



Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Marine mollusc exploitation in Mediterranean prehistory: An overview

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ARTICLE INFO

Article history:

Available online xxx

ABSTRACT

Marine molluscs have been recovered from sites around the Mediterranean Sea dating as far back as the Lower Palaeolithic, when hominins might have started consuming them (ca. 300 ka). During the Middle Palaeolithic and the early Upper Palaeolithic, humans (*Homo neanderthalensis* and *Homo sapiens*) ate molluscs at many sites across the Mediterranean at least as early as the Last Interglacial, although the scale of this exploitation is still unclear, due to biases produced in the coastal archaeological record by Late Glacial and post-Glacial sea level rise. The exploitation of marine molluscs apparently increased in the Late Glacial and Early Holocene, when humans collected them in relatively large quantities and from all available ecosystems. The consumption of shellfish, and of other small animals (aquatic and continental), probably contributed to the success of the flexible and opportunistic subsistence strategies adopted by Mediterranean hunter–gatherers for much of prehistory. This is particularly evident in later foraging economic systems (i.e. late Upper Palaeolithic and Mesolithic), in which coastal resources probably acted as buffers against the negative outcomes of environmental and anthropogenic impacts on available resources.

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1. Introduction

The role of marine molluscs in hunter–gatherer diets has generated more debate among archaeologists than that of any other aquatic resource exploited by humans in the past (Erlandson, 2001). In spite of this, “there is no established consensus on the dietary contribution of marine molluscs to early human subsistence economies, mainly due to differing methods of analysis and inherent biases” (Fa, 2008). Much of the debate on the role of marine resources has centred on oceanic regions, characterized by high levels of primary productivity and, as a result, by the presence of large shell middens containing astronomical numbers of molluscs (e.g. Bailey and Milner, 2002/2003; Bailey and Flemming, 2008; Rick and Erlandson, 2008).

The role of marine resources in prehistoric Mediterranean subsistence and of molluscs, in particular, has received far less attention. This is partly due to the fact that large shell middens,

similar to those present in oceanic regions of the world, are not apparently present along the coasts of the Mediterranean Sea (Bailey and Flemming, 2008). As a result, the contribution of shellfish to the subsistence of Mediterranean hunter–gatherers has rarely been considered in sufficient detail. This tendency has favoured, especially in the past, simplistic interpretations attributing a marginal role to coastal resources in prehistoric Mediterranean diets. Some studies (e.g. Stiner, 1994, 1999; Aura et al., 2002a, 2009; Stringer et al., 2008), however, have reevaluated the contribution of marine foods, including molluscs, by demonstrating the antiquity of their exploitation and highlighting their potential as key resources at times of climatic and environmental change, and/or during demographic crises. A recent study by Fa (2008), on the effects of tidal amplitude on intertidal resource availability, has demonstrated that the nature of the coastal habitats has a direct effect on mollusc biomass and productivity. This should be taken into account, especially in the case of the Mediterranean Sea, which compared to oceanic regions is nutrient-poor and characterized by restricted tidal ranges.

A detailed evaluation of the potential role of marine resources in the Mediterranean is, therefore, necessary and overdue considering that the basin is one of the key areas for understanding the human

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cultural processes that took place during the Quaternary. Its geographic position has favoured long-term cultural interactions between Europe, Africa and Asia, with coastal areas operating as corridors for human migrations (e.g. Bailey et al., 2008; Barton et al., 2008; Carrión et al., 2008), but also as settings for the development of complex hunter–gatherer adaptations during the Palaeolithic and Mesolithic. The present article is a review of the exploitation of marine molluscs by prehistoric Mediterranean hunter–gatherers. The aims of this paper are to evaluate what changes in marine mollusc exploitation occurred through time, to hypothesize what contribution marine molluscs made to the subsistence and diet of Mediterranean hunter–gatherers at different stages in prehistory and to propose new avenues of research which should be pursued to improve understanding of prehistoric shellfish exploitation in the region.

Although the present paper will focus on the exploitation of marine molluscs and of other coastal resources, numerous lines of evidence indicate that the diet of Mediterranean hunter–gatherers was centred mainly upon terrestrial resources (e.g. Payne, 1975; Tagliacozzo, 1993; Stiner, 2005; Guixé et al., 2006; Martini et al., 2007a, 2007b; Craig et al., 2010). The ample geographical and chronological scope of this paper precludes providing a detailed account of the zooarchaeology of Mediterranean prehistory, a topic which has been covered by other studies (e.g. Stiner, 1994, 2001, 2005; Stiner et al., 1999, 2000). In the discussion, however, the role of marine molluscs in hunter–gatherer diets will be evaluated in relation to other sources of evidence ('terrestrial zooarchaeology', isotope evidence, etc.). Before starting to review the archaeological evidence for the exploitation of marine molluscs, it is necessary to describe the defining features of present and past Mediterranean coastal environments, as this is indispensable for a detailed understanding of prehistoric hunter–gatherer adaptations.

2. Environmental setting

The Mediterranean Sea is a semi-enclosed basin (roughly between 30° and 45°N) surrounded by Europe, Asia and Africa. It has an area of about 2.5 million km² and extends over 3700 km in longitude and 1600 km in latitude (Fig. 1). With a coastline of 46,000 km, the basin is connected to the Atlantic Ocean by the Strait of Gibraltar on the west and to the Sea of Marmara and the Black Sea by the Dardanelles and Bosphorus respectively, on the north-east. The Mediterranean Sea is formed by two major basins (western and eastern), which are divided at the Strait of Sicily and at the Strait of Messina. For the purposes of this paper the basin is divided

according to its dominant coastlines: western (coasts of Spain, France, Morocco and Algeria), central (coasts of Italy and of the Adriatic Sea in the north, Tunisia in the south) and eastern (including the Mediterranean from Greece and Libya to the Levant).

2.1. The present-day Mediterranean coasts

The coasts of the Mediterranean Sea are characterized by complex physiographic, geological and ecological features. The complex orography of Mediterranean coastal areas, in which extensive reliefs alternate with small coastal plains, favours the presence over short distances of different coastal ecosystems and elevated biodiversity (e.g. Blondel and Aronson, 1999; Bianchi and Morri, 2000; Spalding et al., 2007). In spite of the rich marine biodiversity, the productivity of the Mediterranean Sea is low (e.g. Zenetos et al., 2002), mainly due to the scarce continental runoff into the basin and the absence of significant upwelling (e.g. Caddy, 1993; Ibañez et al., 2000). Primary productivity displays a west–east gradient, with the highest levels being present in the westernmost part of the Mediterranean (i.e. the Alboran Sea) and the lowest in the east (Antoine et al., 1995; Danovaro et al., 2008). At the local level, higher productivity is encountered in areas characterized by wide continental shelves and along coasts with freshwater outputs. Transitional waters are usually present along these shores (e.g. Basset et al., 2006), which in the Mediterranean, as elsewhere, constitute some of the most productive environments (e.g. Blondel and Aronson, 1999; Roberts and Reed, 2009). Another limiting factor for the productivity of Mediterranean littoral zones is the low tidal amplitude (usually less than 30 cm), which is due to the weak influence of astronomic forces on the coastal waters of this enclosed basin (Ibañez et al., 2000; McCully, 2006).

The generally steep coastal morphology, low productivity and restricted tidal range of the Mediterranean Sea all have a significant impact on the availability and biomass of marine molluscs in the Mediterranean compared to oceanic regions (Fa, 2008). This implies that what is ecologically possible in terms of mollusc productivity and, consequently, for the potential role of marine molluscs in human subsistence in oceanic regions is probably not possible in Mediterranean settings.

The marine molluscs of the Mediterranean Sea include around 1800 native species (Sabelli et al., 1990; Gofas and Zenetos, 2003). In the eastern basin there are no more than 900 species today, including Lessepsian migrants (Galil, 2007). Only a few of these species of gastropods and bivalves have been exploited by humans for food and occur in high frequencies in archaeological deposits

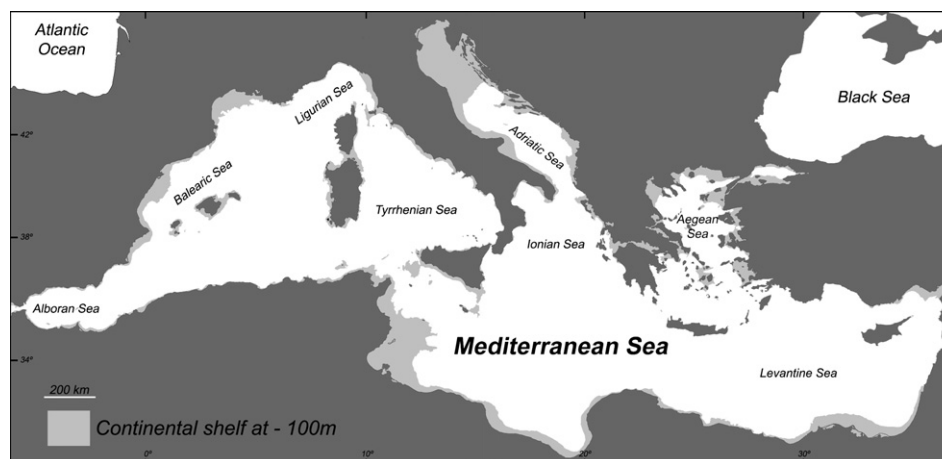


Fig. 1. Map showing the Mediterranean basin and smaller water bodies, and illustrating the continental shelf at –100 m.

Table 1

Main marine mollusc species exploited for food during the Palaeolithic and the Mesolithic in Mediterranean regions. Also reported are principal Habitat type codes according to the European Union Habitats Directive (source http://ec.europa.eu/environment/nature/natura2000/marine/index_en.htm) – 1110: Sandbanks which are slightly covered by sea water all the time; 1130: Estuaries; 1150: Coastal lagoons; 1160: Large shallow inlets and bays; 1170: Reefs. Substrate – H: hard; S: soft.

Family	Genus	Species	Habitat type code	Substrate
Gastropoda				
Patellidae	<i>Patella</i>	<i>P. caerulea</i> Linnaeus, 1758	1170	H
		<i>P. ferruginea</i> Gmelin, 1791	1170	H
		<i>P. rustica</i> Linnaeus, 1758	1170	H
		<i>P. ulysiponensis</i> Gmelin, 1791	1170	H
Trochidae	<i>Gibbula</i>	<i>G. divaricata</i> (Linnaeus, 1758)	1170	H
		<i>G. rarilineata</i> (Michaud, 1829)	1170	H
	<i>Osilinus</i>	<i>O. articulatus</i> (Lamarck, 1822)	1170	H
		<i>O. turbinatus</i> (Von Born, 1778)	1170	H
Cerithiidae	<i>Cerithium</i>	<i>C. vulgatum</i> Bruguière, 1792	1110, 1160	S
Muricidae	<i>Hexaplex</i>	<i>H. trunculus</i> (Linnaeus, 1758)	1110, 1160	H,S
Bivalvia				
Cardiidae	<i>Acanthocardia</i>	<i>A. tuberculata</i> (Linnaeus, 1758)	1110, 1160	S
	<i>Cerastoderma</i>	<i>C. glaucum</i> (Bruguière, 1789)	1110, 1130, 1150, 1160	S
Veneridae	<i>Callista</i>	<i>C. chione</i> (Linnaeus, 1758)	1110	S
	<i>Chamelea</i>	<i>C. gallina</i> (Linnaeus, 1758)	1110, 1160	S
	<i>Ruditapes</i>	<i>R. decussatus</i> (Linnaeus, 1758)	1110, 1160	S
Glycymerididae	<i>Glycymeris</i>	<i>G. bimaculata</i> (Poli, 1795)	1110, 1160	S
		<i>G. insubrica</i> (Brocchi, 1814)	1160	S
Spondylidae	<i>Spondylus</i>	<i>S. gaederopus</i> Linnaeus, 1758	1170	H
Mytilidae	<i>Modiolus</i>	<i>M. barbatus</i> (Linnaeus, 1758)	1170	H
	<i>Mytilus</i>	<i>M. galloprovincialis</i> Lamarck, 1819	1170	H
Ostreidae	<i>Ostrea</i>	<i>O. edulis</i> Linnaeus, 1758	1110, 1160, 1170	H,S
Pectinidae	<i>Pecten</i>	<i>P. jacobaeus</i> (Linnaeus, 1758)	1110, 1160	S
		<i>P. maximus</i> (Linnaeus, 1758)	1110, 1160	S

(Table 1; Fig. 2). The most easily gathered taxa are intertidal rocky shore molluscs, the most productive of which in terms of biomass in Mediterranean coasts are in order *Mytilus* sp., *Patella* spp. and *Osilinus* spp. (Fa, 2008). The western and eastern Mediterranean share the same species of intertidal rocky shore molluscs, with the exception of *Patella ferruginea*, which is by far the largest *Patella* and occurs only in the western basin (Guerra-García et al., 2004). On soft bottom shores, intertidal species are also the easiest to exploit, and the main taxon is the bivalve *Cerastoderma glaucum*, a typical inhabitant of brackish water lagoons (e.g. Brock, 1987; Gontikaki et al., 2003; Derbali et al., 2009). This species may be present in dense populations and provide considerable biomass seasonally

(e.g. Derbali et al., 2009). Rocky and soft bottom shore species living in the sub-littoral require a greater effort to collect, negotiation with deeper waters and, even swim. It is possible that some of these species could occasionally be collected live on the shore, washed up in very low numbers after storms and rough seas.

2.2. Sea levels in the Mediterranean during the Pleistocene and Early Holocene

The main transformations registered in Mediterranean coastal areas during the Quaternary are represented by eustatic–isostatic–tectonic sea level fluctuations, which produced significant

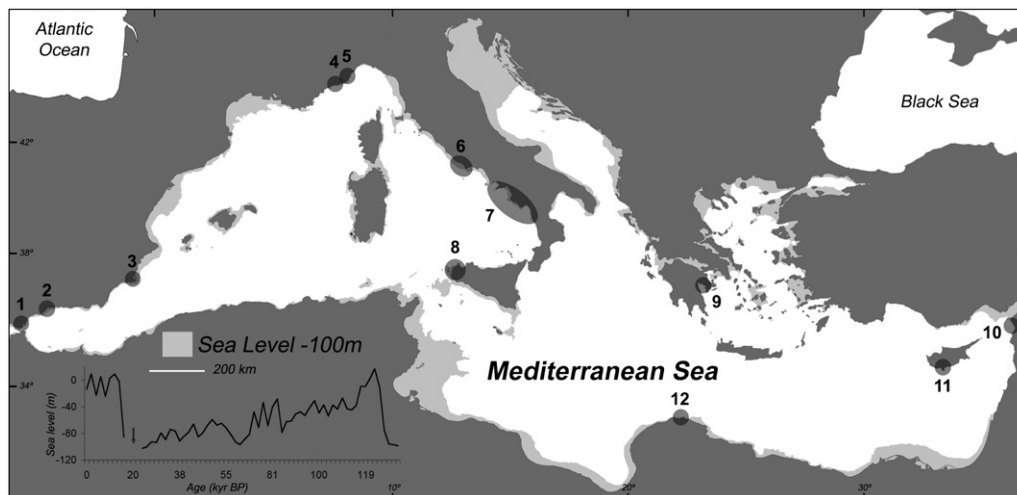


Fig. 2. The Mediterranean basin and main sites, and groups of sites, cited in the text: 1) Gibraltar caves; 2) Cueva de Nerja; 3) Cueva Perneras and Cueva de los Aviones; 4) Terra Amata and Grotte du Lazaret; 5) Riparo Mochi; 6) Grotta dei Moscerini and Riparo Blanc; 7) Grotta del Mezzogiorno, Grotta della Serratura and Grotta della Madonna; 8) north-west Sicilian sites; 9) Franchthi Cave; 10) Ksar 'Akil and Üçağızlı; 11) Aetokremnos; 12) Haua Fteah. The continental shelf at –100 m and the Late Pleistocene–Holocene sea level fluctuations (Siddall et al., 2003) are also illustrated. The arrow in the sea level trend indicates an interruption of the record (see Siddall et al., 2003). Sea level fluctuations operated against the survival of the earliest shellfish assemblages, some of which have been preserved because they were relatively far inland or located on steeply-shelving shorelines, each of which may have imposed particular biases on the resulting mollusc assemblages.

environmental changes in littoral ecosystems, but also had an impact on the archaeological record (e.g. van Andel, 1989; Lambeck, 1996; Lambeck and Bard, 2000; Flemming et al., 2003; Bailey and Flemming, 2008). Sea level has been quite stable during the last 7000 years, but in the Early Holocene and for most of the Pleistocene it was much lower than at present, being as low as –120 m during the Last Glacial Maximum (LGM) around 20 ka cal BP (Siddall et al., 2006). As a consequence, large extensions of the Mediterranean continental shelf emerged, favouring littoral ecosystems which are no longer present and which would have been inhabited and exploited by prehistoric humans (e.g. van Andel and Shackleton, 1982; van Andel, 1989; Lambeck, 1996; Faure et al., 2002; Flemming et al., 2003; Bailey and Flemming, 2008). The melting of northern hemisphere ice sheets, after ca. 20 ka BP, produced a rapid and progressive rise in sea level, which reduced the extent of coastal plains and caused the submergence of many prehistoric sites. This has a direct bearing on the ‘visibility’ of evidence for marine resource use (e.g. Bailey and Flemming, 2008). Bailey and Craighead (2003) have illustrated how such evidence decreases rapidly with increasing distance inland. Given that remaining sites with evidence of marine exploitation would have been some distance inland from Marine Isotope Stage (MIS) 2 and 3 coastlines, a significant under-representation of these activities is to be expected, particularly where the continental shelf is shallow and wide. The relative scarcity of proof of marine resource utilisation during the Palaeolithic at these sites only then serves to further emphasise the apparent lateness and geographical marginality of coast-oriented subsistence economies (Bailey and Milner, 2002/2003).

In the following sections of this paper, evidence for the exploitation of marine molluscs will be presented for sites from the Lower Palaeolithic to the Mesolithic and from the three areas of the Mediterranean defined above (western, central and eastern). Few studies in the literature report information on the mollusc assemblages other than quantitative descriptions, usually based on MNI counts, and limited taphonomic observations. The dearth of systematic taphonomic studies makes it difficult to assess how many of the taxa recovered in prehistoric Mediterranean sites were actually collected for dietary purposes. However, as the objective of the present review is to assess the role of marine mollusc exploitation in the subsistence of the hunter–gatherer of the Mediterranean Basin, the focus is mainly on edible taxa (Table 1), which are usually medium-to-large sized and which generally dominate the mollusc assemblages. Where possible, the focus is on cases for which the recovery of molluscan remains was thorough and taphonomic evaluations are available.

3. Lower Palaeolithic

Hominins possibly started exploiting shellfish along Mediterranean shores as early as the Lower Palaeolithic. The oldest Mediterranean site at which, to the authors’ knowledge, shells of marine molluscs have been recovered is Terra Amata near Nice (southern France) dating to around 300 ka and associated with Acheulean industries, which are known to have been produced by pre-Neanderthal hominins (i.e. *Homo erectus*, *Homo heidelbergensis*). The molluscs found are Ostreidae, Mytilidae and Patellidae (de Lumley, 1966), but given the lack of more detailed information on these finds it is not possible to conclude whether they were eaten by the Lower Palaeolithic occupants of the site. A few shells were also found at another Lower Palaeolithic site near Nice, Grotte du Lazaret, in Acheulean horizons dating to MIS 6 (ca. 186–127 ka). The molluscs recovered include intertidal rocky shore taxa (Patellidae, Trochidae and Littorinidae) and taxa that live on seaweed, such as *Bittium reticulatum* (Barrière, 1969). Patellidae and Trochidae might have been collected for food, although this has not been clearly

demonstrated. On the other hand, *B. reticulatum* is a small gastropod which lives amongst seaweed and seagrasses and, for this reason, it has been hypothesised that it was introduced accidentally into the cave along with *Posidonia oceanica* foliage, which according to Barrière (1969) was used by humans as a form of bedding.

4. Middle Palaeolithic

4.1. Western Mediterranean

Recent studies on Middle Palaeolithic sites, attributable to the Mousterian, in Gibraltar (e.g. Stringer et al., 2008) and in the Murcia province of Spain (Zilhão et al., 2010) have demonstrated that marine molluscs were exploited by Neanderthals in the southern Iberian Peninsula. In Gibraltar, three sites (Devil’s Tower, Gorham’s Cave and Vanguard Cave) contained evidence for the exploitation of marine resources, including mammals (Pinnipedia and Delphinidae), fish and molluscs. The Mousterian layers at Devil’s Tower contained mollusc remains, mainly of *Mytilus galloprovincialis* and of different species of *Patella*, including both Atlantic (*Patella vulgata*) and Mediterranean (e.g. *P. ferruginea*) taxa (Garrod et al., 1928), which were probably collected for consumption. Soft bottom species, although scarce in Mousterian deposits, include *Acanthocardia* spp., *Callista chione*, *Lucinoma borealis*, *Pecten maximus*, *Pecten jacobaeus*, and *Spondylus gaederopus* (Fa, in press). Fa (in press) suggests that the observed constancy of the same species between sites, albeit present in low frequencies, may be indicative of low-level exploitation for food, irrespective of how they were collected.

The Middle and Upper Palaeolithic layers of Gorham’s Cave were characterized by an assemblage (1423 shell fragments of 14 mollusc species) composed almost exclusively of rocky shore taxa such as *M. galloprovincialis*, the Atlantic species *Modiolus modiolus*, and *Patella* spp. (Baden-Powell, 1964). As reviewed by Erlandson and Moss (2001), the same deposits contained several pinniped (*Halichoerus grypus*, *Monachus monachus*) and cetacean bone fragments, as well as abundant bird bones, some of which are seabirds and carrion feeders (e.g. Accipitridae, Corvidae, etc.). The lack of a detailed taphonomic study of the shells from Waechter’s excavations at Gorham’s Cave and the presence of seabirds, carrion feeders and bone accumulators (Hyaenidae, Ursidae, etc.) has led Erlandson and Moss (2001) to suggest that “Gorham’s Cave – as well as many other early coastal localities – probably contains a complex amalgamation of faunal remains from both aquatic and terrestrial species that accumulated through a combination of cultural and non-cultural processes”. Recent investigations of mollusc remains from Middle and Upper Palaeolithic levels at Gorham’s Cave confirm that out of at least 14 species found, the main species exploited for dietary purposes are *Patella* spp. (including *P. caerulea*, *P. depressa*, *P. ferruginea*, *P. ulissiponensis*, *P. vulgata*), followed by *Mytilus* spp. (*M. galloprovincialis*, *M. edulis*) and *Osilinus turbinatus*, all easily-collected taxa living on rocky shores (Fa, 2008, in press). These recent investigations have taken place in an area not previously excavated, deep within the cave. Dates for excavated Mousterian levels place the last Neanderthal presence at this site at around 28 ka BP, possibly as recently as 24 ka BP (Finlayson et al., 2006; Finlayson et al., 2008), making it to date the most recent site of Neanderthal occupation in the world. Above this level, there is no evidence of human occupation at the site until levels dated to around 18 ka–11 ka BP, with Upper Palaeolithic (Solutrean) technologies. Based on data from rocky shore molluscs collected for consumption, Fa (in press) has reported no significant differences in either types or relative proportions of these species between Mousterian and Solutrean levels, suggesting that, at least at this site, the mode and tempo of exploitation

of these marine resources remained remarkably consistent. Similar results were obtained by Brown et al. (in press) for the exploitation of small game such as lagomorphs and birds by both Neanderthals and Anatomically Modern Humans (AMHs), the birds being dominated by rock dove (Columbidae) and choughs (Corvidae), as well as including cryptic, ground-dwelling species such as quail and partridge (Phasianidae), marine species such as gannet (Sulidae) and cormorants (Phalacrocoracidae) and lagoon/estuarine species such as ducks (Anatidae).

The only subtidal, soft bottom species reported in this Mousterian level to date is *P. maximus*, also present in the Solutrean level (Fa, in press). All shells of genus *Pecten* found, both in Mousterian and Solutrean levels, were right (curved) valves. Whether collected live from the seabed or washed up on the shore, the noticeable lack of left (flat) valves suggests that some selection process (anthropic, natural or a combination of both) was operating (Fa, in press). Marine molluscs recovered from Mousterian deposits at Vanguard Cave, which accumulated between MIS 5 and 3, are dominated by *M. galloprovincialis* (Stringer et al., 2008), followed by *Patella* spp. (Barton, 2000). According to Stringer et al. (2008) molluscs were gathered and transported to the cave by humans, where fire was used to cook and open the shells. The apparently large size of *M. galloprovincialis* in question has led Barton (2000) and Fernández-Jalvo and Andrews (2000) to suggest that these molluscs must have been collected in an estuarine environment, rather than on the nearby rocky shore, but Fa (in press) reports that large *M. galloprovincialis* (>10 cm shell length) are very numerous along the rocky seaboard immediately outside the site today. He notes that at more temperate latitudes, *M. galloprovincialis* of the size obtained at Vanguard are usually from more productive, estuarine environments and suggests that this observation was probably a case of mis-application of ecomorphometric data, an additional aspect that needs to be considered when critically assessing environmental interpretations. Moreover many other possible factors can affect marine mollusc shell size, including physical, chemical and biological factors (e.g. Rhoads and Lutz, 1980; Ricciardi and Bourget, 1999). Additional evidence for the exploitation of animals from littoral environments has been retrieved from all the Middle Palaeolithic deposits explored at Gibraltar, attesting that Neanderthals also exploited crustaceans (*Eriphia verrucosa*), echinoderms (*Paracentrotus lividus*) and fish (e.g. *Diplodus* spp., *Thunnus thynnus*) (Brown et al., in press), as well as marine mammals (*M. monachus*, *Tursiops truncatus*, *Dephinus delphis*) and seabirds (e.g. *Alca impenis*), the acquisition of which might have taken place during seasonal forays primarily aimed at shellfish collection (e.g. Stringer et al., 2008; Brown et al., in press).

Other sites in southern Iberia have yielded marine molluscs from Middle Palaeolithic deposits, as in the case of two caves (i.e. Cueva Pernerias and Cueva de los Aviones) along the coast of Murcia (Montes Bernárdez, 1989). The marine mollusc assemblages from both these sites are dominated by rocky shore species of the genera *Ostrea*, *Patella* and *Mytilus*. At Cueva de los Aviones, at ca. 50 ka cal BP, about 96% of the molluscs were probably taken back to the cave by the Neanderthals (Zilhão et al., 2010). Of the food taxa, 98% are rocky shore species (*Patella* spp., *O. turbinatus*, *M. galloprovincialis*) and only 2% are specimens of *C. glaucum*, a tidal flat and coastal lagoon species. According to Zilhão et al. (2010), the remaining marine molluscs were either introduced accidentally (i.e. *Nassarius incrassatus* and *Gibbula* sp.) or, in the case of the subtidal genera (*Acanthocardia tuberculata*, *Glycymeris insubrica* and *S. gaederopus*), were probably beach-collected. Some of these shells might have been used as ornaments, while others have been found to contain pigments (e.g. *G. insubrica* and *S. gaederopus*) and might have been receptacles for body paints (Zilhão et al., 2010). Use of intentionally perforated marine shells (*Nassarius gibbosulus*

and possibly *Columbella rustica*), presumably for personal decoration, is documented for Aterian deposits dated ca. 82 ka at sites in Morocco (Bouzouggar et al., 2007; d'Errico et al., 2009).

4.2. Central Mediterranean

The earliest Middle Palaeolithic evidence for the exploitation of marine molluscs by humans in the Mediterranean basin is represented by shells recovered at the coastal cave of Grotta dei Moscerini in Latium, western-central Italy, the only case from the region that has also been investigated fully from a taphonomic point of view (Fig. 3). Humans producing Mousterian artefacts occupied Grotta dei Moscerini from around 115–110 ka to around 65 ka (Stiner, 1994). Shells of marine molluscs were recovered in every archaeological level, albeit in low quantities. Most of the molluscs, including the infralittoral and circalittoral taxa (*C. chione* and *Glycymeris* sp.) were taken back to the site by Mousterian groups for consumption (Stiner, 1994). In addition to clear evidence of fresh fractures and burning damage indicating dietary use mainly of the genera *Callista* and *Mytilus*, some shells of the bivalve *C. chione* from Grotta dei Moscerini were used as raw materials for the production of tools, retouched to make scrapers (Vitagliano, 1984; Stiner, 1994; see also Darlas, 2007, on Kalamakia Cave in Greece). Apart from these sandy shore bivalves, the occupants of Grotta dei Moscerini mainly consumed rocky shore intertidal taxa such as *M. galloprovincialis*, *O. turbinatus* and *Ostrea* sp., as well as

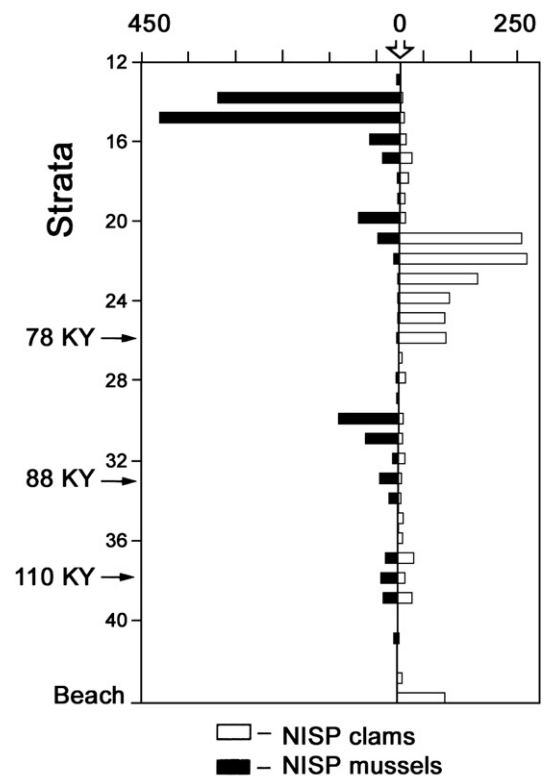


Fig. 3. Bar chart showing the relative frequencies of smooth-shelled sand clams (*Glycymeris* spp., *C. chione*) and mussels (*M. galloprovincialis*) in the stratigraphic sequence of Grotta dei Moscerini. Specimens in stratum 41 and upwards were collected and eaten by the Middle Palaeolithic occupants. Values are shell NISP for each bivalve group, representing the contrast between soft-substrate (sandy bottom) and hard-substrate (rocky surfaces and gravel) habitats respectively. Three averaged ESR dates are shown on the stratigraphy axis. Frequencies in each group rise gradually and decline suddenly through the sequence, in parallel with the aggrading and erosional tendencies in global sedimentary systems. Hunter-gatherers responded opportunistically to changes in local foraging opportunities (adapted from Stiner, 1994; Fig. 6.20).

lagoonal taxa such as *Cerastoderma* sp. The frequencies of these taxa vary through the sequence, probably as a direct consequence of the changes in sea levels, which altered shoreline habitats in the vicinity of the cave between 115 and 65 ka. The mollusc assemblage from Grotta dei Moscerini shows that Mousterian groups made dietary use of marine molluscs, possibly seasonally, as only a few hundred individual molluscs were retrieved from a sequence spanning over thousands of years (Stiner, 1994). The contribution of marine foods to the essentially terrestrial meat-based diets of Neanderthals was limited to shoreline foraging (Stiner, 1994), given that, apart from the molluscs mentioned above, the only other remains of aquatic fauna are a few bone fragments of *M. monachus* at Grotta dei Moscerini and one cut-marked specimen at the nearby coastal site of Grotta di Sant'Agostino (Stiner, 1994).

4.3. Eastern Mediterranean

There is currently little evidence for the consumption of marine molluscs in the Middle and Upper Palaeolithic from the eastern Mediterranean. Shellfish exploitation may have occurred at some southern Levantine localities during the Palaeolithic, but to the best of current knowledge, shellfish were seldom, if ever, a major source of meat for foragers of that area (Stiner, 2005). Another reason for the dearth of molluscs from Near eastern sites could be the relatively poor marine productivity to support a consistent exploitation (see for instance Zenetos et al., 2002). In the southern Levant there currently is no evidence for the presence of shells in Middle Palaeolithic sites associated with Neanderthals, while shells have been recovered at Skhul Cave and at Qafzeh Cave, two Middle Palaeolithic sites in Israel attributed to AMHs (Bar-Yosef Mayer, 2005). The shells recovered at Skhul only include sandy shore species, some of which were probably collected for ornamental purposes (Vanhaeren et al., 2006). These shells were recovered in layers attributed to a period between 100 and 135 ka and, as a result, this has been taken as evidence that the presence of shell beads is indicative of modern human behaviour. At Qafzeh Cave, where several burials of AMHs were unearthed in a layer dating to 92 ka, a few specimens of *G. insubrica* were found, most of which had naturally produced holes (Bar-Yosef Mayer et al., 2009). These shells were probably used as ornaments and, similar to the Skhul specimens, their presence at these sites indicates that Middle Palaeolithic AMHs visited the Mediterranean shores of the Levant. The abraded condition of *G. insubrica* in other Middle Palaeolithic sites such as Ras el Kelb in Lebanon and Sefunim Cave in Mt. Carmel indicate that humans only collected shells, but did not consume mollusc flesh (Bar-Yosef Mayer et al., 2009).

There is clear evidence of marine mollusc exploitation by Middle Palaeolithic foragers at the northern Levantine site of Üçağızlı II cave on the Hatay coast of Turkey (Stiner, 2009/2010). The shells are from large edible species that inhabit rocky shores, almost exclusively *Patella* spp. and *O. turbinatus*. The cave today rests only about 2 m above sea level, and a series of cultural deposits are underlain by an Interglacial beach that most probably dates to MIS 5a. Small numbers of wave-worn whole shells and fragments occur in the beach deposit, whereas many shells displaying fresh breaks and burning damage occur in the cultural layers above the beach, in connection with hearth features and lithic artifacts. The Middle Palaeolithic occupations of the cave continued sporadically through MIS 4, and possibly into the earliest part of MIS 3 and mollusc collection continued through the later occupations. Lithic artefacts, bones and marine shells occur at especially high densities in the lower layers of the cave. The earlier cultural layers are particularly dense with lithic, bone and shell remains.

Evidence for the exploitation of marine molluscs as food resources during the Middle Palaeolithic comes from Haua Fteah in

Cyrenaica (Libya), on the north African coast of the eastern Mediterranean basin, a site which contains a long depositional sequence spanning at least 100 ky (McBurney, 1967). Shells of marine molluscs collected for dietary purposes were found to occur throughout the sequence, although they were rare in layers attributed to the Mousterian (Middle Palaeolithic) and Dabban (Upper Palaeolithic) cultures, possibly due to the seaward displacement of the coastline during glacial conditions and to lower human population levels during arid phases in this region (Klein and Scott, 1986). The main taxa encountered at Haua Fteah are *P. caerulea* and *O. turbinatus* (Emiliani et al., 1964, 1967; Klein and Scott, 1986), attesting that early AMHs at the cave consumed mainly rocky shore species, as in other parts of the Mediterranean basin. New excavations by an interdisciplinary team (Barker et al., 2009) will provide data that should refine, and perhaps require re-interpretation of, the Haua Fteah sequence.

5. Pre-LGM Upper Palaeolithic

5.1. Western Mediterranean

Gravettian and Solutrean deposits dating to around 29–19 ka cal BP at Cueva de Nerja, in Andalucía (Spain), might contain evidence for shellfish as a source of nourishment, but stratigraphic issues have compromised their chronological attribution (Aura et al., 2002a, 2009). According to Cortés-Sánchez et al. (2008), marine shells from Gravettian layers were exclusively used as ornaments. Evidence for the exploitation of coastal marine resources is provided by fish remains in Solutrean deposits (e.g. Morales-Muñiz and Rosselló-Izquierdo, 2008). Sea levels would have been at their lowest around the Last Glacial Maximum and, therefore, the dearth of evidence for the exploitation of coastal marine resources in the few millennia preceding and following 20 ka BP might not be a true reflection of the role played by such resources in human subsistence, because coastal sites from that period are the most likely to have been furthest from present-day coastlines and submerged by Late and Post-Glacial sea level rise (Bailey and Flemming, 2008). Marine mollusc exploitation is documented at the site of Vale Boi during the Gravettian after 28 ka and through the Solutrean occupations (Stiner, 2003b; Manne and Bicho, 2009). Though this site is located on the Atlantic side of the Strait of Gibraltar, material culture and stone raw material use link these Palaeolithic occupations with those of the Mediterranean proper.

Fa (in press) reports at least 26 marine mollusc species in the Upper Palaeolithic (Solutrean) deposits from Gorham's Cave. Rocky shore molluscs dominate the assemblage, with Patellidae, Mytilidae and Trochidae, in this order, being the most abundant. As previously reported, the proportional representation of each of these species remains essentially unchanged from that observed in Mousterian levels. At least seven soft bottom, shallow-water bivalve species are present (*A. cf. tuberculata*, *Anomia* sp., *Cardita calyculata*, *Chamelea* sp., *Glycymeris bimaculata*, *P. maximus*, *P. jacobus*, *Ruditapes decussatus*). Although present in Mousterian deposits (possibly as accidental inclusions in seaweed such as fucoid algae, or with mussel 'mats'), species like *Littorina obtusata*, *Littorina saxatilis* and *Nucella lapillus* showed evidence of having been collected for decoration during the Solutrean, given that they had been perforated for use as beads.

5.2. Central Mediterranean

Early Upper Palaeolithic sites assignable to the Aurignacian and Gravettian are few and far between in Italy (Mussi, 2001), but locally common in some areas. Not many of these sites are coastal

and the only one containing a mollusc assemblage of any size is Riparo Mochi in Liguria, close to the border between Italy and France. The proto-Aurignacian layer at this site (Layer G; 36–41 ka cal BP) yielded a mollusc assemblage of about 6000 NISP, representing circa 1500 MNI (Kuhn and Stiner, 1998). According to Stiner (1999) and Kuhn and Stiner (1998), taphonomic evidence indicates that molluscs were introduced into the deposit as food items (Patellidae, Mytilidae, Veneridae, Glycymerididae and Pectinidae), as ornaments (gastropods and scaphopods) and accidentally (i.e. Cerithiidae), possibly along with seaweed or seagrass. The dominant species consumed as food were of the genera *Mytilus* and *Patella*. The ornamental taxa are diverse but are dominated by *Cyclope neritea* and *Homalopoma sanguineum*. During the Aurignacian, the marine molluscs exploited for food at Riparo Mochi were nearly exclusively rocky shore species. The fact that thousands of gastropods used for ornamental purposes were collected from soft bottom shore thanatocoenoses but edible species were not suggests: (a) that the collection of shells for ornamental purposes was probably a separate and more wide-ranging activity from collection for subsistence purposes and/or (b) that soft bottom shore molluscs were not generally collected for consumption. Whereas “shelf-life” limitations affect shell transport to a large degree, ornamental shells are easily traded and may remain in general circulation for a significant time (Kuhn and Stiner, 2007; Stiner, 2003a; Fa, 2008, in press).

Similar modes of marine mollusc consumption to those attested in the early Aurignacian (Layer G) were also achieved in the middle Aurignacian (Layer F), while shells of food taxa are less common (6% of marine molluscs) in the Gravettian (Layer D) (Stiner, 1999). The issue of whether the low level of mollusc exploitation at Riparo Mochi in the Gravettian is a local consequence of the dramatic fall in sea level at that time, or a true reflection of the extent of the reliance of Gravettian humans on marine molluscs, cannot be settled with the available evidence. The dearth of coastal sites, and therefore of mollusc assemblages of Gravettian age in this region, might be a consequence of the extremely low sea levels at that time and subsequent inundation. Coastal environments were at least visited to collect shells for the production of personal ornaments.

5.3. Eastern Mediterranean

Some early Upper Palaeolithic sites in the eastern Mediterranean basin have yielded remains of marine molluscs, and those found are almost exclusively intertidal rocky shore species. Two deeply stratified sites in the Levant (Ksar ‘Akil and Üçağızlı) have provided evidence for the exploitation of large marine molluscs for food and the shells of small species for ornaments (Kuhn et al., 2001). Ksar ‘Akil is one of the oldest Upper Palaeolithic sites in the Levant and, although, it is located a few kilometres inland from the coast, many ornamental shells occur in the deposits along with around one hundred remains of edible types, mainly of the rocky shore species *O. turbinatus* and *Patella* spp., but alimentary use of molluscs at this site is not certain (Kuhn et al., 2001). The coastal cave site of Üçağızlı I on the Hatay coast of southern Turkey, on the other hand, is very rich in both edible and ornamental mollusc remains (Kuhn et al., 2009; Stiner, 2009/2010). Marine mollusc consumption, mainly of *Patella* and *Osilinus*, occurred after the formation of the oldest Initial Upper Palaeolithic layers, and peaked during the Ahmari occupations.

Marine molluscs of the genera *Patella* and *Osilinus* were exploited, albeit at very low levels, by the early Upper Palaeolithic (Dabban culture) occupants of the Haua Fteah Cave in Libya (Klein and Scott, 1986). Other parts of the eastern Mediterranean, such as in the Peloponnese region of Greece, also provide evidence for the

exploitation of marine molluscs in the early Upper Palaeolithic, but few sites have been explored and published in detail (Karali, 1999). The few sites that have been found to contain mollusc remains mainly contained shells used as personal ornaments such as at Kephalaria Cave (Hahn, 1984), Klissoura 1 Cave (Koumouzelis et al., 2001; Stiner, in press), and Franchthi Cave (Shackleton, 1988).

6. Post-LGM Upper Palaeolithic and Epi-Palaeolithic

6.1. Western Mediterranean

The consumption of marine molluscs is attested at several Upper Palaeolithic sites on the Spanish and French coasts (e.g. Martínéz Andreu, 1989, 2002; Davidson, 1989; Moreno, 1995; Cade, 1998; Aura et al., 2002a, 2006; Jordá et al., 2003; Casabó i Bernard, 2004; Cortés-Sánchez et al., 2008; Fa, in press) and there are some limited data for the Mediterranean coasts of Morocco and Algeria (e.g. Camps, 1966, 1974; Saxon et al., 1974; Hachi et al., 2002; Hachi, 2006). So widespread is the evidence from Europe that only selected areas will be considered here.

The mollusc assemblage from Cueva de Nerja constitutes the most detailed and long-term evidence of Upper Palaeolithic shellfish exploitation in the western Mediterranean (e.g. Aura et al., 2002a, 2002b; Jordá et al., 2003; Cortés-Sánchez et al., 2008). The palaeoeconomic importance of marine molluscs apparently increased through the Magdalenian (ca. 14.5–13 ka cal BP) and in the Epipalaeolithic (ca. 8 ka cal BP). The exploitation of marine molluscs intensified noticeably during the Magdalenian occupation, as demonstrated by the thousands of specimens harvested over a shorter time interval (Aura et al., 2002a; Cortés-Sánchez et al., 2008). During the Magdalenian *R. decussatus* became particularly abundant along with *M. galloprovincialis*, *C. glaucum* and *Patella* spp. This indicates that molluscs were collected in both transitional waters and in intertidal rocky and soft bottom biotopes, in response to available coastal environments (Aura et al., 2002a; Jordá et al., 2003).

The increase in marine mollusc exploitation at Cueva de Nerja also coincides with the local intensification of fishing in the Magdalenian (Aura et al., 2002a; Cortés-Sánchez et al., 2008), with transport of marine foods over long distances from the coast (Aura et al., 2006), and with the consumption of marine mammals (e.g. *M. monachus* and *D. delphis*). Fish species also suggest the existence of estuaries and lagoons (Aura et al., 2002a). The exploitation of resources from the whole range of coastal habitats present in the vicinity of the cave, suggests that a key component of the food economy of the occupants of the site was represented by marine resources, even though terrestrial animals were still the main source of dietary protein (Aura et al., 2002a, 2002b; Cortés-Sánchez et al., 2008; Morales-Muñiz and Rosselló-Izquierdo, 2008).

6.2. Central Mediterranean

The late Upper Palaeolithic marine mollusc assemblages available for the central Mediterranean all come from Italy, where a few thousand years after the LGM there was a significant increase in the number of sites (Mussi, 2001), many of which are located in steep coastal areas characterized by limestone bedrock. These geographical locations made it more likely for the occupants of the caves to exploit rocky (*Osilinus* and *Patella*), rather than soft bottom shore molluscs, and to deposit them in sites relatively close to the sea (Emiliani et al., 1964, 1967; Durante and Settepassi, 1972; Tozzi, 1975; Stiner, 1999; Palma di Cesnola, 2001; Mannino and Thomas, 2004, 2007, 2009, in press; Colonese and Wilkens, 2005; Martini et al., 2007a, 2007b, in press-a, in press-b; Colonese, in press-a, in press-b; Colonese and Tozzi, in press).

Exploitation clearly intensified in the Epigravettian at some coastal sites in northern Italy, such as at Riparo Mochi in the Balzi Rossi area (Stiner, 1999). At Grotta della Serratura, on the Tyrrhenian coast of southern Italy, the collection of marine molluscs intensified around 13 ka cal BP (Colonese and Wilkens, 2005). During this phase the main species exploited for food were lagoonal types, such as *C. glaucum*, which is represented by thousands of individuals – in some levels accounting for up to ca. 90% – and *Ostrea* sp., which in some levels accounts for up to ca. 22% (Colonese and Wilkens, 2005). At this time rocky shore intertidal taxa (e.g. *O. turbinatus* and *Patella* spp.) were rarely collected, as they only represent between 9% and 3% of the mollusc assemblage (Fig. 4). The pattern of exploitation changed dramatically at ca. 12 ka cal BP, with a sudden replacement of the lagoonal species by rocky shore intertidal species, with *O. turbinatus* and *Patella* spp. accounting for about 80% of the assemblage. The marked change in the mollusc assemblage, probably caused by modifications in local coastal environments likely related to sea level rise, is mirrored by changes in the fish and bird bone assemblages (Wilkens, 1993).

The exploitation of *C. glaucum* is also attested at other late Upper Palaeolithic sites in Italy, for example at Grotta del Mezzogiorno and Grotta Erica (Martini et al., 2007a; Colonese and Tozzi, in press). At Grotta del Mezzogiorno mollusc harvesting started around 12.5 ka cal BP and increased after that. Upper Palaeolithic exploitation focused on rocky shore intertidal species, including *O. turbinatus* (ca. 50%) and *Patella* spp. (ca. 20%), while species from

lagoons and intertidal soft bottom were collected less and were represented mainly by *C. glaucum* (ca. 15%).

At Grotta della Madonna, mollusc collection started around 12 ka cal BP and increased through time at least until the Early Holocene. Invariably, the marine molluscs most commonly exploited for food were rocky shore intertidal species, represented by *O. turbinatus* and *Patella* spp., including *P. ferruginea* which disappeared in the Early Holocene (Durante and Settepassi, 1972). The increase in marine molluscs was paralleled by an increase in fish and bird bones, attesting the exploitation of a wide range of coastal fauna (Durante and Settepassi, 1972).

Other evidence regarding the nature of coastal adaptations by Late Glacial hunter–gatherers is offered by excavations undertaken in the early and mid-twentieth century at Grotta Romanelli, a cave in Apulia (SE Italy). According to Blanc (1930), marine molluscs were frequently exploited by the Late Epigravettian occupants. The faunal assemblage has been studied in detail, and out of 52,238 bone remains, 31,984 belonged to birds (Cassoli and Tagliacozzo, 1997). The assemblage also included a few fish bones, and bones of marine mammals such as *M. monachus* and Delphinidae. The birds consumed for food comprise numerous species of waterfowl (e.g. Anatidae), showing that the hunter–gatherers of Grotta Romanelli frequently hunted birds, which would have been found around transitional waters.

Recently, Mannino and Thomas (2009) have studied shells from Upper Palaeolithic (Late Epigravettian) sites in north-west Sicily

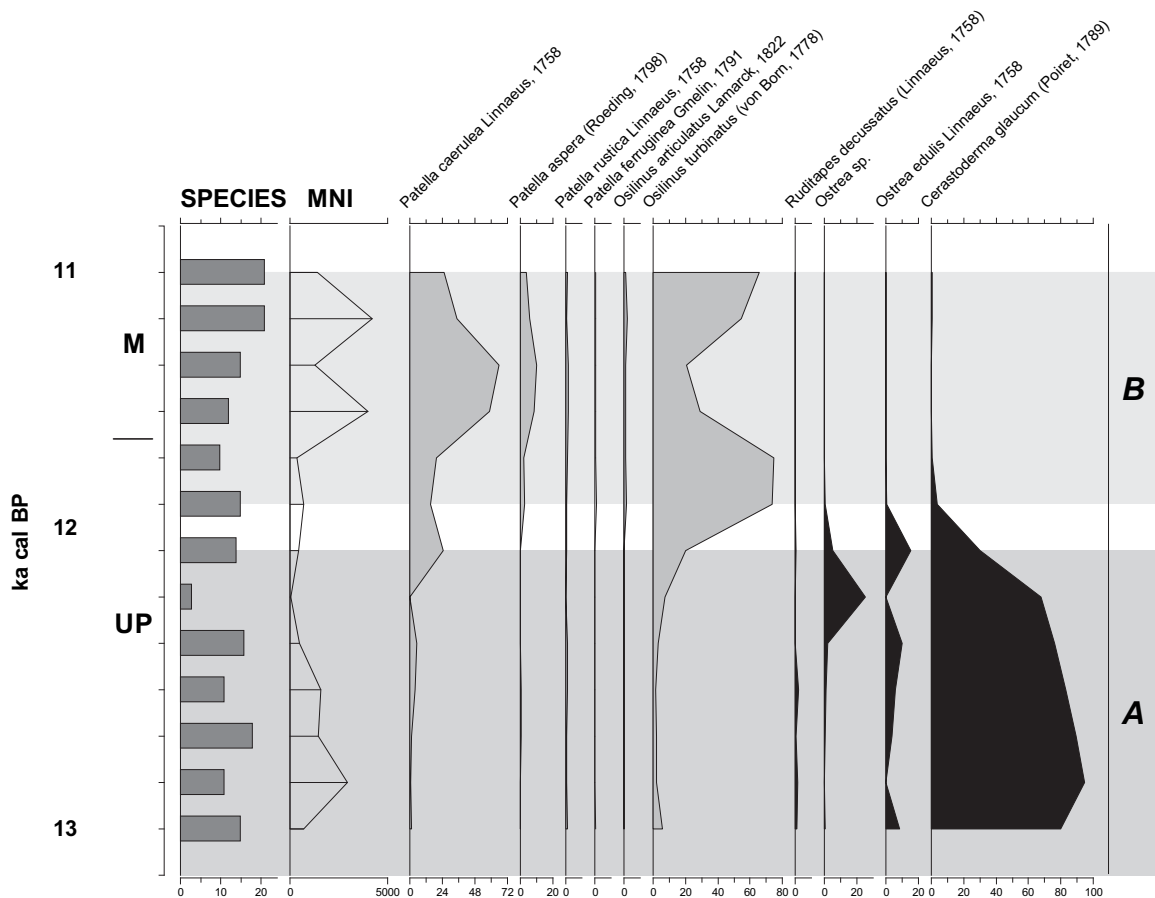


Fig. 4. Frequencies of the main species from the Upper Palaeolithic (UP) and Mesolithic (M) layers of Grotta della Serratura. From the left to the right the numbers of species identified are reported, the MNI for each layer and oscillations in MNI (%) of the most abundant species through the stratigraphy. Marine shell remains from Grotta della Serratura have very good preservation, which enabled species-specific identifications. Gastropods (e.g. *Patella* spp., *Ostilinus* spp.) were counted using apex, bivalves were counted using left valves or fragments with the umbo. Coastal lagoon species (e.g. *C. glaucum*) dominate in the first stage of exploitation by Upper Palaeolithic groups (stage A). The soft bottom shore taxa were suddenly replaced by rocky shore intertidal species (e.g. *Patella* spp. and *Ostilinus* spp.), which prevail in the Mesolithic (stage B) (after Colonese and Wilkens, 2005).

(Grotta dell'Addaura, Grotta delle Incisioni, Grotta di Cala dei Genovesi). Assemblages dated to 14–12 ka cal BP were composed of rocky shore species, represented by *P. ferruginea*, *P. caerulea*, *P. rustica* and *O. turbinatus* and *Osilinus articulatus*. The most notable finding is the presence of relatively high numbers of *P. ferruginea*, the largest species which would have been available. Large *P. ferruginea* shells (>50 mm) have also been found in late Upper Palaeolithic deposits at Grotta Racchio (Martini et al., in press-b), and, although data are preliminary, this suggests that the rocky shores close to the caves had probably not been subject to human predation prior to the initial exploitation by Epigravettian hunter–gatherers. This hypothesis is supported by the absence of humans in Sicily before the Late Epigravettian (Mannino and Thomas, 2007).

Some studies on the marine molluscs from late Upper Palaeolithic sites in Sicily have included oxygen isotope analyses on the shell carbonates of *O. turbinatus* to reconstruct the season of collection (Martini et al., 2007b; Mannino and Thomas, 2009, in press). The results of the oxygen isotope analyses show that intertidal mollusc collection usually occurred between the end of autumn and the beginning of spring when sea surface temperatures are lower. Intertidal molluscs were, therefore, a markedly seasonal resource and the temporal pattern of their exploitation was probably a consequence of the fact that humans moved away from the seashore during the summer, possibly in order to exploit the main sources of dietary protein, such as red deer (*Cervus elaphus*), aurochs (*Bos primigenius*) and the European wild ass (*Equus hydruntinus*).

6.3. Eastern Mediterranean

In eastern Mediterranean regions, Upper Palaeolithic marine mollusc exploitation is known at sites in the Balkan Peninsula, particularly in the Peloponnese (e.g. Bailey et al., 1984; Shackleton, 1988; Karali, 1999), Libya (Emiliani et al., 1964, 1967; Klein and Scott, 1986; Barker et al., 2009), Turkey (Albrecht et al., 1992; Stiner et al., 2000, 2002; Kuhn et al., 2009) and on the island of Cyprus (Reese, 1999).

The most detailed and long-term record of exploitation in the eastern Mediterranean basin for the late Upper Palaeolithic is that of Franchthi Cave, in the southern Argolid (Greece) (Shackleton, 1988). Marine mollusc exploitation at this site is attested from ca. 13 ka cal BP, when a broad range of vegetal and animal resources were part of the subsistence economy of local human groups, which apart from hunted wild mammals also included wild plants, fish and land snails (Jacobsen, 1973; Payne, 1975; Perliès, 1995; Rose, 1995; Stiner and Munro, submitted for publication). As at other Mediterranean sites, marine mollusc exploitation was important in the final Upper Palaeolithic and Mesolithic and it focused principally on rocky shore intertidal species, represented by *O. turbinatus*, *Gibbula divaricata*, *Gibbula rarilineata*, but also sporadically on taxa from lagoons or muddy shores, such as *Cerithium vulgatum* and *Hexaplex trunculus* (Shackleton, 1988). The end of the Upper Palaeolithic occupation was marked by an increase in *Cerithium*, the use of which is uncertain, but may have been a source of bait for inshore fishing. Shackleton and van Andel (1986) have explained the sudden onset of shellfishing at Franchthi Cave as being a direct consequence of the changes produced by Late Glacial sea level rise on the coastal ecosystems of the Argolid. A significant increase in dietary breadth in favour of other marine resources also occurred at this time (Stiner and Munro, submitted for publication). Rather than maintaining an exclusively terrestrial focus in foraging, and retreating from the southern Argolid as terrestrial resources became impoverished, the later occupants at Franchthi turned increasingly to the sea, beginning with shellfish collecting and

shoreline fishing in the late Palaeolithic and expanding later to include open water fishing in the Mesolithic (Rose, 1995).

As in previous periods, at Haula Fteah marine mollusc exploitation at the end of the Pleistocene, during the Capsian period, was characterized by the collection of intertidal rocky shore species of the genera *Patella* and *Osilinus* (Emiliani et al., 1964, 1967; Klein and Scott, 1986; Barker et al., 2009). The same taxa were exploited during the Late Pleistocene (ca. 12 ka cal BP) at the site of Aetokremnos in southern Cyprus (Reese, 1999). The main species consumed by the occupants at this site were *O. turbinatus* (20,750 individuals), *P. caerulea* and *P. rustica* (total of 640 individuals). The size of the mollusc assemblage pushed Simmons (1999) to hypothesize that the settlement at Aetokremnos was in part justified by its proximity to the coast, which provided people with access to marine molluscs. The estimates made by Fa (2008), on the potential offered by Mediterranean rocky shore intertidal habitats for human subsistence, suggest that if the diets of the hunter–gatherers at Aetokremnos were centred mainly on shellfish, then the occupations at the site could only have been short-lived. It seems clear, however, that shellfish were an important supplementary source of protein at this site.

The Epipalaeolithic cultures of Aegean Turkey and the Levant occur at the same time as the late Upper Palaeolithic of Europe. Data on coastal Epipalaeolithic sites are few for Turkey, but moderate to heavy exploitation of rocky shore species is indicated by one Epipalaeolithic fauna dated to ca. 20 ka cal BP at Üçağızlı I Cave on the Hatay coast of Turkey, in the northernmost Levant (Stiner et al., 2000, 2002; Kuhn et al., 2009).

In the southern Levant, there is ample evidence for exploitation of mollusc shells as ornaments, and scaphopods and small gastropods (especially *Columbella* and *Nassarius*) dominate the assemblages. However, there is no evidence for shellfish consumption (Bar-Yosef Mayer, 2005, 2007). A similar situation was observed at Öküzini cave, and level B of Karain cave in southern Turkey (Albrecht et al., 1992).

The Natufian culture (14.5–11.5 ka cal BP) is famous for the use of scaphopod shells as ornaments (Bar-Yosef Mayer, 2008), but recently it has been found that there is evidence for other uses of marine molluscs. In addition to ornamental shells, several shells of *P. caerulea* were discovered at El-Wad cave and El-Wad Terrace in Mt. Carmel. The Mediterranean coast would have been over 10 km away from the site during Natufian times and, therefore, it is assumed that the specimens found represent 'keepsakes' of molluscs consumed by the shore. However, if sites with evidence for the consumption of marine molluscs along the coast existed, they are probably submerged now. On the other hand, other kinds of marine exploitation are apparent from the remains of fish (Serranidae, Sparidae, Sciaenidae and Mugilidae) at the Natufian sites of Hayonim Cave, Kebara Cave, Hilazon Tachtit cave and Hatoula. Fishing is further attested by the presence of fishing instruments at these sites, which, in turn, suggests that marine molluscs could have been exploited along the coast (Lernau and Lernau, 1994; Bar-Yosef Mayer and Zohar, 2010).

7. Mesolithic (early Holocene)

As recently summarized by Pluciennik (2008), defining the chronological boundaries of the Mesolithic in the Mediterranean is somewhat arbitrary, because the broadening in the subsistence base in favour of small game and aquatic animals, which was originally proposed as a distinguishing feature of this prehistoric period, has been pushed back to the early Upper Palaeolithic and was a protracted process that accelerated with time (Stiner, 2001). The beginning of the Mesolithic has been set to coincide with the start of the Holocene (ca. 11.5 ka cal BP), but its duration varies from

the east to the west of the Mediterranean, because the Neolithic started to spread about 10.5 ka cal BP in the Near East, but only reached the Iberian peninsula a few millennia later (e.g. Pèrles, 2001; Lubell, 2004a, 2004b; Linstädter, 2008; Zeder, 2008; Pluciennik, 2008). Coastal Mesolithic sites are present across the whole basin from Greece westwards and, particularly, in the central and western Mediterranean where there was continuity in the exploitation of marine molluscs coupled with an increase in the exploitation of other aquatic resources as well as an increased variety of terrestrial ones such as land snails (Lubell, 2004a, 2004b).

7.1. Western Mediterranean

In the western Mediterranean, marine molluscs from Epipaleolithic and Mesolithic sites have been found mainly along the Iberian and French coasts (e.g. Aparicio, 1989; Moreno, 1995; Cade, 1998; Casabó i Bernard, 1999, 2004; Aura et al., 2002a, 2006; Jordá et al., 2003; Vaquero, 2006; Cortés-Sánchez et al., 2008; Stiner et al., 2003; Stiner, 2003b). Rocky shore intertidal species dominate mollusc assemblages in most cases, for example at Cueva de Nerja (Aura et al., 2002a), Santa Maira (Aura et al., 2006) and Le Rouet (Cade, 1998).

As for the end of the Pleistocene, the site in the western Mediterranean with the longest sequence containing evidence of shellfish exploitation in the Early Holocene is Cueva de Nerja. The number of molluscs from Epipaleolithic levels is higher than that attested for previous occupations and the most common species is *M. galloprovincialis* (accounting for about 90% of remains). Soft bottom intertidal and lagoonal species (i.e. *R. decussatus* and *C. glaucum*), which are well represented in Magdalenian horizons, were not frequently collected during the Early Holocene (Jordá, 1985; Aura et al., 2002a; Cortés-Sánchez et al., 2008). The rise in the number of molluscs in Early Holocene deposits might be a consequence both of the reduced distance of the cave from the coast and of the more important economic role of these resources at that time (Aura et al., 2002a, 2009). The prevalence of *M. galloprovincialis* suggests that changes in local coastal environments were produced by sea level rise, which probably submerged progressively wider expanses of soft bottom shores and lagoonal habitats. According to Cortés-Sánchez et al. (2008), the intensification in mollusc collection is synchronous with a marked increase in the exploitation of small animals, mostly lagomorphs, and with an abrupt drop in the numbers of ungulates, which might indicate that marine resources were more important at this time.

7.2. Central Mediterranean

Marine molluscs, mainly of intertidal rocky shore species, were exploited by Mesolithic hunter–gatherers along coastal areas of the Italian Peninsula (e.g. Radmilli and Tongiorgi, 1958; Palma di Cesnola, 1962; Taschini, 1964; Bonuccelli, 1971; Durante and Settepassi, 1972; Tozzi, 1975; Cremonesi et al., 1984; Boschian and Pitti, 1984; Wilkens, 1993; Colonese and Tozzi, in press), Istria (Miracle, 2001), Dalmatia (Radić, 2002) and central Mediterranean islands (Compagnoni, 1991; Mannino et al., 2006, 2007; Mannino and Thomas, 2009, in press; Colonese, in press-a, in press-b; Colonese et al., in press; Martini et al., in press a,b). Many sites show a continuity in the mode and intensity in which marine molluscs were exploited from the late Upper Palaeolithic to the Mesolithic (e.g. Grotta del Mezzogiorno, Grotta della Serratura and Grotta della Madonna in southern Italy; Addaura caves and Grotta Racchio in Sicily; Grotta di Cala dei Genovesi, Grotta delle Uccerie and Grotta d'Oriente on the Égadi Islands). Most of these sites are characterized by the intensive exploitation of rocky shore intertidal taxa, mainly represented by *O. turbinatus* and *Patella* spp., with few

sites yielding evidence for the consumption of molluscs from transitional waters (e.g. Riparo Blanc). Riparo Blanc, a rock-shelter along the Tyrrhenian coast of central Italy, yielded a large assemblage of marine molluscs from rocky and soft bottom shores (Taschini, 1964). The site has been dated to ca. 9.5 ka cal BP and the main refuse of the Mesolithic occupation is represented by thousands of mollusc shells, mainly of marine species, remains of crustaceans and echinoderms, a few fish bones and only a handful of bone fragments of terrestrial mammals. The marine molluscs exploited were intertidal rocky shore (*O. turbinatus* and *Patella* spp.), and soft bottom intertidal and lagoonal species (*R. decussatus* and *C. glaucum*). The abundance of marine molluscs and the presence of other marine resources (crustaceans, echinoderms and fish) at Riparo Blanc was taken by Taschini (1964) as evidence for the complete reliance by Mesolithic hunter–gatherers on marine resources and, particularly, on molluscs for their year-round survival. An ongoing study is demonstrating that the scale of shellfish exploitation during the Mesolithic at Riparo Blanc was probably not different to that attested for Upper Palaeolithic sites, such as Grotta della Serratura (Mannino, personal communication).

Grotta dell'Uzzo, a cave in NW Sicily, has yielded a large mollusc assemblage that has been the object of a detailed study (Compagnoni, 1991), and it is a key site attesting to shellfish exploitation for the study of the Mesolithic–Neolithic transition in the Mediterranean (Mannino et al., 2006, 2007). The exploitation of marine molluscs at this site was not very significant in the early Mesolithic, but increased progressively in the late Mesolithic, in the so-called 'transition' phase and in the early Neolithic, after which the number of molluscs decreased sharply (Compagnoni, 1991). Marine mollusc exploitation at this site was always centred on intertidal rocky shore taxa (*O. turbinatus* and *Patella* spp.). An interesting change within the mollusc assemblage from Grotta dell'Uzzo is the gradual reduction in numbers of the large *P. ferruginea* (Mannino and Thomas, in press). This species represents 63% of all *Patella* spp. in the early Mesolithic, 10% in late Mesolithic, 0.4% in the Mesolithic–Neolithic transition phase and less than 0.3% in the Neolithic (Compagnoni, 1991). Considering that adult *P. ferruginea* are in general substantially larger than other intertidal molluscs in the central Mediterranean, and that humans at Grotta dell'Uzzo targeted the largest taxa and specimens available on the shores, the dramatic decrease in the presence of this species could be explained by over-exploitation (Mannino and Thomas, in press), in a similar way as demonstrated by Espinosa et al. (2009) for modern populations.

The increased reliance on marine molluscs at Grotta dell'Uzzo at a time of resource depression could be associated with demographic pressure and/or reduction of available resources. Currently, there is no archaeological evidence for an increase in sites from the Upper Palaeolithic to the Mesolithic. On the other hand, the study of the animal remains from Grotta dell'Uzzo demonstrates that towards the end of the Mesolithic wild equids (*E. hydruntinus*) and bovids (*B. primigenius*) had become rare, or locally extinct, and red deer (*C. elaphus*) had become depleted by prolonged human exploitation (Tagliacozzo, 1993). At this time marine resources, including rocky shore molluscs, echinoderms, crustaceans, fish, pinnipeds and cetaceans, all either started being exploited or became more frequent prey (Tagliacozzo, 1993). Zooarchaeological data from Grotta dell'Uzzo, therefore, seems to support the hypothesis that the increase in dietary breadth, and of the exploitation of marine molluscs, was probably a consequence of the depression of available resources.

Recent excavations at sites around the lagoon of Sebket Halk el Menjel in Tunisia have provided evidence for the exploitation of molluscs starting around 8 ka BP and continuing at least to around 6 ka BP (Mulazzani et al., 2008; Mannino et al., 2006, in press-a).

Capsian groups inhabited the area around the present-day sebkha and subsisted by hunting mammalian herbivores and by exploiting lagoonal resources and, especially, *C. glaucum*, which is represented by tens of thousands of individuals at sites such as SHM-01. The ongoing studies on the assemblages from the Sebkhet Halk el Menjel sites should allow evaluation of the potential of resources from transitional waters for Holocene hunter–gatherers in the Mediterranean and testing whether these environments were capable of supporting human groups year-round or not.

7.3. Eastern Mediterranean

Marine molluscs have been recovered in Early Holocene deposits on the Ionian island of Corfu (Sordinas, 1969), in the Peloponnese (e.g. Shackleton, 1988; Karali, 1999) and in Libya (Klein and Scott, 1986; Barker et al., 2008, 2009).

The largest mollusc assemblage and detailed study for the eastern Mediterranean basin is that from Franchthi Cave. In the Mesolithic, the intertidal rocky shore taxa (*O. turbinatus* and *Patella* spp.) abundant in the Upper Palaeolithic decrease dramatically and were replaced by coastal lagoon and brackish water taxa (Shackleton, 1988). The Mesolithic mollusc assemblage from Franchthi cave is dominated by *Cyclope* spp., which was not collected for dietary purposes (Perlès and Vanhaeren, submitted for publication), and *C. vulgatum*, which was the most important edible mollusc. Fishing increased through the Mesolithic, as attested at first by the remains of inshore fish such as bream, later by barracuda (*Sphyraena* sp.) and other taxa, and finally by large quantities of tuna fish (*T. thynnus*) bones (Rose, 1995). In the late stages of the Mesolithic (ca. 9.2 ka cal BP) and early Neolithic there is a marked decrease in fishing and an increase in the collection of *C. vulgatum*, which at this stage accounts for 60%–80% of marine molluscs. Shackleton and van Andel (1986) stated that *C. vulgatum* would not have offered great food value and recognized that, although other marine molluscs would have been present in the catchment of the Franchthi Cave, the fact that other species were practically ignored at that time is puzzling. Thomas (1987) has pointed out that a careful taphonomic study should have been undertaken to prove or disprove whether these marine molluscs had been collected for food. The species could have been used as fishing bait (Katsanevakis et al., 2008) or they could have adhered to fishing nets that were pulled to shore. In any case, it seems reasonable to say that, at the end of the Mesolithic sequence, marine molluscs constituted a surprisingly minor item in the diet of the Franchthi Cave hunter–gatherers. Regarding the dominance of *C. vulgatum* in the late Mesolithic and Neolithic, W.R. Farrand (personal communication) points out that because the main occupation during the Neolithic was outside the cave on the Paralia, it is possible that at that time the cave was used mainly for stabling animals (sheep and goats) and, furthermore, that the Neolithic occupants of the site were not descendants of the Mesolithic group.

8. Discussion

Marine mollusc exploitation in the Mediterranean Sea might have started as early as the Lower Palaeolithic (ca. 300 ka), if the marine molluscs from Terra Amata (de Lumley, 1966) were collected by archaic humans for consumption. However, the earliest secure evidence for the consumption of marine molluscs by humans along Mediterranean shores is attested by assemblages from early Mousterian sites (e.g. the Gibraltar Caves, Grotta dei Moscerini), where molluscs were exploited by Neanderthals possibly as early as 110 ka. This evidence is contemporary to that from several Middle Stone Age sites in Africa (e.g. Klasies River Mouth, Boegoeberg II, Blombos Cave, Pinnacle Point, Abdur), where

AMHs exploited coastal resources including marine molluscs, pinnipeds, cetaceans and aquatic birds (e.g. Erlandson, 2001; Marean et al., 2007). The earliest evidence for the exploitation of aquatic resources from the African sites associated with AMHs is similar to that from the Mediterranean Mousterian sites, in that in both instances there is little proof of fishing and the marine fauna exploited required at best the use of “low-tech” technologies (Erlandson, 2001). Overall, the data suggests that Neanderthals probably consumed only marine mollusc that could be easily collected (i.e. intertidal and, possibly, shallow subtidal species), but at no site does shellfish exploitation appear to have been very intensive.

Neanderthals continued exploiting molluscs, mainly of rocky shore taxa, right up to the time of their extinction (ca. 28–24 ka cal BP), as attested by the finds from Gibraltar (Finlayson et al., 2006). Stringer et al. (2008) suggested that relying on marine resources might have facilitated the late survival of Neanderthals in the southern Iberian Peninsula. This is reasonable, taking into account the influence of Atlantic waters on the local marine productivity (Antoine et al., 1995) and the particular thermophilous character of the southern Iberian Peninsula even during glacial conditions (Finlayson, 2006, 2008; Carrión et al., 2008). On the other hand the oligotrophic aspect of the full Mediterranean Sea probably limited such reliance in the rest of the basin. This does not imply that coastal resources did not play a role in the subsistence strategies and diet of Mediterranean Neanderthals, but is likely that shellfish (e.g. molluscs, echinoderms, crustaceans) and other marine animals simply constituted dietary supplements (Stiner, 1994, 2001) and possibly provided nutrients that were not otherwise available in terrestrial foods (Broadhurst et al., 1998, 2002; Hockett and Haws, 2003).

The evidence for marine mollusc exploitation from Mousterian sites is comparable in pattern to that from Upper Palaeolithic sites pre-dating the LGM (e.g. Riparo Mochi, Üçağızlı I, Cueva de Nerja), given that rocky shore species were the most frequently exploited species in mollusc assemblages composed only of few hundreds of specimens (e.g. Aura et al., 2009). As a matter of fact, there is probably more evidence for shellfish consumption by Middle Palaeolithic Neanderthals than by subsequent Upper Palaeolithic populations if the sheer number of preserved sites and occupation layers are considered. This observation should not be taken at face value, because it might simply reflect the bias produced by changing sea levels on the archaeological record (Bailey and Flemming, 2008) and the fact that the post-interglacial Middle Palaeolithic represents a much longer time interval than the Upper Palaeolithic.

The shells from the Aurignacian levels at Riparo Mochi in Italy (Kuhn and Stiner, 1998; Stiner, 1999) and the early Upper Palaeolithic levels of Üçağızlı I in Turkey (Kuhn and Stiner, 2007; Stiner, 2009/2010) testify that early Upper Palaeolithic humans exploited easily-collected gastropods and bivalves from rocky and shallow sandy shore environments, similarly to what is attested for the Middle Palaeolithic. In addition, Upper Palaeolithic foragers frequently visited sea shores in order to collect shells as raw material for the production of personal ornaments. These were used mainly by the people who collected them, but small numbers were exchanged with inland groups, rarely over very long distances to sites hundreds of kilometres inland (e.g. Taborin, 1993). Lithic raw materials were also transported over a few hundred kilometres at this time, suggesting that early Upper Palaeolithic human groups were very mobile (e.g. Féblot-Augustins, 2009), and/or had extensive trading/communications networks. The small numbers of sites currently yielding restricted evidence for the consumption of marine molluscs in the Mediterranean during the Aurignacian (Mussi, 2001) might indicate that overall the subsistence of humans

belonging to this culture rarely included marine foods. The scarce evidence for marine mollusc exploitation in the few millennia prior to and around the LGM might be explained by the submergence of sites from cold climate phases by rising seas. It is likely that Mediterranean coastal regions constituted refugia from the climatic rigors of the Last Glacial Maximum (e.g. Blondel and Aronson, 1999; Hewitt, 2000; Faure et al., 2002). Based on this consideration, it is at least possible that humans were present at higher densities in coastal areas of the emerged continental shelf. Marine foods, including shellfish, would have constituted useful and available sources of protein and this might have been even more so around the LGM, when emerged coastal areas of the Mediterranean probably supported more productive ecosystems compared to inland areas (Faure et al., 2002; Bicho and Haws, 2008; Carrión et al., 2008; Morales-Muñiz and Roselló-Izquierdo, 2008). The fish remains from the Solutrean occupation levels at Cueva de Nerja are useful to elucidate this point. The fact that remains of marine fauna were recovered at this site in considerable numbers, in spite of its distance from the coast, might indicate that marine foods were an important component of the diet of the Upper Palaeolithic occupants of the cave (Morales-Muñiz and Roselló-Izquierdo, 2008). Further evidence of fish exploitation around the LGM is offered by the presence of sea trout (*Salmo trutta morpha trutta*) in Upper Palaeolithic sites in Spain and in Italy, where it stopped being fished in the Early Holocene (Durante, 1978). Carbon and nitrogen isotope analyses on the bones of a Gravettian individual buried at the Arene Candide (Liguria, Italy), known as “The Prince”, show that as much as 20% of this individual’s diet came from the consumption of marine and/or freshwater resources (Pettitt et al., 2003), such as *S. trutta*. Similarly, recent isotope analyses on human bone collagen from a burial in the Evolved Epigravettian deposits at the inland site of Grotta del Romito, in Southern Italy (Craig et al., 2010), have attested that the hunter–gatherer in question consumed significant quantities of marine and/or freshwater fish. This direct and indirect evidence for fishing might imply that Gravettian and Solutrean hunter–gatherers made greater use of marine resources than previously thought, which could indicate that molluscs were also exploited more than can be perceived from the archaeological record. In fact shellfish exploitation is indicated at some coastal Gravettian and Solutrean sites that happen to be situated above the reach of modern sea level (e.g. Riparo Mochi in Italy and Vale Boi in Atlantic Portugal, respectively).

Five or six millennia after the LGM the number of sites attesting the exploitation of marine molluscs increased significantly, as well as the size of mollusc assemblages. This increase might equate to a *per capita* increase in marine resource exploitation. The causes for this have been debated over decades. Other kinds of zooarchaeological evidence indicate that human populations probably expanded at this time (Stiner et al., 1999, 2000; Stiner, 2001) and Late Glacial sea level rises brought the shorelines closer to the sites in question. The main marine molluscs exploited throughout the Mediterranean basin during this period were rocky shore intertidal taxa (*Patella* and *Osilinus*). At a few sites (e.g. Cueva de Nerja, Grotta della Serratura), associated with coastal wetlands (e.g. lagoons, river deltas, coastal ponds), substantial numbers of soft bottom intertidal and lagoonal bivalves, mainly represented by *R. decussatus* and by *C. glaucum*, were exploited (e.g. Aura et al., 2002a; Jordá et al., 2003; Colonese and Wilkens, 2005). The capability of exploiting all the coastal environments in the catchment areas of the sites, including wetland areas, which are highly productive, probably buffered Mediterranean hunter–gatherer subsistence strategies against the adverse effects of Late Glacial environmental changes. In littoral areas characterized by different ecosystems, marine molluscs with other small animals, might have contributed to the success of the flexible and opportunistic strategies that, not

only allowed late Upper Palaeolithic humans to continue subsisting by hunting and gathering (in spite of the progressive reduction in ungulate biomass), but also to increase population levels (e.g. Kuhn and Stiner, 2006).

Seasonality data shows that Upper Palaeolithic groups collected rocky shore intertidal species (i.e. *O. turbinatus*) mostly from autumn to the beginning of spring, with the highest numbers of molluscs being consumed in the winter (e.g. Shackleton, 1974; Deith and Shackleton, 1988; Martini et al., 2007b; Mannino and Thomas, 2009). The main exceptions to this general trend are some cave sites associated with wetlands on the present-day Egadi Islands, Levanzo (Grotta di Cala dei Genovesi) and Favignana (Grotta delle Uccerie), which would have been connected to mainland Sicily until the Early Holocene (Agnesi et al., 1993; Martini et al., 2007b). At Grotta di Cala dei Genovesi (Mannino et al., in press-b) and, in the nearby Grotta Schiacciata, on the island of Levanzo there is evidence for the exploitation of coastal lagoons (shells of *C. glaucum* have been recovered), which might indicate that, at localities where both rocky shores and lagoons were present, marine resources (including molluscs) were exploited at different times of the year. Further work in these and other Mediterranean sites will help to establish the generality (or not) of these results.

Patterns of marine mollusc exploitation similar to those recorded for the late Upper Palaeolithic, are attested for the Mesolithic. Rocky shore species are the main taxa recovered from Mesolithic sites across the Mediterranean basin, but where transitional waters were present hunter–gatherers also exploited molluscs from such environments (e.g. Riparo Blanc). Marine resources, composed almost exclusively by molluscs at sites such as Riparo Blanc (Taschini, 1964), have traditionally been interpreted as the main resources exploited by Mesolithic hunter–gatherers along with small mammals, birds and fish (Radmilli, 1960). Radmilli (1960) even hypothesised that mollusc exploitation made it possible for Mesolithic hunter–gatherers to become sedentary, because marine molluscs were abundant enough to provide food all year round. The observations on the Mediterranean records, made in the present paper, show that such interpretations of the potential role of marine molluscs for hunter–gatherer diets are untenable, as are similar suggestions with regard to the role of terrestrial molluscs (Lubell, 2004b). Sedentism more likely evolved with the transition to farming that begins at about the same time (Bar-Yosef and Belfer-Cohen, 1989). Such extreme claims on the role of marine molluscs for human subsistence are probably unrealistic even in the case of highly-productive oceanic coastal regions, where mega-middens are present (e.g. Jerardino, 1998, 2010; Bailey and Flemming, 2008). This is not to say, however, that in some coastal areas of the Mediterranean, especially those composed of transitional waters, aquatic resources were never an important component of human diets. Carbon and nitrogen isotope analyses on human bone collagen from the shell midden at El Collado in southern Spain prove that, in the case of some of the individuals analyzed, as much as 25% of their dietary protein was derived from marine foods (Guixé et al., 2006).

The pattern of the seasonality of marine mollusc exploitation in the early Mesolithic was in general the same as in the Upper Palaeolithic, with molluscs being collected preferentially between autumn and the beginning of spring (Mannino et al., 2007; Colonese et al., 2009; Mannino and Thomas, 2009). Colonese et al. (2009) have hypothesised that this temporal pattern of exploitation might have been a consequence of the seasonal availability of large mammalian herbivores, which were the most important sources of dietary protein for Mediterranean hunter–gatherers. Barker (1981) has hypothesised that in Italy during the late Pleistocene and Early Holocene hunter–gatherers followed supposedly migratory species, including red deer (*C. elaphus*) and European wild ass (*E. hydruntinus*), between the Apennine uplands in summer and the

coastal plains in winter. This hypothesis has been partly supported by a study on faunal migrations in Late Glacial central Italy based on oxygen and strontium isotope analyses on teeth of *C. elaphus* and *E. hydruntinus* (Pellegrini et al., 2008), which have demonstrated that red deer moved over wider territories than did wild asses, although there is not much isotopic evidence in support of the hypothesis for altitudinal migrations. Similar migratory patterns have been observed in modern populations of *C. elaphus* in the Italian Alps, with long distance altitudinal movements occurring during the summer (Luccarini et al., 2006). In the light of these observations, it seems plausible that marine mollusc collection was a subsistence activity subordinate to the exploitation of terrestrial meat resources (e.g. large ungulates), undertaken at times of the year when hunter–gatherers were present along coastal areas, or at least rocky coastal areas. The available data suggest that in the early Mesolithic marine molluscs were exploited in similar ways and with similar periodicities as in the late Upper Palaeolithic and it is plausible that the role of marine molluscs in the subsistence strategies stayed more or less the same. Similar points have been made with regard to the extensive evidence for consumption of terrestrial molluscs during the late Pleistocene and early Holocene throughout the Mediterranean Basin (Miracle, 2002; Lubell, 2004a, 2004b).

Few sites in the Mediterranean contain late Mesolithic deposits with evidence for the exploitation of marine resources, the most noteworthy exception being Grotta dell'Uzzo in NW Sicily. At this site intertidal molluscs (mainly *Patella* and *Osilinus*) were collected increasingly through the late Mesolithic and into the early Neolithic (Compagnoni, 1991). This intensification is also attested by isotopic studies of the seasonality of mollusc exploitation, which show that molluscs were collected in every season in the late Mesolithic (Mannino et al., 2007). The intensification in mollusc exploitation was probably responsible for the significant decline in intertidal mollusc populations (e.g. *P. ferruginea*) and there was a corresponding increase in the consumption of small animals. Both these alternative resource types occur at higher population densities and in more restricted habitat patches compared to large game animals and their exploitation would have necessitated frequent movements within circumscribed territories. According to Mannino and Thomas (2009), the intensification of marine mollusc exploitation at Grotta dell'Uzzo could be associated with the resource depression experienced by the late Mesolithic hunter–gatherers and caused changes in territoriality. The lowered biomass offered by the otherwise not very productive intertidal rocky shore molluscs, in conjunction with the decrease in terrestrial resources registered in Sicily at the end of the Mesolithic, made it difficult to continue hunting and gathering, and probably favoured the adoption of an agro–pastoral economy on the island (Mannino and Thomas, 2009).

9. Conclusions

The evidence for marine mollusc exploitation by prehistoric Mediterranean hunter–gatherers, reviewed in this paper, is clearly dominated by sites on steeply sloping rocky shores and areas characterized by wide continental shelves are probably under-represented as an artefact of the geologic and climate history of the Mediterranean basin (e.g. Gulf of Lion, south-west of Sicily, Gulf of Gabes, North Adriatic, North African coasts from Tunisia to the Levant, coasts of Greece and southern Turkey). This bias raises the possibility of a severe underestimation of the importance of marine molluscs to prehistoric Mediterranean diets along gently sloping and sandy or muddy bottom shores, as previously noted by Bailey and Flemming (2008).

The fact that the archaeological record of marine mollusc exploitation reviewed in this paper is constituted by a heterogeneous dataset originating from both recent and earlier excavations,

might also seem to bring about biases stemming from ambiguous formation histories or recovery practices. To circumvent these possibilities, analysis has concentrated on sites with the most complete stratigraphies and with the best recovery of mollusc remains, even in the case of earlier excavations (e.g. Riparo Mochi and Grotta dei Moscerini). It is important that the mollusc assemblages from diverse sites converge in showing that marine molluscs were exploited commonly along rocky and soft bottom shores (Table 1). The consistencies in the data indicate that the records chosen for comparison are reliable. The dearth of systematic taphonomic studies might also have caused a bias in the archaeological record against those taxa with structurally-weaker shells, but in fact these mollusc groups dominate much of the coastal zooarchaeological record (e.g. some Patellidae, Mytilidae, Ostreidae). The evidence reviewed in this paper suggests that for most of these taxa (e.g. Patellidae, Mytilidae), taphonomic agents have not operated to such an extent as to subvert significantly their proportions within the assemblages, given that at many sites these species are by far the most abundant (e.g. Riparo Mochi, Cueva de Nerja). In addition, shells from Mediterranean assemblages prevalently come from cave sites and are generally well-preserved.

The last main bias which might affect the mollusc assemblages reviewed in this paper is anthropogenic post-depositional disturbance caused by millennial cave occupation and use, typical of Mediterranean coastal regions (e.g. Waele, 2009). Pedoturbation is likely to have affected to a greater extent the uppermost layers and, therefore, the more recent prehistoric mollusc assemblages, in other words those from the Neolithic, Mesolithic and late Upper Palaeolithic. Given that evidence for mollusc exploitation increases significantly in deposits which accumulated during the Late Glacial and early Holocene it is unlikely that anthropogenic mixing of cave deposits has distorted the long-term patterns in the record significantly.

Taking current evidence from coastal Mediterranean sites, with the above mentioned biases in mind, it can be stated that marine molluscs constituted quantitatively unimportant but qualitatively useful supplementary resources due to their nutritional peculiarities in a diet otherwise dominated by terrestrial foods and mammalian protein. The history of mollusc exploitation along Mediterranean coasts stems back to the Last Interglacial, at the very least. The quantitatively limited presence of marine molluscs, and other easily exploited coastal resources, has been interpreted as a sign of low population pressure, while high population pressure and resource depression has in other instances been taken to suggest intensive exploitation of marine molluscs. One of the most important lessons from the Mediterranean data is the long-standing importance of marine molluscs as a supplementary source of protein in forager diets. Molluscs are not necessarily a low-quality food, nor a particularly expensive type of food to collect from rocky shores. Interpretations of harvesting pressure are compelling in a handful of situations and, as such, revealing about the human circumstances in specific times and places. The validity of such interpretations is strongly dependent, however, on extensive knowledge of the environment in question. Ecological knowledge and modelling of the potential offered by marine molluscs for human diets show that Mediterranean coastal environments are noticeably less productive compared to the nearby oceanic regions (e.g. Zenetos et al., 2002; Fa, 2008 and references therein). Based on these considerations, it can be proposed for Mediterranean environments that the null hypothesis – that marine molluscs were not a major resource during the Palaeolithic and Mesolithic in absolute terms – is a valid generalization. This hypothesis is supported by the doubts on the importance of marine molluscs even for the diets of humans inhabiting the most productive coastal regions in the world (i.e. where mega-middens

are present, but see [Jerardino, 2010](#)) and can only be rejected in the unlikely case that the submerged sites will produce evidence of large shell accumulations. Healthy diets are built, however, upon a combination of nutritional quantity and quality, and the latter is no less important in the quest for complete protein and other rare nutrients.

The importance of marine mollusc exploitation should therefore be viewed in relative terms in the context of hunter–gatherer subsistence strategies as a whole. This is particularly necessary in the case of the Mediterranean region, not only because of its low mollusc biomass, but also because the topography of its basin is characterized by a complex mosaic of marine and terrestrial habitats, with the sea never being very far away. In other words, the value of marine molluscs for prehistoric Mediterranean human diets should also be assessed by verifying the periodicity of their exploitation, which will provide more elements to judge what part shellfish played in the scheduling of resource exploitation by the hunter–gatherers in question. This can be accomplished by establishing the seasonality of mollusc collection through isotopic and sclerochronological studies, which unfortunately have rarely been undertaken. The utility of this kind of information, combined with other data (e.g. mollusc MNI, shell biometric data, seasonality data from other fauna, etc.), can potentially allow assessment as to whether shellfish were consumed preferentially or only when other resources (e.g. terrestrial mammals) were low or not available.

In the case of the Middle Palaeolithic, marine molluscs were a low-cost (high return) supplement to large game hunting. The main hypothesis for explaining the late Upper Palaeolithic and early Mesolithic seasonality data is that, in Mediterranean environments characterized by low marine productivity, temporal regularity in the exploitation of marine molluscs might reflect coastal hunter–gatherer economies successful in responding to changing environments, increasing population levels and decreasing resources. In some cases, nevertheless, the consumption of marine molluscs might have been less opportunistic and it might have had a more incisive role in the local subsistence system (e.g. near transitional environments).

In some environmental settings (e.g. islands), irregular exploitation characterized by temporally haphazard collections seems to be associated to resource-stressed hunter–gatherers in the late Mesolithic (e.g. [Mannino and Thomas, 2009](#)). The biased dataset currently available suggests that it was also at that time that, with a more detailed knowledge of the marine environment, coastal adaptations evolved favouring considerable advances in maritime technologies ([Broodbank, 2006](#)). Further investigations are necessary to establish exactly when in time and where along the Mediterranean basin, coastal adaptations of such scale started developing and what role they played in how humans responded to Quaternary environmental dynamics.

Acknowledgments

ACC thanks the Lab. d'Arqueozoologia (UAB, Spain) and Museo e Istituto Fiorentino di Preistoria “Paolo Graziosi” (Italy). MAM acknowledges a Marie Curie Intra-European Fellowship within the 7th European Community Framework Programme. DBYM thanks the Israeli Ministry of Science, Culture & Sport for supporting the national collections of natural history at Tel Aviv University as a biodiversity, environment, and agriculture research knowledge center. Authors are very grateful to J.E. Estévez (Universitat Autònoma de Barcelona, Spain), B. Wilkens (Università di Sassari, Italy), K.D. Thomas (University College London, UK), J. Nadal (Universitat de Barcelona, Spain), C. Dupont (UMR 6566 CREAAH, France), C. Perlès (Université Paris X-Nanterre, France), J. Linstädter

(Universität Köln, Germany), N. Barton (University of Oxford, UK), G. Barker (University of Cambridge, UK), C. Hunt (Queen's University of Belfast, UK), M. Sahnouni (Indiana University, USA), E. Gontikaki (University of Aristotle, Greece), F. Martini (Università di Firenze, Italy), D. Lo Vetro (Museo e Istituto Fiorentino di Preistoria “Paolo Graziosi”, Italy) and W.R. Farrand (University of Michigan, USA) for their kind support in the production of this paper. Authors also thank the guest editors for their invitation and two anonymous reviewers for their comments and suggestions, which improved the quality of the manuscript.

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