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

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

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

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

2.2. Environmental setting

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

3. Materials and methods

3.1. Faunal remains

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

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

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

In order to explore diachronic variations within each faunal category we standardised the faunal indicators (NISP, MNI) for the total volume of sediment (m^3) for each archaeological sublayer (e.g. Zangrando, 2009; Jerardino, 2016; Perlès, 2016). This approach inherently assumes constant deposition rates, in addition to minimal differences in sedimentary matrix, preservation conditions through the succession (Jerardino, 1995; 2016) and the non-contiguous distribution of the remains when the sedimentary deposits include structures such as hearths and pits. Due to the limited number of radiocarbon dates, the deposition rate could be estimated only between sublayers 6B and 6D (2.06 m/ka). However, the average volume 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 (0.11 m^3, sublayers 7D and 7E) suggest comparable depositional rates in most parts of the deposit. The nature of the sedimentary matrix has not been studied in detail, however according to field observations there were few differences between layers 5 and 6, which were mainly composed of silts and sand typically found in active karst settings (Woodward and Goldberg, 2001). In contrast, layer 7 showed an increase in clay and considerably lower anthropogenic deposits (for faunal remains see below). Finally, the presence of fish and small fragile shell remains (e.g. freshwater) is clear evidence of good overall preservation (see below). Shell fragmentation is minor and prevalently related to food processing (in the case of *P. turbinatus*) as well as *post-mortem* taphonomic processes prior to shell transport into the cave for non-food taxa (see below).

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

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

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

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

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

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

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

After rinsing and air-drying, shells were partially embedded in an epoxy resin (Araldite rapid epoxy) and sectioned perpendicularly to the growth lines at the aperture, using a Buehler Isomet 1000 Precision Saw. Four samples were taken from the inner nacreous aragonite layer, starting from the shell aperture toward the apex, with an interval of ~1 mm using a manual microdrill with a 0.4 mm drill bit following the method described in Mannino et al. (2007) and Colonese et al. (2009). In short, samples taken at the shell aperture were milled in order to collect only the most recent shell deposits (Fig. 2A). The aperture $\delta^{18}O$ values are used to interpret the season of collection. One shell per sublayer was selected for sequential isotope analysis (~30 samples) using the sampling techniques described above (Fig. 2B). The sequential $\delta^{18}O$ values provide the intra-annual range of temperature against which the aperture $\delta^{18}O$ values can be compared.

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

4. Results

4.1. Shellfish remains

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

Upper Palaeolithic deposits (sublayers 7B to 7E; Fig. 3) contained the least number of mollusc remains of the entire sequence (MNI = 1306; MNI/m^3 = 1711) and a relatively high taxonomic variability (average Shannon index = 1.54). These were dominated by small-sized species typically found in lagoons, estuaries, large shallow inlets and bays such as *Pirenella conica* (52%) and *Bittium* spp. (23%). Their shells were fragmented and abraded due to exposure to near-shore waves or currents (Bosch et al., 2015b), and were likely transported incidentally into the cave, thus they are hereafter considered non-food taxa (Jerardino, 1993; Stiner, 1999). Taxa possibly exploited as food (17%) included *Cerithium vulgatum, Porchus turbinatus*, *Phorcus articulatus, P. caerulea/ulyssiponensis*, collected in large shallow inlets, bays and lagoons, and intertidal reefs. Few shells of *P. turbinatus* (8.8%) were fractured or had their apex sectioned for removing the animal flesh as observed in other Upper Palaeolithic and Mesolithic sites in Sicily (Compagnoni 1991; Mannino et al., 2011). Crustaceans (MNI = 78) and echinoderms (MNI = 127) were similarly retrieved from these deposits, and were represented by *Eriphia verrucosa* and *Paracentrotus lividus*, respectively (Fig. 4). Freshwater molluscs were found in several Upper Palaeolithic layers and included the genera *Stagnicola* (*Stagnicola* cf. *fuscus*) *and Lymnea* (*Lymnaea* (*Galba*) *truncatula*), very likely transported incidentally to the cave (Supplementary table 2).

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

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

4.2. Fish remains

Fish remains (n = 2570) were retrieved from Upper Palaeolithic, Early Mesolithic and Late Mesolithic/Early Neolithic deposits (Fig. 5; Supplementary table 3). The number of identified specimens (NISP = 616) could only be established for 23.9% of the remains. Fish were mainly represented by postcranial elements in all phases (~78%), followed by cranial elements (16.5%) and undetermined fragments (5.3%). This pattern is suggestive of fish consumption and refuse in place, instead of processing for consumption elsewhere (Stewart, 1991; Zohar et al., 2001). Burn marks were also observed on ~41% of the remains, with this value remaining fairly consistent throughout the stratigraphy. The taxonomic composition includes sea breams (Sparidae; 35%), morays (Murenidae; 29%), grey mullets (Mugilidae; 20%), wrasses (Labridae; 8%), combers (Serranidae; 7.7%) and gobids (Gobiidae; 0.2%). With the exception of large-eye dentex (*Dentex macrophthalmus*), all these taxa could have been captured from the shore, in shallow waters using a variety of tools, including nets, traps, weirs, harpoons and hooks (Morales Muñíz, 2007). The number of remains and the taxonomic diversity increased progressively from the Upper Palaeolithic to the Late Mesolithic/Early Neolithic deposits. The distribution pattern observed in the CA provides two main ordination axes that cumulatively explain more than 70% of the variability in species composition among the sublayers (Supplementary figure 1B). However there is no clear environmental gradient suggesting that fish were captured in a variety of coastal environments through the sequence, although reef environments seem to be more represented in Late Mesolithic/Early Neolithic deposits.

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

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

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

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

Diagenetic indices measured on the FAA and THAA fractions from all the 13 shells show very good covariation (Fig. 6; Supplementary table 4). FAA and THAA values fall on a definite diagenetic trajectory, thus displaying excellent closed-system behaviour. This indicates that the inner nacreous aragonite sublayer was not compromised during the burial history (Bosch et al., 2015a) and that it is likely that the original oxygen isotope composition is retained. This was confirmed by XRD indicating that the inner shell deposit used for stable isotope analysis was pure aragonite. Moreover, microscopic analysis did not reveal any recrystallized or dissolved carbonate, and microgrowth increments were clearly visible on the inner nacreous aragonite sublayer of the sectioned shells. We also note that Ala and Asx D/Ls and [Ser/Ala] values offered the best resolution between sublayers 5A and 6B, and show that shells from sublayer 5A are less degraded (and therefore younger) than those from sublayer 6B and sublayer 7D. Despite the limited resolution of the method over these timescales, this can be considered as independent evidence for supporting the radiocarbon dates for the sublayers and the general integrity of the stratigraphic sequence.

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

5. Discussion

5.1. Upper Palaeolithic (Late Pleistocene)

Shellfish and fish were seldom processed/consumed as food at ORT during the Upper Palaeolithic at ~14.2 ka cal BP, presumably due to a combination of the distance of the cave from the coast and the intermittent nature of its occupation, likely used in the context of foraging trips (e.g. as a campsite or location *sensus* Binford, 1980). This is supported by the dearth of terrestrial faunal remains (NISP = 125; Martini et al., 2012), as well as by oxygen isotopic data from *P. turbinatus* shells (sublayer 7C) attesting to short episodes of collection during the coldest months of the year, as also detected in other Upper Palaeolithic sites the NW Sicily (Mannino et al., 2011a).

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

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

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

5.2. Early Mesolithic (Early Holocene)

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

5.3. Late Mesolithic/Early Neolithic (Late Holocene)

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

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

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

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

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

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

6. Conclusions

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

Acknowledgements

The excavation of Grotta d'Oriente in 2005 was funded by the *Regional Operational Programme for Sicily 2000/2006, II, 2.0.1.* (European Commission), under the authorization of the Soprintendenza ai Beni Culturali e Ambientali di Trapani (Regione Siciliana, Assessorato ai Beni Culturali e Ambientali). The AAR analyses were supported by the EU (Re)Integration grant mAARiTIME PERG07-GA-2010-268429; Sheila Taylor is thanked for her help in the laboratory. The authors thank Sebastiano Tusa and Rossella Giglio for their logistic and administrative support during and after the fieldwork. The authors also wish to thank all the people involved in the archaeological excavation and in the multidisciplinary research at Grotta d'Oriente since 2005. We thank Giovanni Mannino for his useful information about the 1972 excavation, Catherine Perlès for commenting on the early draft of this manuscript, Ivan Briz Godino for analytical support of radiocarbon dating of the two *Pirenella* shells and Krista McGrath for reviewing the English. Finally we thank the reviewers for their constructive comments on the manuscript.

Contributions

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

Figure captions

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

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

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

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

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

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

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

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

Table captions

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

Supplementary information (Figures)

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

Supplementary information (Table)

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

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

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

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

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

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