Molluscs in the Levantine Upper Palaeolithic: implications for modern human diets and subsistence behaviour

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Chapter 1 ・ Introduction

From the Late Pleistocene onwards, Early Upper Palaeolithic (EUP) *Homo sapien*s groups (e.g., Levantine Early Ahmarians) dispersed into Eurasia around 50–40 thousand years ago (kya) (e.g., Klein 2008; Hublin 2013). These groups generally consisted of small populations often dispersed over large territories. Contrary to earlier humans dispersing into Eurasia, e.g., Levantine Initial Upper Palaeolithic (IUP) groups, EUP human settlement is characterised by increasing site counts and occupation intensity which has been interpreted as a sign of increasing population density (Powell et al. 2009; Mellars and French 2011; but see Dogandžić and McPherron 2013; Vaesen et al. 2016) throughout Marine Isotope Stage (MIS) 3 [~57–29 kya; Lisiecki and Raymo (2005)]. Thus, it appears thats EUP *Homo sapiens* were better adept to tackle the difficulties of dispersal and long-term survival in new habitats than their IUP forbearers. What were the underlying adaptations that made this possible? To start addressing this question, we need to improve our understanding of the timing of human dispersal events, the routes involved in these events, and the environmental conditions under which successful dispersal events occurred. Equally important is to investigate behavioural adaptations (e.g., technology, social interaction, and subsistence strategies) to shed light on some of the potential factors underpinning the success of these dispersals.

This thesis contributes to our understanding of early Upper Palaeolithic (including both Levantine IUP and EUP) adaptations through interdisciplinary research on materials from the archaeological site of Ksâr 'Akil, Lebanon. The choice of this site is based on several important factors. First, it has played a central role in the *Homo sapiens* dispersal debate because of its location in the Levantine Corridor on the edge of Europe (e.g., Bar-Yosef 1987; Mellars 2004). Second, Ksâr 'Akil is well known for its rich early Upper Palaeolithic deposits, including multilayered IUP and EUP/Early Ahmarian deposits that are associated with *Homo sapiens* fossils. The IUP and EUP of the Levant are key in the debate around Upper Palaeolithic human dispersals into Europe because both technocomplexes have been connected to *Homo sapiens* dispersal events based on similarities in lithic technologies between the Levant and Europe (e.g., Bar-Yosef 1998, 2007; Tostevin 2003; Mellars 2006; Kuhn and Zwyns 2014; Hublin 2015).

The IUP/Emirian in the Levant has been argued to be the source of the Bohunician in Central Europe and to represent the archaeological signature of a population dispersal (Svoboda and Bar-Yosef 2003; Tostevin 2003; Škrdla 2013). Along the same lines, it has been argued that the appearance of the Proto-Aurignacian in Europe is connected to a dispersal of Early Ahmarian human groups into Europe (e.g., Belfer-Cohen and Goring-Morris 2003; Mellars 2006; Zilhao 2006; Le Brun-Ricalens et al. 2009; Tsanova et al. 2012). Ksâr 'Akil is one of the few sites in the Levant (in addition to Manot Cave, Israel, and Üçağızlı I Cave, Turkey) that contain deposits spanning these critical time periods associated with human remains.

1.1 The role of shellfish in Palaeolithic diets

Exploitation of shellfish and other aquatic resources in general is thought to have been important in early hominid encephalization (e.g., Brenna and Carlson 2014; Cunnane and Crawford 2014; Joordens et al. 2014; Kyriacou et al. 2016). Marine molluscs and other aquatic resources are rich in polyunsaturated (omega-6 and omega-3) fatty acids in the form of arachidonic acid (AA) and docosahexaenoic acid (DHA). These are important in human brain development, and some of them, especially DHA, are difficult to obtain from other sources (e.g., Kyriacou et al. 2014). Recent archaeological discoveries indicate that the exploitation of aquatic resources has a long history among various hominid species. The earliest current evidence for the exploitation of freshwater fish is at FwJj20 (Koobi Fora, Kenya), dating to approximately 1.95 million years ago (Braun et al. 2010) and associated with the Oldowan. *Homo erectus* individuals may have consumed freshwater molluscs from approximately ≥400 kya in Trinil (Java, Indonesia) (Joordens et al. 2014).

The exploitation of coastal habitats has also featured in hypotheses concerning the interaction between *Homo sapiens* groups during the Southern African Middle Stone Age (MSA) (e.g., Marean 2014, 2015). Marean's (2014) hypothesis is that consistent use of these coastal habitats gave rise to the need to defend these territories, which likely led to intergroup conflict. A similar scenario for lakeshore access has recently been proposed for early Holocene groups in the Turkana Basin (Lahr et al. 2016). Intergroup competition over shore access could also have stimulated intragroup cooperative behaviours and so-called hyperprosociality (*sensu* Richerson and Boyd 2008), which Marean (2015) sees as one of the trademarks of modern human uniqueness. This hypothesis assumes reliance on intertidal marine recourses and a central role of the coastal zone in hunter-gatherer mobility. Evidence for MSA coastal exploitation dates back to MIS 6 and 5 (roughly 190–125 kya and 125–80 kya, respectively) when several coastal South African sites show evidence for shellfish gathering (e.g. Klein et al. 2004; Avery et al. 2008; Jerardino and Marean 2010; Langejans et al. 2012; Clark and Kandel 2013; Kyriacou et al. 2015; Jerardino 2016).

Furthermore, intertidal marine molluscs may have served as fall-back resources to tap into in times of dietary stress (e.g., Meehan 1977; Waselkov 1987) because they are easily acquired predictable resources that are available year-round (e.g., Shackleton and van Andel 1986; Kyriacou et al. 2014; Marean 2014; Jerardino 2016). In the eastern Mediterranean, for example, intertidal marine molluscs were predominantly gathered in winter during both the Epipalaeolithic Capsian and Neolithic phases at the Haua Fteah (Libya), whereas seasonality data for terrestrial fauna indicate that hunting was practised mainly during the summer, leading Prendergast et al. (2016) to suggest that shellfish were dietary supplements at times of resource depression. In the Mediterranean region in general, marine shellfish were exploited during the Middle Palaeolithic by both *Homo sapiens* and *Homo neanderthalensis* from MIS 5 onwards (e.g., Emiliani et al. 1964; Klein and Scott 1986; Stiner 1999; Finlayson et al. 2006; 2008; Colonese et al. 2011; Cortés-Sánchez et al. 2011; Barker et al. 2012; Fa et al. 2016).

The predictable availability of inter-tidal molluscs in coastal habitats has further been argued to facilitate human dispersals along coastal routes (e.g., Stringer 2000; Finlayson 2005; Mellars 2006a). In unknown terrain, coastal habitats may have provided a predictable source of molluscs that can readily be exploited (e.g., Fa 2008). In other words, whereas hunting terrestrial fauna in novel surroundings might prove difficult, marine molluscs are generally abundantly available on intertidal rocky shores. However, Fa (2008) argues that the low tidal amplitude of the eastern Mediterranean shores, due to the reduced intertidal zonation, would have supported fewer edible littoral molluscs than for example the western Mediterranean shores. He argues that these coastal habitats would therefore have been depleted rapidly, which would have necessitated moving to new coastal patches, thus promoting hunter-gatherer mobility along this type of coast. Similarly, Mannino and Thomas (2002) suggest that in a rocky shore context, if large-scale human dispersals along coastal routes are the result of many small-scale dispersal events, and if subsistence practices relied substantially on exploiting coastal resources, localised over-exploitation and patch depletion would have resulted in increased (residential) mobility (*sensu* Binford 1981). Although availability of edible shellfish would in these scenarios influence human mobility and dispersals, short-term local over-exploitation would not necessarily be evident in the archaeological record, if humans were passing through rapidly, and such episodes might not have had a long-term impact on mollusc communities (Fa 2008).

Finally, evidence of intensified use of coastal resources is often taken to be an indicator of reduced residential mobility and/or population pressure (e.g., Stiner 2001, 2009; Steele and Klein 2013; Marean 2014). Similarly, incorporation of shellfish into the diet and broader use of the carrying capacity of a site's catchment area would arguably allow support of a higher population density (e.g., Stiner 2001) or would sustain smaller groups for a longer time (e.g., Finlayson et al. 2006; Fa 2008; Prendergast et al. 2016).

Thus, the archaeological record suggests that aquatic resources played a role in hominid diets of great antiquity, though their contribution has been considered marginal for most of the Palaeolithic (e.g., Erlandson and Moss 2001; Colonese et al. 2011; Clark and Kandel 2013; Jerardino 2015). This is especially true when optimal foraging models are used, which primarily consider the caloric value and energy intake of foodstuffs (see also Stiner, 2001, 2010). However, shellfish are a rich source of many essential nutrients: next to the aforementioned AA and DHA fatty acids, they are also rich in vitamins D, B12, C, A, and E; as well as iron, folate, potassium, and calcium (e.g., Hockett and Haws 2003; Haws and Hockett 2004). Hockett and Haws (2003) suggest that broader and nutritionally rich diets are important because they increase hominid fitness and help to reduce child mortality and interbirth intervals. In turn, when minimum energy requirements are met (including those from other food sources), this could have allowed for the population increase in Europe thought to coincide with the start of the Upper Palaeolithic.

Against this background, the primary goals of the research programme were to (1) provide a new chronology for the IUP and EUP occupations of Ksâr 'Akil, and (2) to analyse selected faunal assemblages from Ksâr 'Akil with the aim of providing insights into subsistence strategies of Levantine early Upper Palaeolithic *Homo sapiens* and understanding the implications of their dietary choices for human nutrition, health, and population density. The following sections briefly present the theoretical background relevant to the Ksâr 'Akil project.

1.2 Theoretical framework

Many scholars have argued that at the onset of the Upper Palaeolithic, parts of Eurasia saw an increase in population density. This is based in part on the number of sites and archaeological artefact densities, as well as calculations of effective population sizes from genetic data (e.g., Bocquet-Appel et al. 2000, 2013; Lahr and Foley 2003; Mellars and French 2011, 2013; French 2015). Others argue that the increase in population density was less extensive than has been proposed. For example, Dogandič and McPherron (2013) argue that the tenfold increase proposed by Mellars and French (2011) is an overestimation, as the numbers for several Upper Palaeolithic phases were collated and not all proxies used are independent (but see French 2015). Davies (2007) argues for small ephemeral initial *Homo sapiens* dispersals at the start of the European Aurignacian based on site distributions and density. What were the underlying factors that facilitated these dispersals? Did, for example, past human diet play a role, and how can zooarchaeological data contribute to answering these questions?

Fluctuations in prehistoric human population densities have been investigated from zooarchaeological data sets worldwide using optimal foraging theory (OFT) and diet breadth approaches (e.g., Stiner et al. 2000; 2012; Stiner 2001, 2010; Munro 2004; Lyman 2008; Clark and Kandel 2013). OFT, follows the economic principle of optimisation, i.e., the action of making the best or most effective use of a situation or resource (MacArthur and Pianka 1966). Translated in archaeological terms, OFT rests on the assumption that an organism or population always tries to optimize subsistence practices, generally in terms of the capture of energy. Following the diet breadth model, overall foraging time depends on two factors: (1) the time it takes to encounter a suitable prey, i.e., 'search time', and (2) the time it takes to capture and process the animal after it has been located, i.e., 'handling time' (Fig. 1.1). Diet breadth models are built on the presumption that, in ideal circumstances, a hunter will only exploit the most profitable prey. In this way, the hunter's decision is based on whether it is more profitable to go after the encountered prey or to keep searching for a higher-ranked species (e.g., Winterhalder 1987; Kaplan and Hill 1992). A (substantial) rise in human population density would require a higher return rate, which in turn would lead to diversification of the diet to cope with the population's increased energy (i.e., calorie) requirements. The inverse of Simpson's (1/D) index (Simpson 1949), an index of taxonomic dominance in faunal assemblages, is often used to assess dietary breadth and the optimality of subsistence practices (e.g., Stiner 2001; Dusseldorp 2010; Lyman 2013). Following these assumptions, an 'optimal' diet consists of a small number of high-ranked taxa exclusively. Inversely, an abundance of many different lower-ranked taxa (e.g., small-bodied taxa low in energy yield or fast-moving taxa high in capture cost) would be indicative of the need to capture whatever hunter-gatherers could get their hands on, which suggests dietary stress (e.g., Broughton and Grayson 1993; Kelly 1995; Bird and O'Connell 2006).

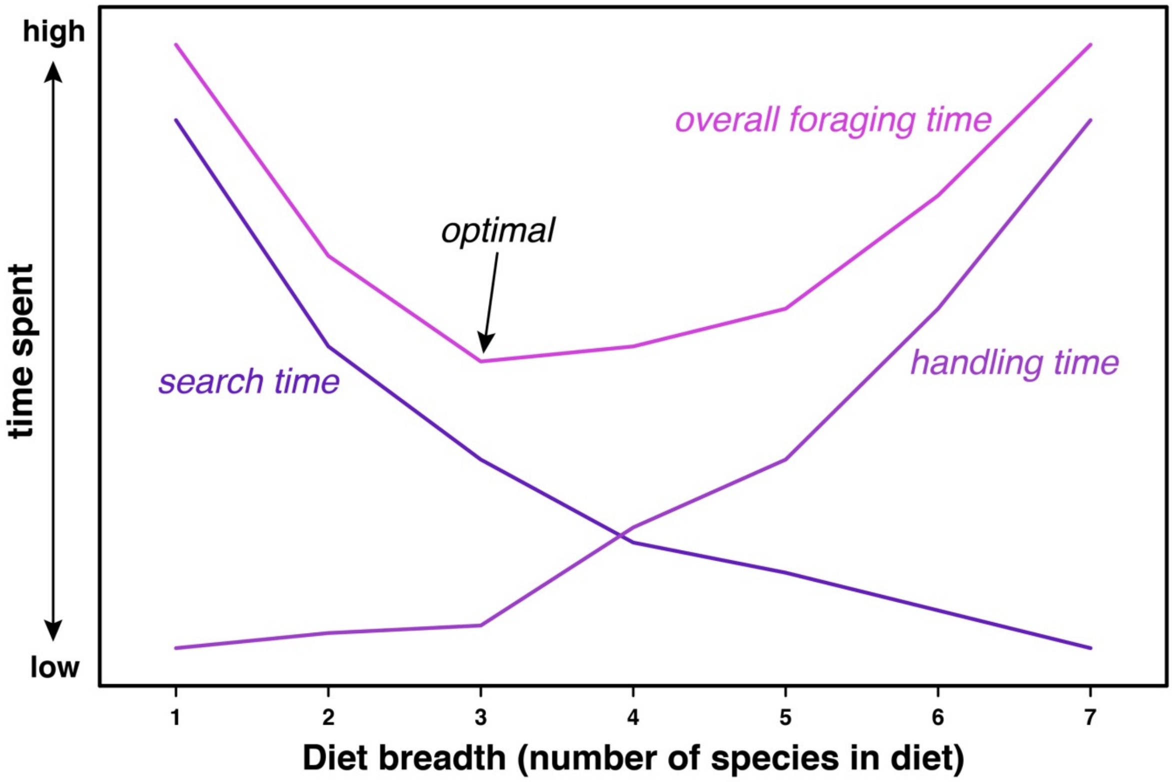

Figure 1.1: Diet breadth model.

Optimal foraging approaches have been criticised as too simplistic and not representing the full scope of hunter-gatherer subsistence behaviour that comprises more than just the optimal capture of energy (Smith 1983). However, these models have proven adequate to predict contemporary hunter-gatherer subsistence behaviour (see, e.g., Winterhalder 1987; MacArthur and Pianka 1966) and are likely equally useful when one seeks to understand the mechanisms and factors important in past hominid foraging behaviour (see also Dusseldorp 2009; 2010). In other words, OFT is a way of addressing subsistence data that can indicate if people are not foraging optimally from an economic perspective as well as if they are. Therefore, OFT forms a good starting point to understand the factors important in past foraging behaviour, including those that are not directly related to nutrition. Moreover, tools used in investigating optimal foraging—taxonomic dominance and evenness indices—have the additional benefit that they are useful for comparing patterns of animal exploitation between faunal assemblages through time at either a single site or between sites (see e.g., Lyman 2013). Based on these considerations, an optimal foraging approach is used to interpret the faunal data from Ksâr ‘Akil.

Adding to the OFT debate, Hockett and Haws (2003) argue that it is not the capture of energy that should be optimized but rather the nutritional value of the diet (e.g., the intake of essential nutrients such as minerals, vitamins, and amino acids). Changing the 'currency' of the foraging model opens up a new area of exploration in human dietary studies. Using so-called nutritional ecology theory (NET), Hockett and Haws (2003; Haws and Hockett 2004) suggest that a broadening or diversification of the diet would result in a more varied and nutritious diet incorporating more essential nutrients. In turn, this would result in healthier populations with greater reproductive success (especially if they also invested in methods to decrease child mortality and interbirth intervals *sensu* Kaplan et al. 2000), ultimately contributing to population increase. Unlike in most OFT models, the decision to diversify the diet in a NET model is not necessarily a conscious one. In other words, even if a subsistence strategy is driven by non-dietary objectives (e.g., obtaining secondary products such as animal skins, tortoise carapaces for containers, mollusc shells for tools or ornaments, prey encountered on a search for other raw materials), the benefits of a varied diet will still affect the overall health of a population.

It is challenging to assess nutritional value of foods in past hunter-gatherer diets from the archaeological record, let alone to assess who ate what within the group. For example, organ meat is high in rare essential nutrients, but from bones remaining in a site, it is not always possible to discern if the organs were consumed in addition to the muscle and fat resources. Similarly, plant foods were likely a (substantial) part of Palaeolithic diets, but they are rarely adequately preserved at archaeological sites (Jones 2009; Henry et al. 2014). In contrast, shells generally preserve well archaeologically, and they constitute small food packages high in essential nutrients. Moreover, these essential nutrients need not be eaten in great quantities to have a positive effect on human health. Therefore, even the presence of low quantities of nutrient-rich foodstuffs—as they are often found at Palaeolithic sites—is informative about the dietary nutritional value. Thus, to assess dietary adaptations and their implications for early Upper Palaeolithic hunter-gatherers, I chose to focus on mollusc exploitation. To gain insight into the broader faunal-based subsistence practices, I complemented the results on mollusc exploitation with investigations of diet breadth and habitat exploitation of terrestrial fauna from the same archaeological context.

1.3 Thesis summary

This thesis investigates the subsistence behaviour of early Upper Palaeolithic (including IUP and EUP) *Homo sapiens* based on the remains of molluscs and terrestrial animals recovered from Ksâr 'Akil. A major aim in this respect is to gain insight into the timing and intensity of shellfish exploitation. I also aim to discuss the influence that dietary choices may have had for past hunter-gatherers in terms of health and development and whether these dietary adaptations could have influenced population density at the site, given the Upper Palaeolithic *Homo sapiens* dispersal events into Europe. More specifically, this thesis addresses the following research questions:

(1) When were early Upper Palaeolithic foragers using the Ksâr 'Akil rockshelter?

(2) What do both the mollusc and vertebrate faunas from Ksâr 'Akil tell us about how early UP foragers exploited those resources, in terms of selection and frequency?

(3) What role does shellfish exploitation play in early Upper Palaeolithic subsistence practices?

(4) Are there differences between IUP and EUP subsistence strategies, and if so, how may they be explained?

(5) Are there general inferences from the Ksâr 'Akil case study for wider debates about landscape use, human health, demography, and their potential relationships to human dispersals?

To pursue these research questions, I conducted zooarchaeological investigations combining an OFT diet breadth approach with NET to evaluate subsistence practices and dietary adaptations of IUP and EUP groups. Specifically, I analysed shell assemblages to investigate mollusc use and consumption using a combination of zooarchaeological (including taphonomic), radiometric, and stable isotopic methods. The results are interpreted in the context of data from the vertebrate faunal assemblage, using a diet breadth approach to evaluate the exploitation of both sets of animal food resources.

In this thesis, I hold general conditions, such as geography, access to fresh water and raw materials, distance to the coast, and access to other habitats, as constant as possible by studying IUP and EUP assemblages from the single site of Ksâr 'Akil. As discussed above, this site was chosen on the basis of several important factors. However, the excavations took place in the 1930s and 1940s, and the site is no longer accessible. Therefore, before any zooarchaeological study could commence, the integrity of the site, its chronology, and potential biases of the recovered faunal assemblages had to be evaluated. These issues, as well as the results of the various analyses, are presented in the following chapters.

Chapter 2 provides an overview of the Palaeolithic sites in the Antelias Valley in which Ksâr 'Akil is situated. This includes a summary of the various notes and interpretations of the rockshelter's stratigraphy and a brief account of the site's history of research, with a focus on faunal studies. It details the sampling rationale for the studied vertebrate assemblage and the cleaning and curation protocols. It also provides a basic account of the taphonomic signatures of the IUP and EUP assemblages studied and an overview of the faunal composition in terms of NISP (Number of Identified Specimens) and relative abundance. Data recording protocols for both the shell and bone assemblages and their rationale are provided in the Appendix A.

Chapter 3 discusses the site's chronology and implications of the age of specific Upper Palaeolithic technocomplexes and human fossils for understanding the timing and patterning of the Upper Palaeolithic human colonisation of Europe. A new chronology of Ksâr 'Akil is presented based on 16 AMS radiocarbon dates and Bayesian modelling. A thorough evaluation of sample integrity using three different independent data sets—amino acid racemization, geochemical characterization of all dated shells, and oxygen isotope analyses—is also discussed. At the start of this project, no direct dates were available on either IUP or EUP material, and the site's chronology was built on assumed ages that were in part extrapolated from dates from other parts of the sequence (Mellars and Tixier 1989). Because the Ksâr 'Akil stratigraphic sections are no longer available and because the materials we used for dating were excavated long ago (1937–1938 and 1947–1948), I and my collaborators developed novel ways using different lines of evidence to assess the site's chronology; we also invested substantial effort in detecting compromised samples. Detailed descriptions of the fresh approaches developed in the framework of this thesis are provided in Chapter 3.

While we conducted our study, Douka et al. (2013) published a chronology based on AMS radiocarbon dates on beach-collected shells from the same excavation campaigns that were potentially used for ornamental purposes. Our new data set of AMS radiocarbon dates on the live-collected *Phorcus turbinatus* molluscs that were consumed by Upper Palaeolithic humans provided significantly older (3000–4000 radiocarbon years) age estimations for both the IUP and

EUP deposits. Chapter 4 discusses discrepancies between our chronology and those of other scholars and proposes some steps towards resolving the remaining questions.

Chapter 5 evaluates the integrity of the mollusc assemblage as well as potential biases (e.g., post-depositional processes, excavation, and collection bias). This chapter also assesses the comparability of assemblages from different layers, excavation years, and recovery histories. Although there is in some instances evidence of extensive time averaging in the way that assemblages formed over a certain amount of time but appearing to be from a (semi) continuous event), there is no tangible evidence for the actual mixing of cultural material either post-depositionally or post-excavation. The mollusc assemblage is described in terms of taxonomic diversity and evenness, taphonomic signatures of different taxa and the ways in which humans used them (e.g., tools, ornaments, and food). The chapter especially focusses on the proportional use from a chronological perspective of both terrestrial and marine molluscs as a food resource relative to their exploitation as a raw material. Investigations include identification of anthropogenic modifications and determination of whether molluscs were gathered alive, which are prerequisites for demonstrating shellfish exploitation by humans. Finally, metric analysis of both live- and beach-collected taxa is used to highlight chronological trends in average mollusc size to investigate potential overharvesting of marine coastal resources (e.g., Mannino and Thomas 2002; Klein and Steele 2013).

Chapter 6 discusses the nature and timing of human shellfish gathering throughout the Upper Palaeolithic and explores how shellfish consumption would have affected hunter-gatherer diets. Seasonality of shellfish exploitation is investigated through the use of oxygen isotope analysis. These data help us better understand the role of this foodstuff throughout the year, and they provide indications on the timing of site occupation, past hunter-gatherer mobility, and overall landscape use. These data are substantiated with evidence from other faunal categories, such as avian, micro- and macro-vertebrate assemblages, that help us understand habitat diversity and human diet breadth. The emerging patterns gleaned from the data are compared with subsistence data from other eastern Mediterranean Palaeolithic sites. Finally, I discuss the implications of shellfish exploitation for past hominid diets in general from a NET perspective and highlight the differences between the IUP and EUP at Ksâr 'Akil.

Chapter 7 summarises the results of the previous chapters and presents a broad discussion of their implications for human subsistence strategies at Ksâr 'Akil. A particular focus is on the discussions on the role that shellfish played in past hunter-gatherer lifeways and on different dietary adaptations of IUP versus EUP groups. The implications of these differences with regard to human health, life history, and dispersal events are explored.

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Chapter 2 • Ksâr 'Akil: Site background, sampling strategy, taphonomy, and vertebrate fauna

In the following chapter, background on Ksâr 'Akil as well as its surroundings, the history of research, the archaeological materials, and the stratigraphic sequence are provided. Further, the employed sampling strategy and its rationale for both the vertebrate and invertebrate assemblages are discussed. Throughout this thesis, information derived from the vertebrate fauna assemblages has been used to identify taphonomic possesses that affected the archaeological material. In addition, investigations of habitat exploitation patterns and taxonomic evenness of the vertebrate fauna have served to place the molluscan data into a broader context of past hunter-gatherer subsistence behaviour. From subchapter 2.6 onwards, the results of these zooarchaeological investigations are briefly described.

2.1 Ksâr 'Akil and the Antelias Valley

The Ksâr 'Akil rockshelter is situated roughly ten kilometres northeast of Beirut (Lebanon), on the Eastern Mediterranean coast. It is located in the Antelias Valley which terminates in the Bay of St. George (Fig. 2.1). Approximately two kilometres inland from this bay, the valley widens and the rockshelter is roughly one kilometre further inland in the northern slope of the valley (Ewing 1947, 1948, 1949). In prehistoric times, a limestone hill in the middle of the valley caused bifurcation of the Antelias River at the height of the rockshelter at about 80 metres above the current sea level. The name of the site is a contraction of the words *Qasr*, meaning inaccessible or fortified place, and *Aqil*, meaning intelligent or wise. The name probably refers to the Semitic 'high place' that used to be situated on the top of the central limestone hill that has since been quarried away. Although the high place no longer exists, the Ksâr 'Akil rockshelter itself still survives, albeit hardly accessible and filled with rubble from extensive quarrying activities (Bergman et al. 2012).

In the past, the south-facing opening of the rockshelter would have been protected by the hill (now quarried away) in the centre of the valley. Freshwater supply would likely have come from the adjacent Antelias River running down the valley. Furthermore, the Ksâr ‘Akil occupants would have had access to the small coastal plain (sahil), the steep slopes of the Lebanon Mountains, and the open highlands of the Beqaa Valley (Fig. 2.1). That the valley was attractive for prehistoric hunter-gatherers is evident from the rockshelter’s 23-metre stratigraphy containing abundant archaeological material remains and from other archaeological sites known in the vicinity. The faunal assemblages of these other sites are mentioned in Hooijer’s (1961) study of the Ksâr ‘Akil vertebrates. The Mugharet el-Bileni*,* or ‘wet cave’ (also known as Antelias Cave), is situated opposite Ksâr ‘Akil on the valley’s southern slope (Braidwood et al. 1951). Antelias Cave, formed by an underground stream, was excavated by the French geologist/archaeologist Zumoffen at the end of the nineteenth century. It contained late Palaeolithic to Neolithic deposits, spanning the time window of roughly 40–5 kya. Faunal remains include Mesopotamic fallow deer (*Dama mesapotamica*), roe deer (*Capreolus capreolus*), wild goat (*Capra aegagrus*), an indeterminate gazelle (*Gazella* sp.), wild boar (*Sus scrofa*), and the large landsnail *Helix pachya* (Hooijer 1961). Human remains include several long bones, a mandible, and a partial skeleton of an 8-month old foetus that probably originates from the Neolithic layers.

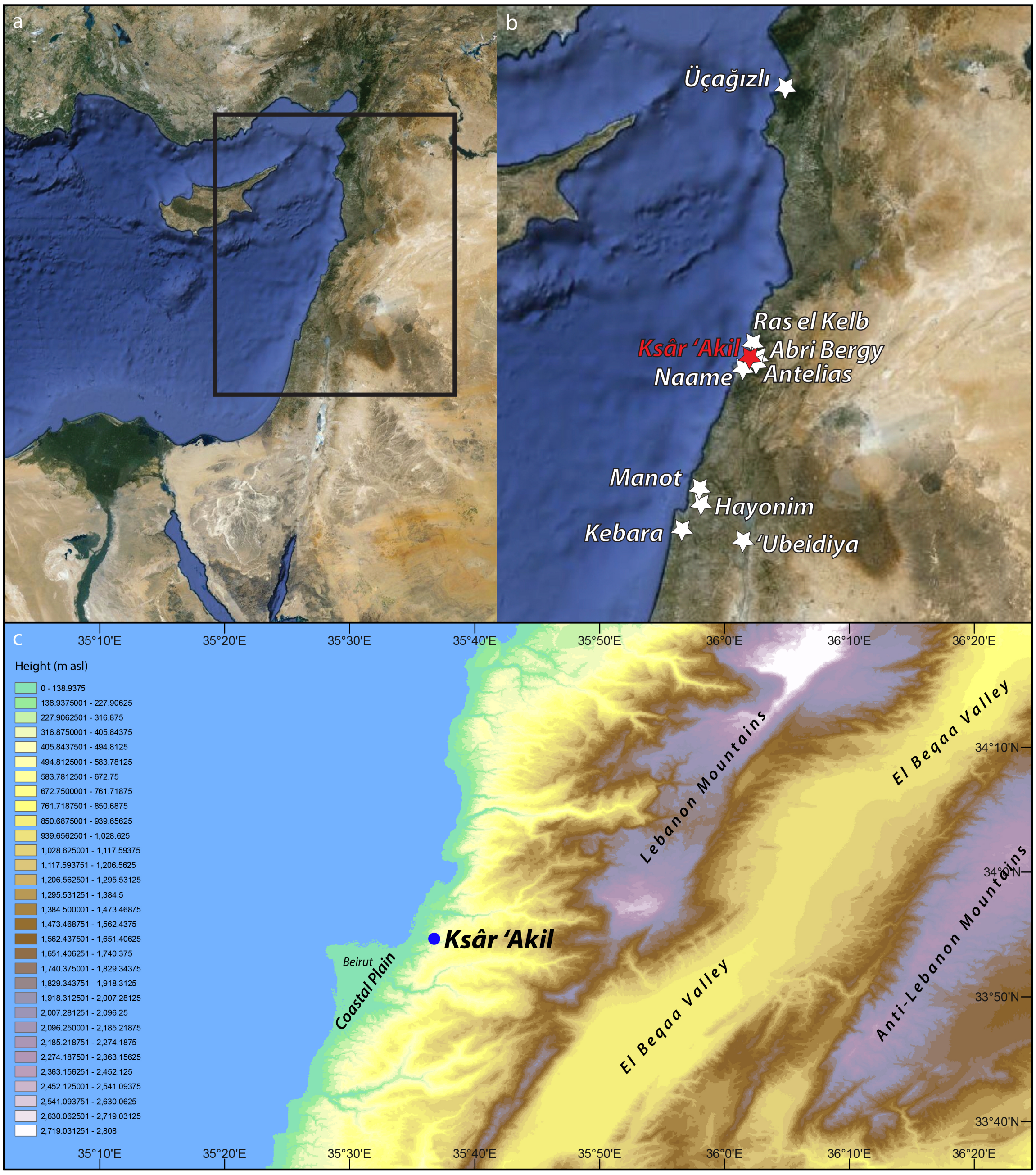

Figure 2.1: Maps showing the geographical location of Ksâr 'Akil and other sites mentioned in the text. (a) and (b): satellite image from http://maps.google.com; (c): Digital elevation data based on NASA's Shuttle Radar Topography Mission (SRTM) (downloaded from: https://lta.cr.usgs.gov/SRTM).

Approximately 400 metre upstream from Antelias Cave, another rockshelter, Abri Bergy, named after the French archaeologist Bergy (1873–1955), can be found. Here, Kebaran artefacts (dating to approximately 20–15 kya) were uncovered. The faunal assemblage comprises *Dama mesapotamica, Capreolus capreolus, Capra aegagrus, Sus scrofa, Ursus* sp., the terrestrial molluscs *Pomatias olivieri* (n = 2) and *Sphincterochila cariosa* (n = 1; although the latter was absent from the collection during this study). Several human remains were uncovered, among which a skull, mandible, and four cervical vertebrae of an adult male were noted (Hooijer 1961; van Regteren Altena 1962). Of these sites, however, the Ksâr 'Akil sequence is extremely rich in archaeological remains and shows by far the longest series of occupations spanning the Middle Palaeolithic to the Epipalaeolithic.

2.2 History of research

Ksâr 'Akil was discovered in 1922 by looters who bought the site and, in their search for gold, dug a 15-metre deep pit at the back of the cave (approximately squares D&E3–4 in the later excavation grid used by Doherty and colleagues). Professor Day, a geologist at the University of Beirut, was able to acquire some of the uncovered lithics and faunal remains and send them on to Paris and London (Ewing 1947). Abbé Breuil saw the material and recommended the site to one of his students, Rev. Doherty. Subsequently, a team from Boston College under the direction of Doherty conducted two field campaigns in 1937 and 1938. The site was larger and richer in archaeological deposits than anticipated, and although during the two extended field seasons excavations had reached a depth of 19 metres, there was still no bedrock in sight. After a break forced by World War II, the team finally reached bedrock at a depth of 23 metres in a final excavation season in 1947–1948 (Ewing 1947, 1948, 1949, 1960). In 1969, Tixier reopened the site and continued excavations until 1975. His team excavated down to a depth of nine metres, when they were forced to leave Lebanon due the outbreak of civil war (Tixier and Inizan 1981; Mellars and Tixier 1989).

2.3 The sequence of Ksâr 'Akil

The 23-metre sequence of Ksâr 'Akil contains deeply stratified deposits from the Middle Palaeolithic to the Epipalaeolithic (Fig. 2.2). The lowermost seven metres (16–23 metres below datum) mostly consist of reddish alluvial deposits that were formed by occasional flooding events of the nearby stream. Within these deposits, several Middle Palaeolithic layers (Layers XXXVII–XXVI) were uncovered (Ewing 1949; Wright 1962).

Above 16 metre, the sediments containing Upper Palaeolithic artefacts are generally brown-greyish in colour and intersected by complexes (e.g., at 16–17 metre and 10–11 metre) of red clay bands underlying a deposit of angular limestone blocks. Both Wright (1962;

Braidwood et al. 1951) and Ewing (1960) hypothesized that these periods of clay formation coincided with humid climatic conditions, potentially representing wetter phases of the last glaciation, but at present this cannot be verified. In the lowest complex, comprising archaeological Layers XXV–XXIV, a *Homo sapiens* maxilla fragment, named, was found accompanied by IUP artefacts. In addition, several faunal taxa including a large gazelle (*Gazella* cf. *gazella*), ibex (*Capra ibex*), hare (*Lepus* sp.), fox (*Vulpes vulpes*), and wild cat (*Felis silvestris*), appear at the start of the Upper Palaeolithic (Fig. 2.2; Table 2.4). In general, the IUP lithic artefacts (Layers XXV–XXI) are characterised by blade cores with opposed platforms and blanks with facetted platforms. Retouched tool types include the *chanfreins* (chamfered pieces)—typical for the Levantine IUP—which are retouched distally by an oblique or *tranchet* flake removal, endscrapers, and burins (Azoury 1986; Bergman 1988).

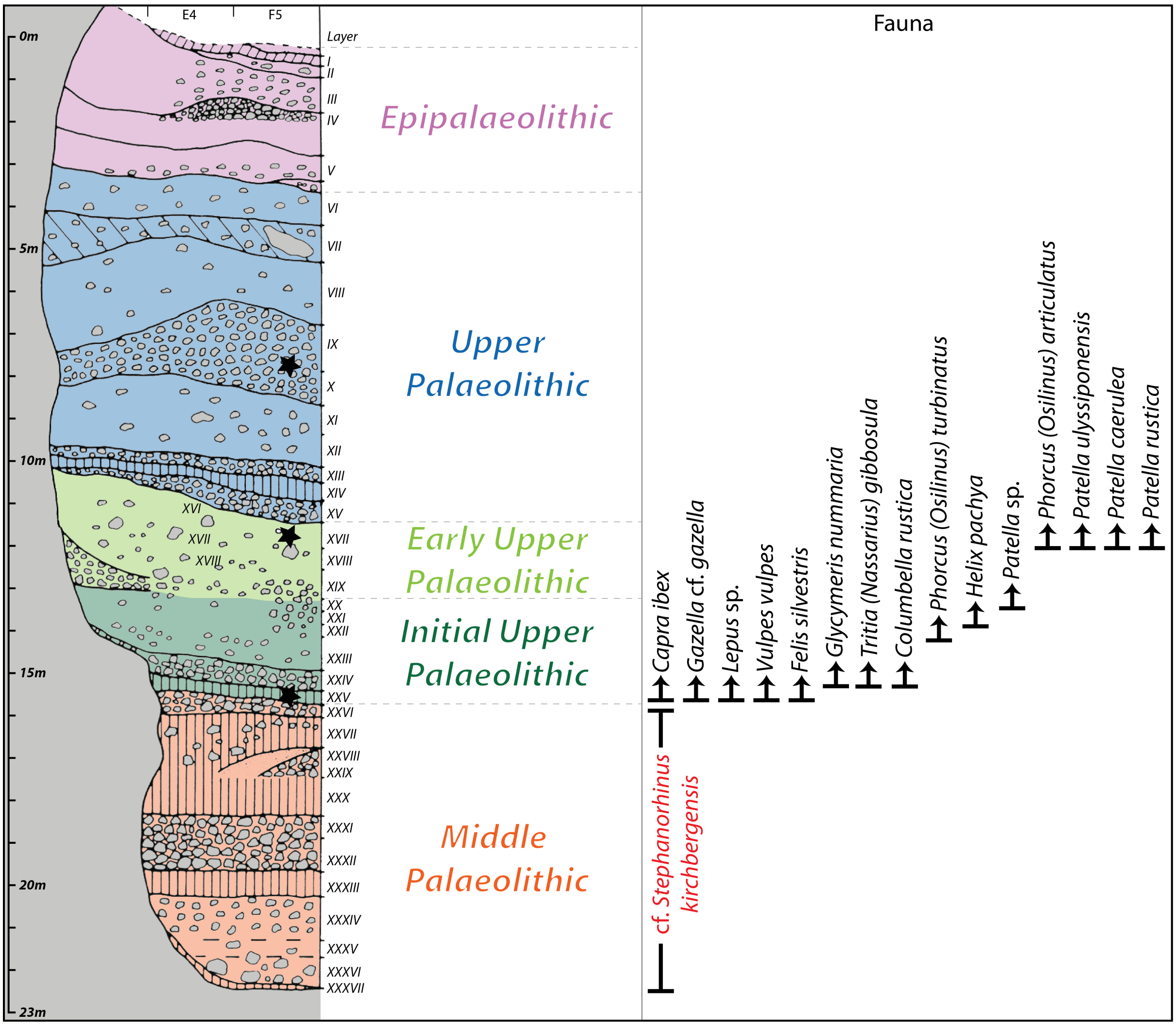

Figure 2.2: Ksâr ʻAkil stratigraphic sequence (redrawn after Mellars and Tixier 1989) with reference to the major archaeological divisions, stratigraphic position of the human remains (stars), and last (red) and first (black) appearance of several faunal taxa.

Subsequent archaeological layers (i.e., Layers XX–XIV) contain Early Ahmarian or Early Upper Palaeolithic lithic artefact assemblages. These assemblages are characterized by opposed platform cores and blanks with plain platforms. Retouched tool types mainly consist of endscrapers, retouched blades and bladelets, including so-called el-Wad points, which have fine and/or steep, usually dorsally retouched tips (Azoury 1986; Bergman 1988). A partial skeleton of an eight-year-old boy named Egbert and some remains of a second individual were found at the back of the cave, in square F3, in the Early Ahmarian Layer XVII (Ewing 1960; Bergman and Stinger 1989).

Above the 'classic Early Ahmarian', Layers XVIII–XVI, the attribution of Upper Palaeolithic archaeological layers to defined technocomplexes becomes somewhat complicated, and several interpretive frameworks have been put forward (Table 2.1; see also Tixier and Inizan 1981; Azoury 1986; Marks and Volkman 1986; Bergman and Goring-Morris 1987; Kersten 1987; Bergman 1988; Bergman and Stinger 1989; Mellars and Tixier 1989; Ohnuma and Bergman 1990; Kuhn et al. 2001; Williams and Bergman 2010; Douka et al. 2013; Leder 2014; Bosch et al. 2015a). For example, Bergman (1988; Williams and Bergman 2010) does not include Layers XV and XIV in his framework, as he claims those layers are sterile. However, a modest number of faunal remains including vertebrates and a few molluscs have been recovered (n = 344 and n = 3, respectively, for square F4). Most scholars agree that Layers VIII–VII can be assigned to the so-called Levantine Aurignacian (Bergman and Goring-Morris 1987), although some have questioned this name because radiometric data suggest that the Aurignacian first appears in Europe and later spread to the Levant by movement of European Aurignacian groups (e.g., Goring-Morris and Belfer-Cohen 2006). They argue, therefore, that the Levantine Aurignacian as a novel technocomplex does not exist and that it should be named simply Aurignacian.

Layer VI is variably placed in the final Upper Palaeolithic (Bergman 1988), the Epipalaeolithic (Mellars and Tixier 1989), the early or Proto-Kebaran (Kuhn et al. 2001), and the Atlitian (Williams and Bergman 2010). A new radiocarbon date on shell (see Chapter 3) of 32.7–31.9 ka cal BP suggests that this layer was formed prior to the last stages of the Upper Palaeolithic. This issue cannot be resolved without reinvestigation of the archaeological remains as well as a more detailed dating programme of this layer. Layers V–I are rather ephemeral and generally attributed to the Epipalaeolithic. Our new radiometric date for Layer V, i.e., 30.2–29.7 ka cal BP, same as for Layer VI, suggests that this layer is older than previously thought. The abovementioned interpretive schemes are largely based on lithic tool types and/or technology. Hooijer (1961), who studied the 1930s and 1940s vertebrate collections, divided the layers on the basis of changes in faunal composition in Phases 1 to 6, of which 3–6 are Upper Palaeolithic (see Table 2.1). These changes in species availability coincide with some, but not all, changes in lithic technology. Here, we generally follow the most recent division by Williams and Bergman (2010), apart from grouping all named and unnamed Upper Palaeolithic assemblages (Layers XV–VI) into one Upper Palaeolithic (see Bosch et al. 2015a), although in a subsequent paper we have chosen to treat Layer VI as a separate entity due to the substantial uncertainty in technological attribution of this layer (Bosch et al. 2015b). Overall, we have also sought to refer to individual layers so that the conclusions of this thesis may also be used within the frameworks proposed by other scholars.

Table 2.1: Division of the Upper Palaeolithic sequence of Ksâr 'Akil into phases based on lithic typology (Mellars and Tixier 1989; Kuhn et al. 2001; Williams and Bergman 2010) and changes in faunal composition (Hooijer 1961).

Layer	Mellars & Tixier 1989	Kuhn et al. 2001	Williams & Bergman 2010	Hooijer 1961
I	Epipalaeolithic	early Kebaran	Epipalaeolithic (phase 7)	phase 6
II				
III				
IV				
V				
VI	Upper Palaeolithic		Atlitian (phase 6)	phase 5
VII		late Levantine Aurignacian	Levantine Aurignacian (phase 5)	
VIII				
IX			Unnamed Upper Palaeolithic (phase 4)	
X				phase 4
XI		mid Levantine Aurignacian	Unnamed Upper Palaeolithic (phase 3)	
XII		early Levantine Aurignacian		
XIII				
XIV	Transitional phase B	Upper Palaeolithic phase II B		
XV				
XVI			Ahmarian (phase 2)	
XVII				
XVIII				
XIX		Upper Palaeolithic phase II A		phase 3
XX				
XXI	Transitional phase A	Upper Palaeolithic phase I	Initial Upper Palaeolithic (phase 1)	
XXII				
XXIII				
XXIV				
XXV				

2.4 Material

The material studied here originates from the 1930s and 1940s excavations by Doherty, the only expedition to reach the IUP and EUP layers. Although excavation techniques were not up to present-day standards, all sediments were dry sieved, and special care was taken when excavating animal bones in anatomical association (Murphy 1938). Ewing (1947, 1948, 1949) was responsible for curating the faunal (and human) remains in the field from 1938 onwards and made a preliminary, very detailed, and impressively accurate account of faunal distribution throughout the sequence. Faunal remains were subsequently boxed up and sent to a specialist for a detailed paleontological study. This study was originally delegated to Bate, a specialist of Pleistocene Levantine faunas at the Natural History Museum in London, UK. However, she was not able to complete her study before her death in 1951. Therefore, the Ksâr 'Akil fauna was sent on to Hooijer at the Natural History Museum (known today as the Naturalis Biodiversity Center) in Leiden, the Netherlands, who studied the entire vertebrate material (Hooijer 1961). During his investigations, Hooijer separated vertebrates and invertebrates. The latter were handed over to his colleague van Regteren Altena for analysis (van Regteren Altena 1962). In the late 1980s and early 1990s Kersten conducted several faunal investigations specifically looking at Epipalaeolithic wild goat and Mesopotamic fallow deer (Kersten 1987) and sequence-wide studies of the bird remains (Kersten 1991) and microvertebrates (Kersten 1992). She kindly provided me with lists based on notes from the original excavators that correlate depths per square to the layers assigned by Ewing, thus linking the material from the 1937–1938 and 1947–1948 excavations. Both the vertebrate and invertebrate assemblages from Ksâr 'Akil remain stored in the Naturalis Biodiversity Center in Leiden (the units of fossil vertebrates and fossil mollusca, respectively). After the initial investigation by van Regteren Altena (1962), the invertebrates were studied by, amongst others, Reese, and were published in a comparative study of the Üçağızlı Cave I (Turkey) and Ksâr 'Akil early Upper Palaeolithic ornaments (Kuhn et al. 2001).

2.5 Sampling strategy

A substantial amount of faunal material has been retrieved during the Doherty and Ewing excavations of the 1930s and 1940s. These collections are stored in two full rows in the Naturalis depot (about 200 large depot boxes; see Fig. 2.3). Within these depot boxes, the bones were largely kept in their original small cartons with glued-on excavation labels containing information on provenience including the square, layer, and/or depth below datum. In determining what to study in the time available, several factors were taken into account. The aim was a comparative study of the earliest Upper Palaeolithic faunal assemblages to gain insight into the subsistence strategies used during these occupation phases. From excavation notes, it is clear that different datums, about a metre apart in depth, were used in subsequent field seasons. The excavators were aware of the problem and made lists correlating layers between squares still available today (see Hooijer 1961; Kersten 1991, 1992, 1987; Bosch et al. 2015a, b). Nevertheless, to overcome potential problems with correlating material from different squares and different excavation seasons, and due to the sheer amount of material available, we decided to take a vertebrate sample from a single square. The 1930s and 1940s excavation campaigns used a 2 × 2 metre excavation grid, thus constituting the smallest sampling unit (Fig. 2.4).

Figure 2.3: Naturalis biodiversity Center (Leiden, NL), fossil vertebrate unit, where the Ksâr 'Akil bones are housed. The left side of the corridor is dedicated to the Ksâr 'Akil collection.

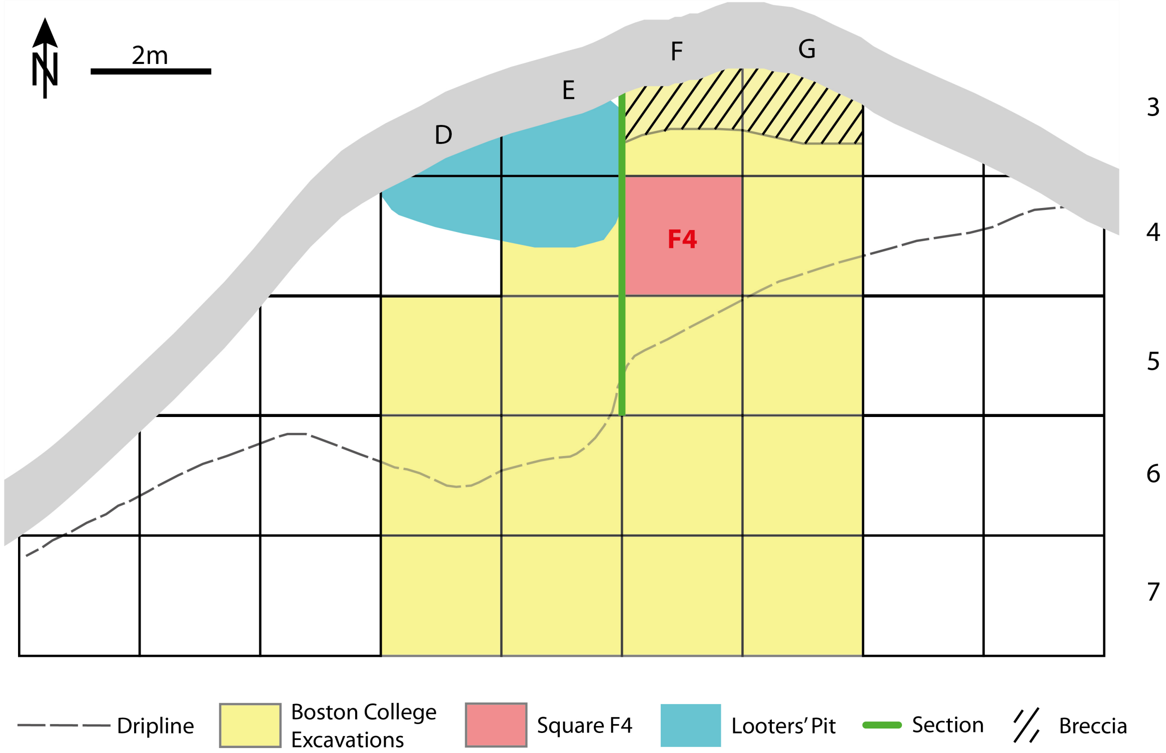

Figure 2.4: Map of the site Ksâr 'Akil (redrawn after Mellars and Tixier 1989) showing the extent of the Boston College excavations (yellow), the looters' pit (blue green), the brecciated area along the rockshelter's wall (hatched), the square F4 from which the sampled bone assemblages originate (red), and the location of the drawn Stratigraphic profile (green).

Excavation notes state that deposits close (up to 30–50 cm) to the rockshelter's wall were highly brecciated, which led to problems in recovering faunal remains, so I excluded all of row 3, i.e., squares D3, E3, F3, and G3 (Ewing 1947). Furthermore, any material from or close to the looters' pit was avoided (approximately squares D&E3–4), as it had been open since it was excavated in the early 1920s. Lastly, I wanted material from close to the published section drawings, which include squares E4 and F5 (see e.g., Bergman and Stringer 1989). This left squares F4, E5, and F5 to choose from. There is a discrepancy in the published literature regarding which squares were excavated in which years. According to Hooijer's (1961) notes, F3, E5, and F5 were excavated in the 1930s, whereas other squares, including F4, were done in the 1940s; this information was deduced from the labels and provenience data that accompanied the bones sent to him. He further states that the material from the 1930s is in 'better shape' than that of the 1940s excavations (Hoojier 1961: 4). However, Bergman went through an archive of unpublished excavation notes, and in 2010 a plan of the rockshelter was published. This indicated that F3, G3, E4, and F4 were excavated in the 1930s, and squares D5–F5, E6, and F6 were done in the 1940s (Williams and Bergman 2010: Figure 3). Ewing (1947: Figure 2) published a section drawing displaying the state of affairs at the end of the 1938 field season, albeit without mention of the squares used or orientation of the profiles. In the section, he drew the burial of Egbert, which was found in square F3. Moreover, Murphy (1938) writes that they used the section of E4 provided by the wall of the looter's pit as a starting point for their stratigraphy. This suggests that the profiles used formed the border between rows E and F and were drawn facing east (see also Braidwood et al. 1951: Figure 3). The fact that in Ewing's 1947 paper only the uppermost two metres of the square adjacent to E4 have been drawn suggests that the majority of either E5 or F5 was excavated in the 1940s. This in turn supports Bergman's representation of the excavation activities. Unfortunately, I had no access to Bergman's data, as this work was published after I selected my sample.

My decision, therefore, was primarily based on Hooijer's notes, the provenience data accompanying the fauna, and a visual inspection of the bones. Of the remaining optional squares (i.e., F4, E5, and F5), F4 is the only one for which the labels mention the archaeological layer in addition to the square and 'depth below datum' (see also Hooijer 1961). As mentioned above, Hooijer (1961) writes that the 1937–1938 material, which he takes to be F3, F5, and E5, is generally in better condition that the 1947–1948 material. However, on the basis of inspection of the bones in the Naturalis depots, cortical surface preservation is sufficient to detect cutmarks and other anthropogenic modifications and, moreover, does not appear to differ substantially between squares E&F5 on the one hand and square F4 on the other. Therefore, it could be that Hooijer's remark refers to the proportion of identifiable bones in the 1930s and 1940s assemblages. Certainly, long bone shaft fragments, many of which exhibit green (fresh) breaks, are abundant in the F4 material, especially in the Upper Palaeolithic layers.

The presence of shaft fragments, which are often hard to identify to species, are important in taphonomic studies such as those evaluating density-mediated attrition and the extent of carnivore damage. They further allow for identification of impact fractures relating to bone-marrow exploitation. For these reasons, the 2 × 2-metre square of F4 was selected for study. In total, the faunal assemblage of F4 comprises approximately 85,000 specimens, and although all material was subjected to initial curation activity, including acid treatment of all bones to remove calcretions, a further selection of layers for study was necessary. Of the IUP deposits, Layers XXV and XXII were chosen, and from the EUP, Layers XVIII, XVI, and XIV were selected, resulting in a total of 5,505 vertebrate remains. The invertebrate assemblage of the 1930s and 1940s excavations is much smaller than that of the vertebrates (to date: n = 3,571) and could be studied in its entirety. Overall, the abundance of both vertebrate and invertebrate remains per layer follows the same trends throughout the sequence, although Layers V, IX, and XVI show a higher relative proportion of shells; Layer XX displays a higher relative (estimated) abundance of bones (Fig. 2.5).

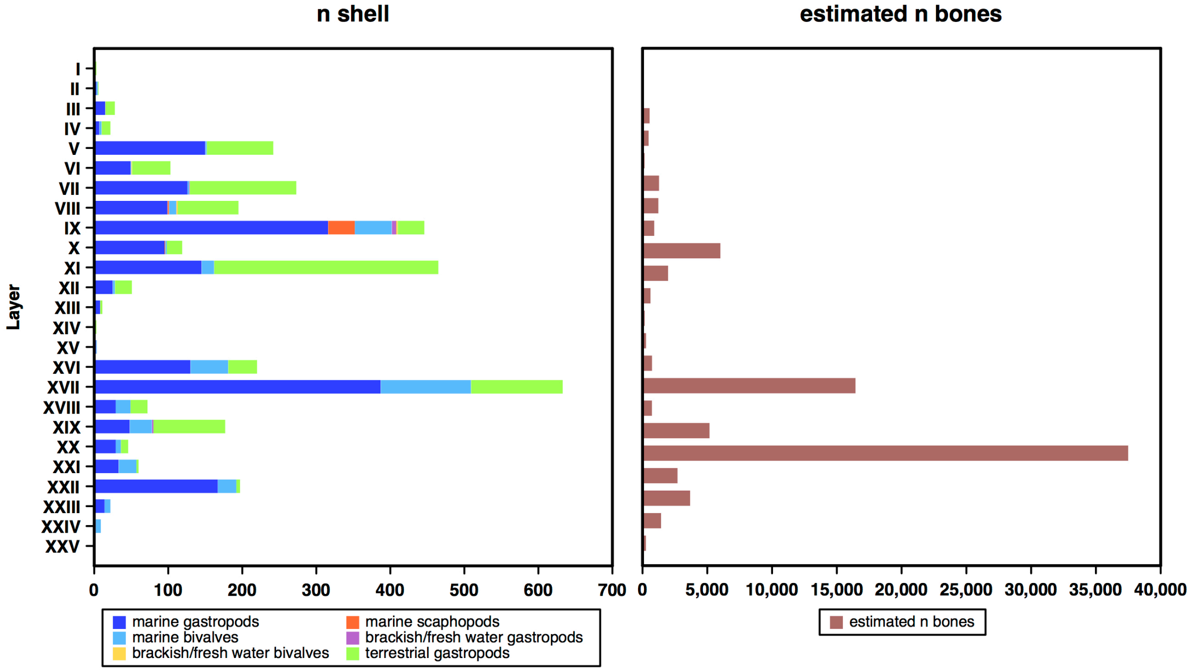

Figure 2.5: Comparison of the frequency of invertebrates (divided by class and habitat) of the total Ksâr 'Akil shell assemblage and estimated frequency of vertebrate remains (only from square F4).

2.6 Vertebrate fauna

The study of the sampled vertebrate fauna does not feature prominently in the chapters that follow, which focus on analyses of the mollusc assemblages. However, I have repeatedly relied on vertebrate data to place the molluscan data into context. These remains yielded clues on post-depositional processes and the extent of human involvement in various layers, and they provide quantitative data on hominin habitat exploitation and dietary breadth. Moreover, during treatment with 10% acetic acid and curation of the vertebrates, a modest number of shells and shell fragments (n = 767) was uncovered and published as the '2015 collection' (2015). Thus, although an in-depth zooarchaeological account of the vertebrates was beyond the scope of this thesis, a brief overview of the research methodology, taphonomy, and faunal composition is provided below (see also Appendix A for the data recording protocol).

All available material from square F4 was selected from the Naturalis Biodiversity Center depots in Leiden and transported to the Max Planck Institute for Evolutionary Anthropology in Leipzig for study. All exported units, whether individual bones or boxes of bones with a shared provenience, were assigned a lab number (DMB1–855, and 999). The faunal remains from the Middle Palaeolithic and Epipalaeolithic layers, as well as those of Layers VI, VII, IX, XV, XVI, and XVIII (n ~4,000), were previously cleaned using acid (Kersten 1987), but the majority (n ~80,000) of Upper Palaeolithic remains (Layers VIII, X–XIV, XVII, and XIX–XXV) were still covered in abundant concretions. To enable identification and inspection of cortical surfaces, these bones were also subjected to acid treatment. Whenever possible, fragile specimens including toothrows, shell fragments, and bones found in anatomical association were extracted and sediment samples (n = 10) were taken. The use of acid is sometimes criticised because it might hamper certain methods of chemical analysis and might affect the preservation of bone surfaces. Therefore, I only treated the F4 assemblage, leaving many thousands of bones from other squares untreated and accessible for other types of analyses. I further conducted a series of experiments to use just enough acid to loosen most attached sediments while leaving cortical surfaces intact.

The acid-treatment protocol involved submerging bones in a 10% acetic acid solution for at least eight hours, and subsequently, any remaining reaction was stopped with a base wash (10% sodium carbonate solution) for two hours. After this, the bones were thoroughly rinsed with normal tap water, dried, and bagged together with separately bagged labels containing information on the find category, layer, square, and the Naturalis inventory number or unique museum identification (RGM) number. Lithics, stones, and sediment samples were bagged per layer. Studied shells and bones were assigned an RGM number that was both written on the labels and included in a two-dimensional barcode.

2.6.1 Taphonomy

Taphonomic investigations focussed on evaluating natural processes and anthropogenic processes that affected the bone. These include breakage types, cortical surface weathering and preservation, burning, and human and animal modifications (Table 2.2). Overall the taphonomic signature of the faunal assemblages is very similar. Most (>90%) of the bones are fragmentary.

2.6.1.1 Breakage patterns

Evaluation of breakage patterns included the recording of the most prominent (i.e., primary) and secondary breakage types. Fresh or green breaks, often identified through spiral fractures of the cortical bone, occur when bone is still greasy, potentially when meat and bone marrow are available for humans, carnivores, or scavengers to eat. Dry breaks occur when the bones are devoid of flesh, no longer greasy, and become increasingly brittle due to a lack of organic content. This type of break can be caused by, for example, post-depositional processes such as trampling or crushing, but it cannot be directly linked (in most cases) to human and animal subsistence-related activities. Lastly, recent breaks are those that occurred during the excavation, curation, and storage of the bones. The category na consists of bones which show no primary and / or secondary breakage, or in few cases, the break was obscured by adhering sediment so that assessment of the breakage type was not possible. Among the Ksâr 'Akil fauna, dry breaks are most common (i.e., roughly 70% of primary breaks), and fresh or green breaks were encountered on approximately 20–30% of the bones depending on the layer (Fig. 2.6).

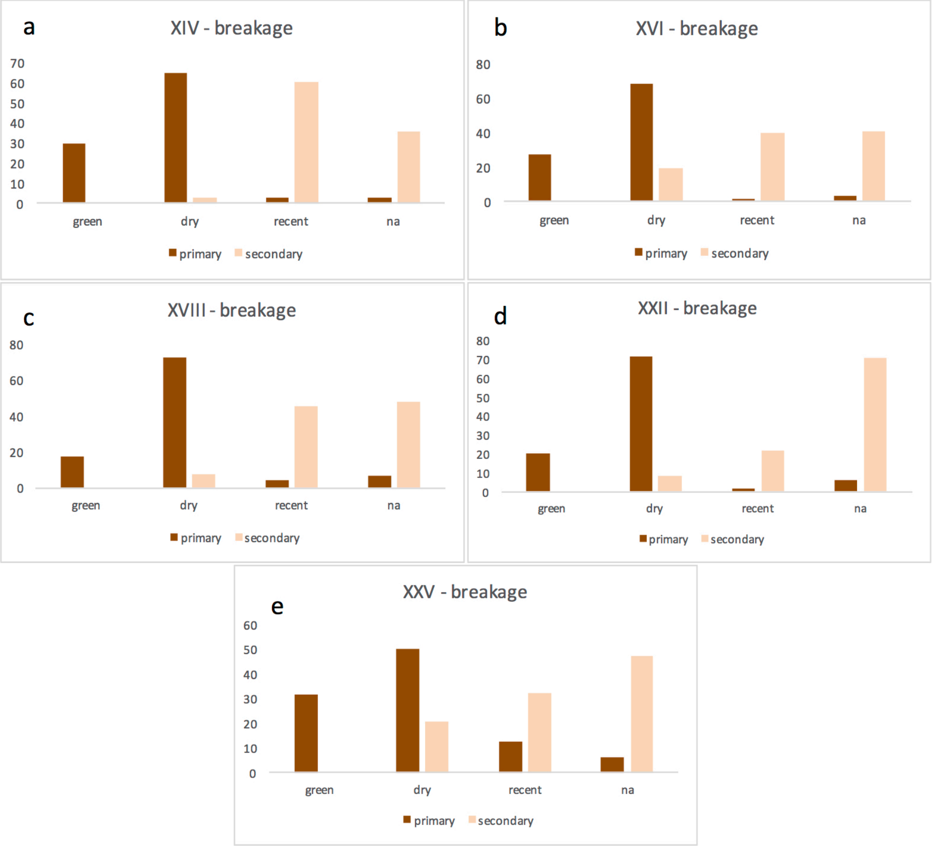

Figure 2.6: Frequency of primary (dark) and secondary (light) breakage types per layer. Green: breaks on fresh bones, Dry: breaks on dried bones devoid of flesh, recent: breaks which occurred during excavation, curation, and/or storage, na: bones without primary or secondary breakage or the type of fracture is obscured by adhering concretions. (a) Layer XIV, (b) Layer XVI, (c) Layer XVIII, (d) Layer XXII, and (e) Layer XXV.

2.6.1.2 Cortical surface weathering and preservation

The state of preservation of cortical bone surfaces was assessed using the stages (0–5) described by Behrensmeyer (1978) that range from no modification (stage 0), cracking of the cortical surface (stage 1) to thin (stage 2) and full (stage 3) cortical surface flaking, through to small rectangular pieces breaking off (stage 4), and finally deep cracks accompanied by flaking of the entire cortical plane (stage 5). In addition, I have added categories 6–8 to record surface modifications caused by smoothing and/or rolling, chemical weathering (including digestion), and geological staining, respectively (Fig. 2.7). Cortical surfaces are generally fairly well preserved, and in all layers, slight cortical surface weathering (i.e., stages 1–2) predominates. In the IUP (Layers XXV and XXII) there is a slightly higher incidence of geological staining, which includes red and black stains, sometimes accompanied by fungal and/or root etching damage, as well as travertine-like concretions. These geological adhesions do not substantially influence the percentage of visible cortical surface per bone between layers. In fact, few bones are fully free of adhering concretions, due to erring on the cautious side while carrying out acid treatment. However, the acid treatment increased the amount of cortical surface (generally >75%; Fig. 2.8) available for inspection for human and animal modifications.

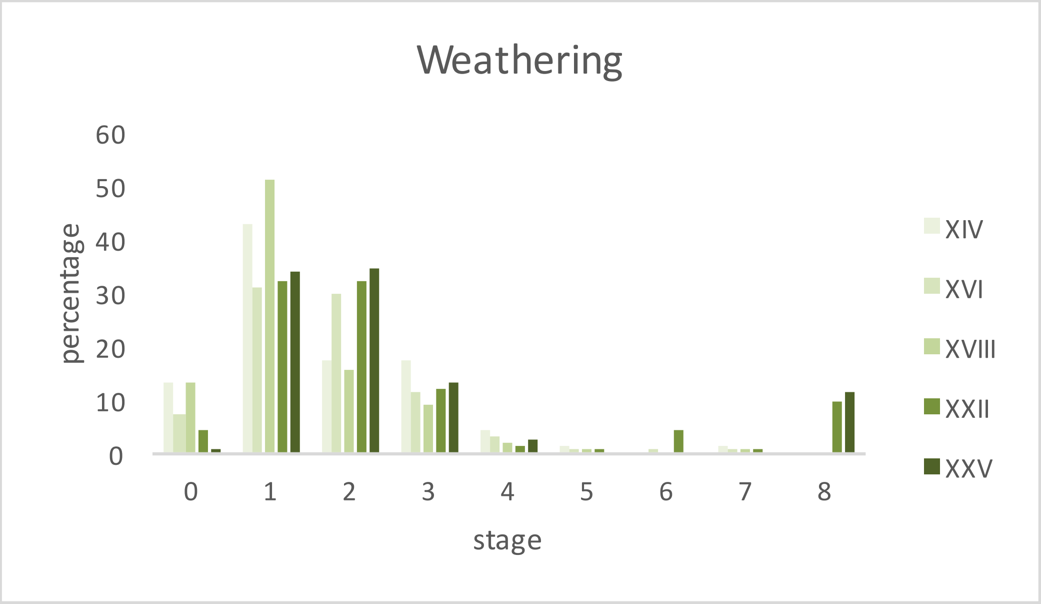

Figure 2.7: Frequency of cortical surface weathering per layer divided into the stages proposed by Behrensmeyer (1978): 0 - none, 1 - cracking of cortical surface, 2 - thin cortical surface flaking, 3 - flaking of cortical surface, 4 - small rectangular pieces breaking of, 5 - deep cracks and flaking of the entire cortical plane; added to Behrensmeyer's stages are: 6 - smoothed and/or rolled, 7 - chemical weathering (including digestion), and 8 - geological staining.

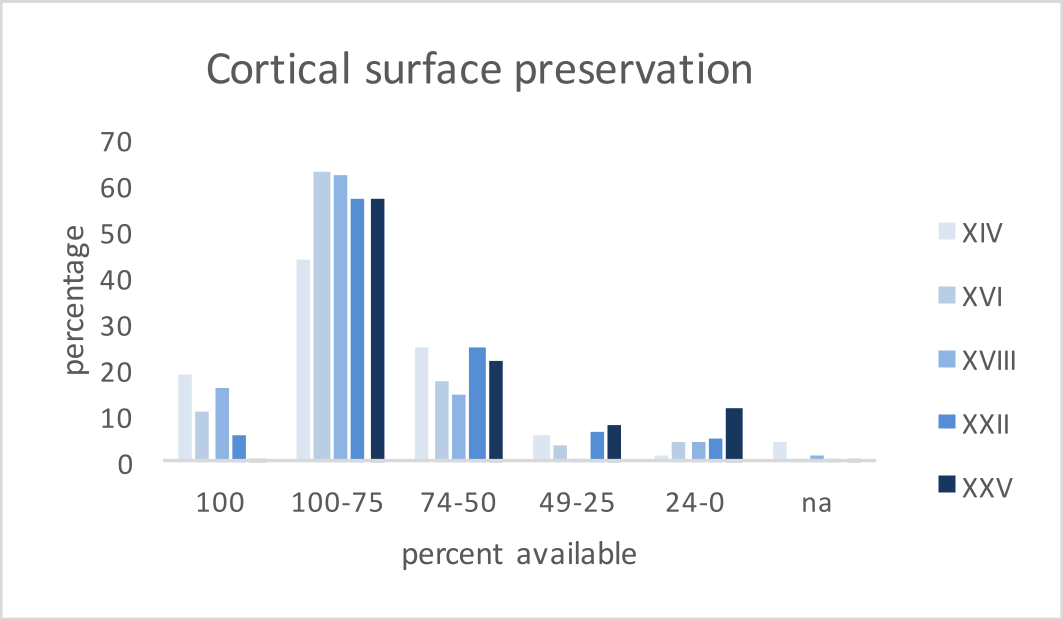

Figure 2.8: Frequency of the extent of cortical surface preservation per layer.

2.6.1.3 Burning

The extent of burning was recorded using the seven-stage system of Stiner et al. (1995) in which stage 0 is not burned, stages 1–3 comprise increasing states of carbonisation (i.e., <50%, >50%, and 100%, respectively) and stages 4–6 refer to calcination or whitening in the same steps. In Layers XXII, XVIII, and XVI, roughly 30–40% of the bones had been exposed, directly or indirectly, to heat (Fig. 2.9). Of these, approximately 5% shows traces of calcination (e.g., whitening of the bone, in combination with cracks and potlids), which has been argued to be a sign of direct exposure to a fire (Stiner et al. 1995), whereas carbonisation or darkening/blackening of the bone can occur while bones are buried (e.g., a fire is lit on top of a bone-bearing layer). In Layers XXV and XIV no calcined bones were recorded, and carbonisation drops to 12% in Layer XIV and one percent in Layer XXV. Several interpretations could explain the lower percentages: humans did not light fires, humans were altogether absent (but see below), or they made their fires in other parts of the rockshelter.

2.6.1.4 Human and carnivore modifications

Stratigraphically, both Layers XXV and XIV are part of so-called complexes thought to coincide with more humid climatic conditions and perhaps a less intense occupation or even a hiatus in the occupation of the rockshelter (Ewing 1947; Wright 1951). However, human modifications occur in the form of both impact fractures, caused by humans bashing bones open to reach the marrow inside, and cutmarks across all layers (Table 2.2). Inversely, modifications made by carnivores are extremely rare (<1%) in all studied IUP and EUP assemblages, and they are absent in Layers XXV and XIV, suggesting humans were the main contributor to the accumulation of bones.

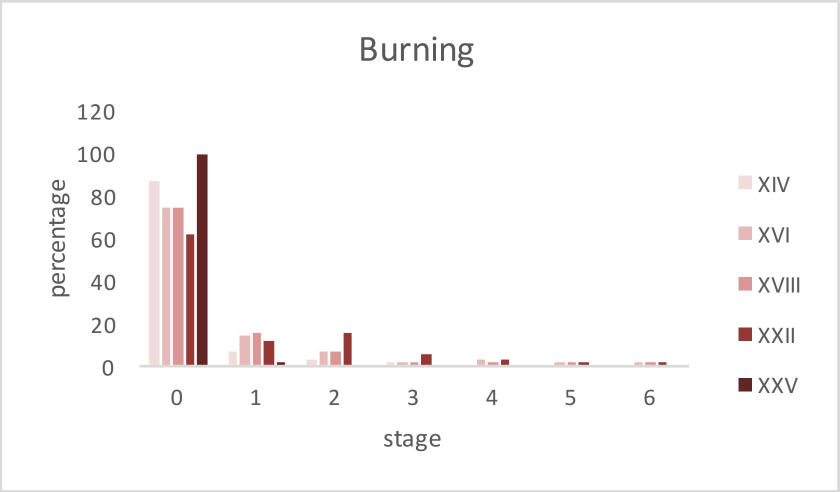

Figure 2.9: Frequency of burned remains per layer divided in the stages proposed by Stiner et al. 1995, 0 - not burned, 1 - <50% carbonised, 2 - >50% carbonised, 3 - 100% carbonised, 4 - <50% calcined, 5 - >50% calcined, 6 - 100% calcined.

The percentage of cutmarks lies between three percent and 13% and that of impact fractures between three and eight percent. Approximately one in five green breaks is accompanied by a discernible impact fracture in Layers XXII, XVIII, and XVI, whereas in layers that are part of the so-called stratigraphic complexes, Layers XXV and XIV, the impact fracture: green-break ratio is only one in ten. Perhaps this difference is caused by increased post-depositional edge damage in the latter two layers, although there is no apparent difference in surface weathering between layers belonging to one of the complexes and those which do not. Green breaks can be caused by butchery and bone marrow extraction by humans, but they can also be caused by carnivores (e.g., hyenas) cracking open bones. However, no clear carnivore modifications were discovered in the layers with a lower impact fracture to green breaks ratio. Other possibilities are that these differences are driven by sample size or that bone marrow extraction was practised elsewhere in or outside the rockshelter.

In summary, taphonomic investigations of the vertebrate fauna show that cortical surface preservation, even after acid treatment, is sufficient to convey human and animal modifications. The results show that carnivores contributed little to the formation of the IUP and EUP assemblages and that humans were the main contributor to the accumulation of these archaeological layers. Human modifications on the remains of Layer XIV suggest that, contrary to the assertion of Bergman discussed above (see Table 2.1; e.g., Bergman and Stringer 1989; Williams and Bergman 2010), humans visited Ksâr ‘Akil during the formation of this layer.

Table 2.2 (next page): Summary of the taphonomic signature of the Ksâr ‘Akil bone assemblages per layer. N bones: number of bones studied. Cortical surface weathering stages after Behrensmeyer (1978): 0 none, 1 cracking of cortical surface, 2 thin cortical surface flaking, 3 flaking of cortical surface, 4 small rectangular pieces breaking of, 5 deep cracks and flaking of the entire cortical plane, added to Behrensmeyer’s stages are: 6 smoothed and/or rolled, 7 chemical weathering (including digestion), and 8 geological staining. Burning stages after Stiner et al. 1995: 0 not burned, 1 <50% carbonised, 2 >50% carbonised, 3 100% carbonised, 4 <50% calcined, 5 >50% calcined, 6 100% calcined.

	XIV		XVI		XVIII		XXII		XXV	
	n	%	n	%	n	%	n	%	n	%
n bones	68		732		724		3449		236	
Primary breakage										
green	20	29.41	200	27.32	123	16.99	705	20.44	74	31.36
dry	44	64.71	501	68.44	523	72.24	2467	71.53	118	50.00
recent	2	2.94	5	0.68	31	4.28	59	1.71	29	12.29
na	2	2.94	26	3.55	47	6.49	219	6.35	15	6.36
Secondary breakage										
green	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
dry	2	2.94	142	19.40	53	7.32	287	8.32	49	20.76
recent	41	60.29	291	39.75	327	45.17	733	21.25	76	32.20
na	24	35.29	299	40.85	344	47.51	2429	70.43	111	47.03
Cortical surface weathering										
0	9	13.24	54	7.38	97	13.40	142	4.12	2	0.85
1	29	42.65	229	31.28	372	51.38	1115	32.33	80	33.90
2	12	17.65	220	30.05	112	15.47	1119	32.44	82	34.75
3	12	17.65	85	11.61	64	8.84	422	12.24	32	13.56
4	3	4.41	24	3.28	16	2.21	54	1.57	6	2.54
5	1	1.47	1	0.14	7	0.97	2	0.06	0	0.00
6	0	0.00	1	0.14	0	0.00	146	4.23	0	0.00
7	1	1.47	2	0.27	1	0.14	7	0.20	0	0.00
8	0	0.00	0	0.00	0	0.00	331	9.60	27	11.44
Available cortical surface										
100	13	19.12	80	10.93	117	16.16	199	5.77	2	0.85
100-75	30	44.12	459	62.70	449	62.02	1963	56.92	135	57.20
74-50	17	25.00	129	17.62	104	14.36	863	25.02	52	22.03
49-25	4	5.88	27	3.69	3	0.41	227	6.58	19	8.05
24-0	1	1.47	34	4.64	30	4.14	169	4.90	27	11.44
na	3	4.41	3	0.41	11	1.52	29	0.84	1	0.42
Burning										
0	59	86.76	542	74.04	535	73.90	2141	62.08	233	98.73
1	5	7.35	106	14.48	115	15.88	423	12.26	3	1.27
2	2	2.94	49	6.69	50	6.91	537	15.57	0	0.00
3	1	1.47	6	0.82	8	1.10	206	5.97	0	0.00
4	0	0.00	22	3.01	5	0.69	90	2.61	0	0.00
5	0	0.00	4	0.55	7	0.97	33	0.96	0	0.00
6	0	0.00	6	0.82	4	0.55	20	0.58	0	0.00
Carnivore modifications										
toothmarks	0	0.00	1	0.14	0	0.00	5	0.14	0	0.00
puncture	0	0.00	0	0.00	2	0.28	0	0.00	0	0.00
gnawing	0	0.00	0	0.00	0	0.00	1	0.03	0	0.00
none	68	100.00	731	99.86	722	99.72	3443	99.83	236	100.00
Human modifications										
cutmarks	6	8.82	25	3.41	28	3.86	253	7.28	31	12.97
impact fractures	2	2.94	59	8.05	39	5.37	143	4.12	7	2.93
chopmarks	0	0.00	0	0.00	1	0.14	0	0.00	0	0.00
none	60	88.24	649	88.54	658	90.63	3077	88.60	201	84.10

2.6.2 Compatibility of faunal composition by layer

Overall, the same vertebrate taxa are present throughout the IUP and EUP. They include: red deer (*Cervus elaphus*), Mesopotamic fallow deer (*Dama mesopotamica*), roe deer (*Capreolus capreolus*), aurochs (*Bos* sp.), ibex (*Capra ibex*), wild goat (*Capra aegagrus*), a small gazelle (*Gazella* cf. *dorcas*), a large gazelle (*Gazella* cf. *gazella*), wild boar (*Sus scrofa*), tortoise (*Testudo* sp.), brown bear (*Ursus arctos*), a large bear (*Ursus* sp.), lion (*Panthera leo*), wild cat (*Felis silvestris*), leopard (*Felis pardus*), wolf (*Canis lupus*), and fox (*Vulpes vulpes*), as well as a few bird, reptile (other than tortoise), and microfaunal remains (Table 2.4). Unidentifiable ungulate remains were assigned size classes, UNG1–5, (after Brain 1981: Appendix 1, Table 1), which conveniently separate the various cervids and bovids. Of the identifiable taxa, only Dorcas gazelle remains can be placed in size class 1 (<20 kg); size class 2 (~20–50 kg) comprises mountain gazelle, bezoar goats, and roe deer; size class 3 (~50–200 kg) includes wild boar, ibex, and Mesopotamic fallow deer; and size class 4 (~200–800) includes red deer and aurochs. The large caballine equid (n = 3) reported by Hoojier (1961) would also fall in this size class but was not recovered from the faunal assemblage of F4. Size class 5 (>800kg) would include rhinoceros, which is present in the Middle Palaeolithic but has not been identified in the Upper Palaeolithic deposits.

The aim of studying the vertebrate assemblage is to assess Upper Palaeolithic dietary breadth and what it can tell us about EUP and IUP subsistence behaviour. Optimal foraging theory and taxonomic composition indices have been widely used by archaeologists to investigate subsistence behaviour through time (e.g., Binford 1981; Grayson and Delpech 1998; Stiner 2001, 2005; Dusseldorp 2009; Lyman 2013). However, before comparing the data from several layers, we need to assess whether the assemblages in terms of numbers of identified specimens (NISP) and the minimal number of individuals (MNI) are comparable in quantity and degree of fragmentation.

If an assemblage is fragmentary, as almost all archaeological assemblages are, there is always the possibility that multiple fragments belong to one specimen (e.g., Grayson 1979; Marean 1991). In contrast, if only one fragment of a certain species is recovered, it by definition makes up an MNI of one. This potential interdependence between NISP and MNI (Grayson 1979, 1984) may substantially drive the results. Moreover, it is likely that in smaller assemblages or less fragmented ones, MNI values overestimate and NISP values underestimate the original faunal composition. Fragmentation is often caused by taphonomic processes, but excavation recovery techniques and past hunter-gatherer behaviour potentially contribute as well. Overall, the taphonomic signature between the studied layers is quite similar (see above). However, some of the analysed layers differ substantially in sample size. One way of addressing this issue is to investigate whether the degree of fragmentation between layers is similar across the assemblages that I want to compare. If there is a significant correlation between the natural log of the NISP (lnNISP) and of the MNI (lnMNI) of all studied layers, we can assume that the degree of interdependence is similar across all assemblages and that it does not significantly affect the observed taxonomic abundances. Moreover, especially if NISPs (or MNIs) or derivatives thereof (e.g., Heterogeneity index: H, inverse Simpson's index: 1/D, and Shannon evenness index: e; see Table 2.3) are used to compare samples from the various archaeological layers, the degree of interrelatedness per sample must be assessed.

Table 2.3: Overview of the applied taxonomic abundance indices.

Symbol	name	Other names	Formula/ description	remarks	reference
S	Taxonomic richness		Number of species per layer		Gaston 1996
H	Taxonomic heterogeneity	Shannon or Shannon-Wiener index	H=-∑Pi(lnPi); where Pi is the proportion of taxon i	The higher the value the greater the heterogeneity: values generally, between 1.5–3.5	Magurran 1988
e	Taxonomic evenness	Shannon index of evenness	e=H/lnS	Values between 0–1, where 1 indicates an even and 0 an uneven faunal distribution	Magurran 1988
1/D	Taxonomic dominance	Reciprocal of Simpson's index	$1/D=\sum n_i[n_i-1]/N[N-1]$; where n_i is the NISP of taxon i, and N is 'NISP species'	The lower the value the greater the taxonomic dominance	Simpson 1949

Table 2.4 (next page): Vertebrate numbers of identified specimens (NISPs) and minimum numbers of individuals (MNIs) per layer. UNG: Ungulate, - Ungulate size class 1: ~<20 kg, 2: ~20-50 kg, 3: ~50-200 kg, 4: ~200-800 kg - NID: not identified, total n: total number of specimens.

layer	**XIV**		**XVI**		**XVIII**		**XXII**		**XXV**	
species	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**
ungulates										
Cervus elaphus	2	1	6	1	8	1	47	3	2	1
Dama mesopotamica	12	3	93	3	124	3	860	18	61	5
Capreolus capreolus	1	1	11	1	24	1	24	2	1	1
indet cervid			4		7		12			
Bos sp.	2	1	3	1	9	1	11	2	39	2
Capra aegagrus	6	2	62	2	39	2	502	10	14	2
Capra ibex	1	1	2	1	12	1	51	3		
Gazella cf. *dorcas*	2	1	7	1	10	1	5	1		
Gazella cf. *gazella*	2	1	2	1	9	1	2	2		
Gazella spp.			7		1		11		2	
indet bovid							3			
Sus scrofa	3	1	21	1	24	1	295	6	51	3
total ungulates	***31***	***12***	***218***	***12***	***267***	***12***	***1823***	***47***	***170***	***14***
small mammals										
Lepus sp.					1	1	1	1		
total small mammals					***1***	***1***	***1***	***1***		
reptiles										
Testudo sp.	1	1	5	1	29	2	20	2		
indet reptile					7	1				
total reptiles	***1***	***1***	***5***	***1***	***36***	***3***	***20***	***2***		
birds										
large bird					1	1	2	2	1	1
total birds					***1***	***1***	***2***	***2***	***1***	***1***
microfauna										
Arvicola sp.							1	1		
total microfauna							***1***	***1***		
carnivores										
Ursus sp.					1	1	1	1		
Ursus arctos					1	1	9	1	1	1
Panthera leo			1	1			1	1		
Felis silvestris					1	1	1	1		
Felis pardus							1	1	1	1
Canis lupus					1	1	11	1		
Vulpes vulpes							3	1		
Large carnivore							15		1	
Small carnivore							3			
total carnivores			***1***	***1***	***4***	***4***	***45***	***7***	***3***	***2***
ungulate size classes*										
UNG 1			3				1			
UNG 1-2			1				1			
UNG 2			54		48		137		1	
UNG 2-3	2		13		23		51		7	
UNG 3	30		286		229		1292		70	
UNG 3-4	2		14		14		69		6	
UNG 4	4		31		56		124		7	
total NISP	**70**		**626**		**679**		**3567**		**265**	
NID	2		116		56		116		7	
total n	**72**		**742**		**735**		**3683**		**272**	

In the following analyses (i.e., interdependence, relative abundance, and taxonomic composition indices), NISP is calculated as the number of specimens identified to species level—here called NISP sp.—(after Lyman 2008), thus excluding remains identified to order or family, and those that could only be attributed a size class, which is here called NISP total (Table 2.5). The correlation of lnNISP and lnMNI is evaluated using a simple best-fit regression analysis (Grayson 1984; Lyman 2008). As a significance test, the Pearson's correlation coefficient is used (as the values are not ranked). A strong significant correlation (see Fig. 2.10a; $r^2 = 0.81$; $r = 0.90$, $p = 0.039$) exists between lnNISP and lnMNI, suggesting that interdependence is distributed randomly across all assemblages.

A second method to assess interdependence is to test whether lnNISP and the logged number of species (lnS or lnNtaxa) are significantly correlated. For the Ksâr 'Akil samples the relation is not significant (Fig. 2.10b; $r^2 = 0.63$; $r = 0.79$, $p = 0.11$), indicating that the number of taxa cannot be compared between layers because it is not an interdependent variable. (Table 2.5). Therefore, these results warrant NISP-based faunal comparisons across layers but not based on the number of species per layer. Relative abundance of species across layers can potentially be compared, as they are NISP-based derivatives.

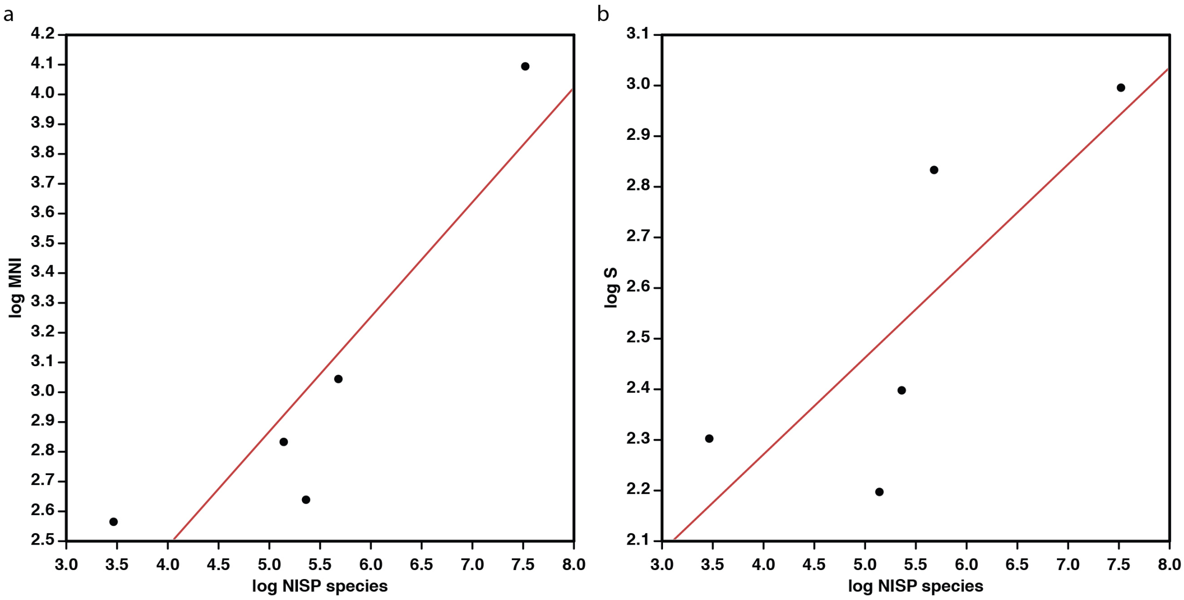

Figure 2.10: Relationship between a) NISP and MNI regression: $r^2 = 0.81$; $r = 0.90$, $p = 0.039$, and b) NISP and S regression: $r^2 = 0.63$; $r = 0.79$, $p = 0.11$ of the five assemblages studied.

Sample size is another potential bias that is evaluated. Similar to the interrelatedness issue, the question here is whether sample size is responsible for an assemblage's taxonomic composition. This issue can be tackled by plotting the frequency of one component within a sample, e.g., the dominant species, against the total NISP of this sample. If multiple components are not significantly related to the total NISP, this would indicate that sample size is not a driving factor in assemblage composition (Lyman 2008). For the Ksâr 'Akil sample we can look at the relative abundance (percent) of several common food species such as *Dama mesopotamica, Capra aegagrus,* and *Sus scrofa*. Again, a simple best fit regression analysis is applied. As a significance test the Spearman's rho (r_s: employing a t-distribution) is used because the values are ranked (Table 2.6). No significant correlations are found for any of the common taxa. The results of both interdependence and taxon relative abundance suggest that sample size is not a significant factor driving faunal distribution.

Table 2.5: The number (n), Number of identifiable specimens including those identified to size class (total NISP), those identified to species level (NISP sp.) and its logged values (lnNISP sp.), the minimum number of individuals (MNI) and its logged values (lnMNI), as well as the taxonomic richness (S) and logged (lnS), the taxonomic heterogeneity (H), evenness (e), dominance (1/D) per layer.

Layer	n	NISP total	NISP sp.	lnNISP sp.	MNI	lnMNI	S	lnS	H	e	1/D
XIV	72	70	32	3.46574	13	2.56495	10	2.30259	1.60779	0.69825	5.63636
XVI	742	626	213	5.36129	14	2.63906	11	2.39790	1.21701	0.50753	3.48157
XVIII	735	679	293	5.68017	21	3.04452	17	2.83321	1.92651	0.67997	4.48595
XXII	3683	3567	1846	7.52078	60	4.09434	20	2.99573	1.44566	0.48257	3.14503
XXV	272	265	171	5.14166	17	2.83321	9	2.19722	1.44284	0.65667	3.69096

Table 2.6 The abundance of the predominant prey species per layer, and the results of the Spearman rho tests. r_s: Spearman correlation, p: probability value.

	XXV	XXII	XVIII	XVI	XIV	r_s	p
NISP species	171	1846	293	213	32		
Dama mesapotamica	61	860	124	93	12	0.8	0.1
Capra aegagrus	14	502	39	62	6	0.3	0.62
Sus scrofa	51	295	24	21	3	0	1

2.6.3 Taxonomic composition

To evaluate faunal composition, I used a combination of several indices, namely S, e, H, and 1/D. (Table 2.5). As all these indices are calculated using NISPs, there is the possibility that these results are also driven by sample size rather than represent species composition. As with interdependence, the way to test this is to run regression analyses of these indices and lnNISP, where a significant correlation would indicate a sample size bias. Table 2.7 shows no significant relationship, which suggests that comparison of these indices across layers is warranted.

However, it is important to note that, although e values give an indication of the faunal distribution within a layer, they should not be compared across layers because they are calculated using both NISPs and S values. As shown above (Fig. 2.11), S values are not interdependent between layers and should therefore not be compared.

Table 2.7: The results of the Pearson's correlation coefficient and r-squared tests of the relation between lnNISP and taxonomic heterogeneity (H), evenness (e), and dominance (1/D).

Index	r	r^2	p
H	−0.12	0.01	0.85
e	−0.73	0.53	0.16
1/D	−0.82	0.68	0.09

2.6.4 Archaeological interpretation

On face value, there seem to be no substantial differences between heterogeneity, evenness, and dominance. All five assemblages are not very heterogeneous, with H values close to 1.5, but with 1/D values ranging between 3 and 4.5, they are not dominated by a single species. Not surprisingly, no significant change in overall taxon abundance could be observed (r_s = 0.5, p = 0.39).

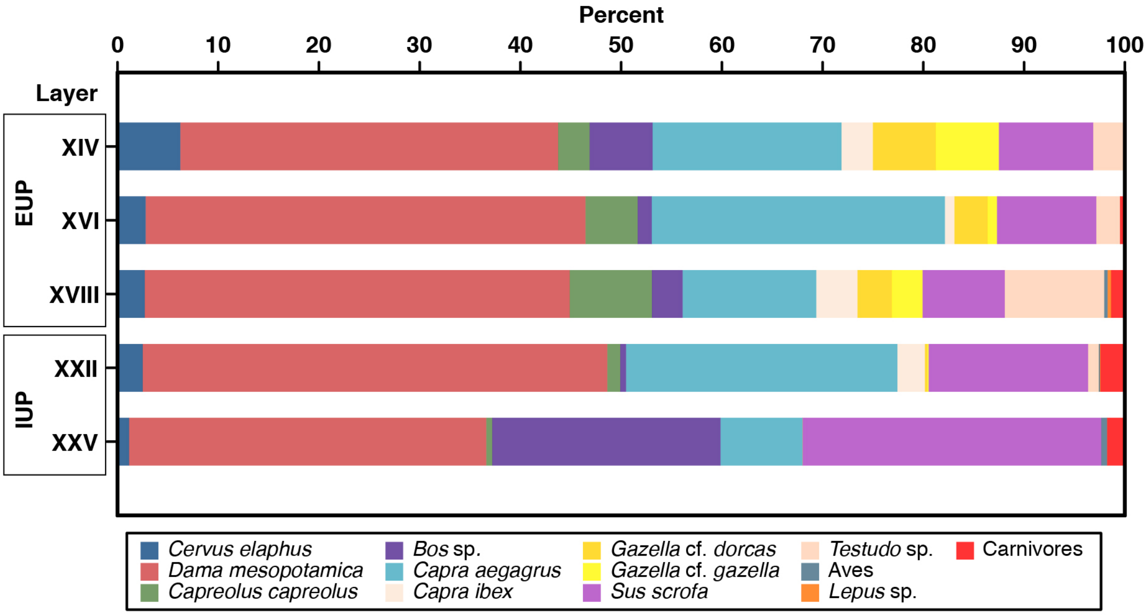

Figure 2.12: Species composition (%NISP) per layer (see Table 2.4 for NISP counts).

When the relative faunal composition is plotted through time (Fig. 2.12), it becomes evident that Mesopotamic fallow deer is always the most frequent taxon. However, in the Early Ahmarian the faunal distribution of the less-common taxa (i.e., excluding *Dama mesopotamica, Capra aegagrus*, and *Sus scrofa*) seems to be more evenly distributed. To test this, I plotted the relative abundance of less common prey-species (Fig. 2.13). The non-significant Pearson's correlation coefficient (for non-ranked variables) of $r = 0.66$, $r^2 = 0.44$, $p = 0.22$ suggests that the patterns observed in relative abundance are not driven by sample size. When plotted through time, the abundance of less-common taxa shows an increasing, but not significant ($r_s = 1$, $p = 0.39$), trend. Due to the low numbers ($n < 5$) of certain taxa, even when collated into broader IUP (i.e., Layers XXV and XXII) and EUP (i.e., Layers XVIII, XVI, and XIV) groups, it is not possible to statistically compare species abundance. Judging from the represented taxa, the non-significant trend involves a higher relative proportion of smaller-bodied taxa such as roe deer, gazelles, and tortoises over larger-bodied taxa such as red deer and aurochs. Indeed, collating the data into broader IUP and EUP categories a χ^2 test reveals a highly significant difference ($\chi^2 = 62.52$, df = 1, $p < 0.001$) between the abundance of larger-bodied prey (i.e., size class 3 and larger) compared with smaller-bodied prey (i.e., size class 2 and smaller).

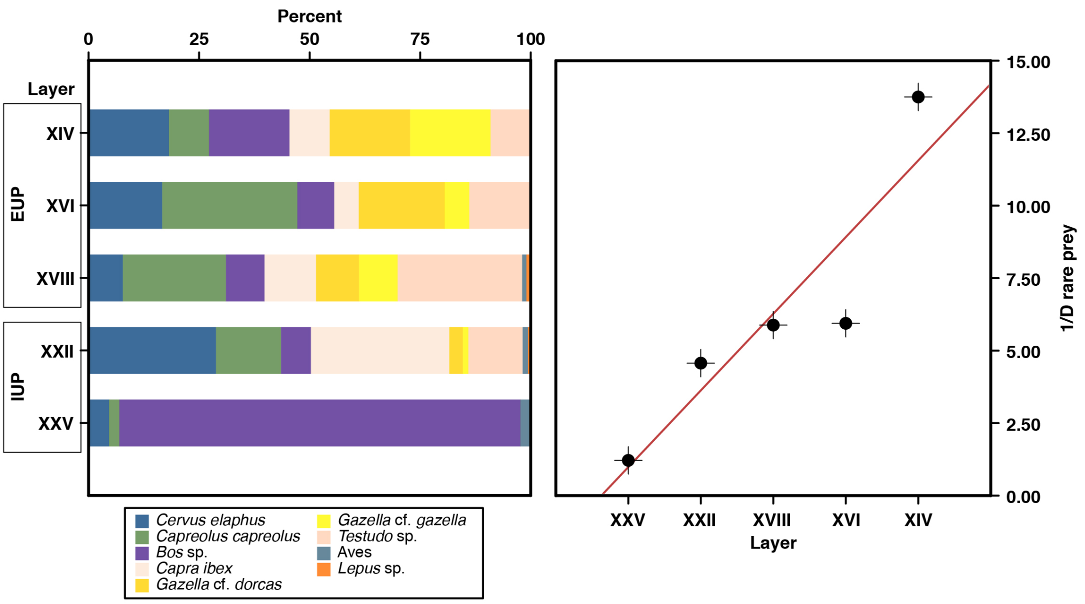

Figure 2.13: Species composition of less-common prey species per layer (left) and relationship of the taxonomic dominance 1/D across layers (right) regression: $r_s = 1$, $p = 0.39$.

Similarly, when plotted by body size (Fig. 2.14) a gradual but not significant ($r_s = 0.8$, $p = 0.10$) shift in faunal exploitation towards smaller-bodied prey becomes evident. When collating the data into broader IUP and EUP categories, a χ^2 test reveals a highly significant difference ($\chi^2 = 115.15$, df = 4, $p < 0.00001$). In other words, the data suggest that during the Early

Ahmarian, larger-bodied prey were on average less often targeted in favour of smaller-bodied prey but that the shift occurred rather gradually. Moreover, the distribution of less-frequently obtained prey is more even in the Early Ahmarian compared to the IUP.

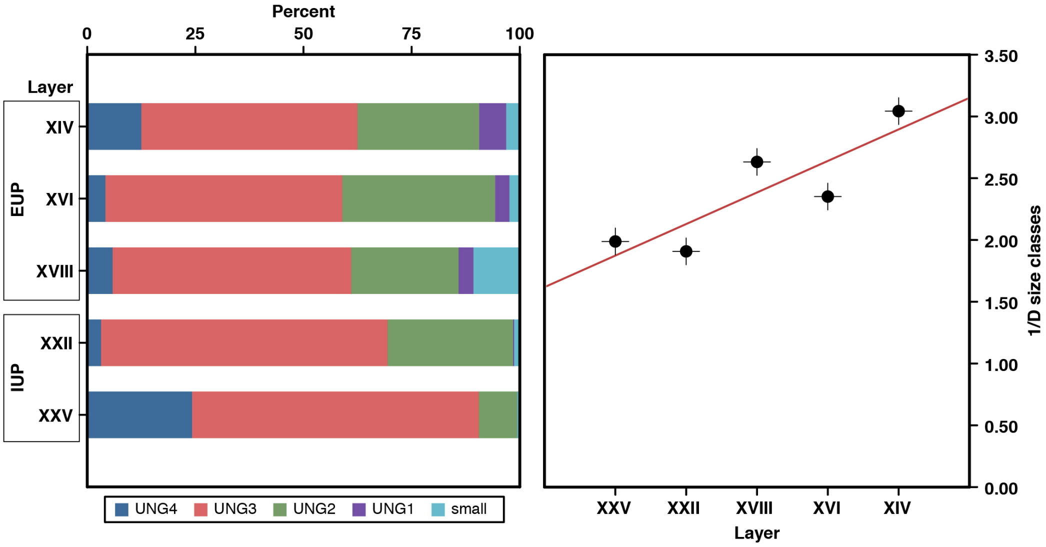

Figure 2.14: Composition of ungulate (UNG) size-class and small bodied prey (small), e.g., tortoise, birds and hare, per layer (left) and the relationship of the taxonomic dominance 1/D across layers (right) regression: $r_s = 0.8$, $p = 0.10$.

In an attempt to use archaeological faunal assemblages as an environmental indicator, Dorothea Bate (1937 in Hooijer 1961) compared relative frequencies of gazelle and Mesopotamic fallow deer using her so-called *Gazella-Dama* graph, the former animal being an indicator of arid and open or steppic conditions and the latter being a temperate woodland taxon. The *Gazella-Dama* graph for Ksâr 'Akil (Fig. 2.15) shows a significant increase ($r_s = 0.9$, $p = 0.04$) in the arid species from the start of the IUP to the end of the Early Ahmarian. Equally, a chi-square test between the collated IUP versus EUP data shows a significant difference ($\chi^2 = 69.42$, df 1, $p < 0.0001$). However, it is likely that this pattern is skewed with the coinciding change in faunal exploitation towards smaller-bodied prey (see Lyman 2008; Yesurun 2017). Shea (2003) suggests evaluating the zooarchaeological evidence, in his example from multiple Levantine Middle Palaeolithic sites, in terms of species' behavioural characteristics. In the northern Levant—Lebanon and northern Israel—he sees a higher frequency of 'territorial species and species that tend to live near or in woodlands' (e.g., *Cervus elaphus, Dama mesopotamica, Capreolus capreolus, Sus scrofa*, and *Gazella gazella*) relative to 'migratory and/or open country/steppic taxa' (e.g., *Bos* sp., *Capra aegagrus*, and *Capra ibex*), whereas the latter dominate the more southern and interior Levantine areas (southern Israel, Syria, and Jordan).

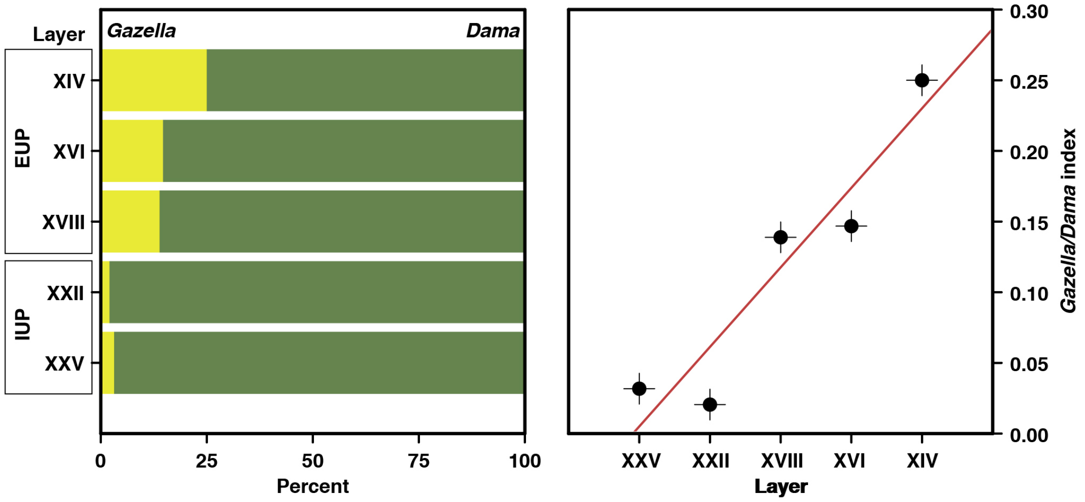

Figure 2.15: The *Gazella-Dama* graph (Bate 1937): the relative frequency (%NISP) of gazelle (i.e., *Gazella.* spp.) against Mesopotamic fallow deer per layer (left) for the five studied layers of Ksâr ‘Akil. The relationship of the *Gazella/Dama* index across layers (right) regression: $r_s = 0.9$, $p = 0.04$).

Consistent with the site’s location in the northern Levantine woodland zone, the relative frequency of territorial/woodland versus migratory/steppe fauna at Ksâr ‘Akil displays a clear woodland dominated profile (Fig. 2.16) but shows no clear chronological trend ($r_s = -0.2$, $p = 0.75$). Moreover, the pattern suggesting increasing aridity throughout the early Upper Palaeolithic previously observed in the *Gazella-Dama* graph disappears. It seems likely therefore, that the *Gazella-Dama* graph is skewed by human change in subsistence practise, namely a preference for smaller fauna, rather than reflecting environmental conditions in a straightforward way.

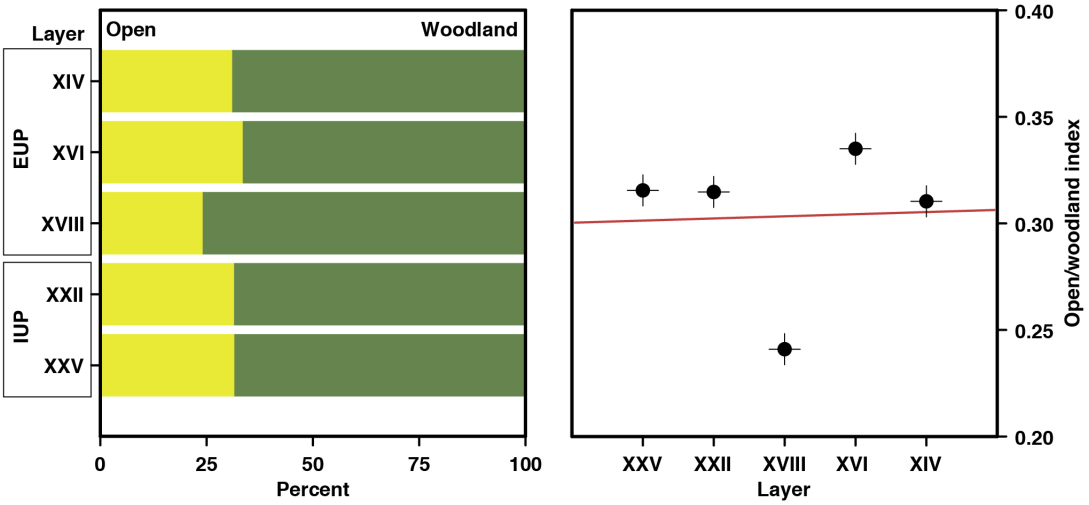

Figure 2.16: Relative frequency (%NISP) of territorial/woodland versus migratory/steppe fauna per layer (left) after Shea (2003). The relationship of the Open/woodland index across layers (right) regression: $r_s = -0.2$, $p = 0.75$.

2.6.5 Vertebrate fauna summary

Ksâr ‘Akil is one of the few sites, together with the Middle Palaeolithic sites of Naame and Ras el-Kelb (both Lebanon), to display a terrestrial faunal composition characteristic of the eastern Mediterranean (temperate) woodland zone (e.g. Shea 2003). This is different from other Levantine sites such as the Mount Carmel Caves of Kebara, Hayonim, and Manot Cave (all Israel), that generally display a high incidence of arid taxa such as gazelle, bezoar goat, and other small bovids (Shea 2003; Rabinovich and Hovers 2004; Speth 2012; Hershkovitz et al. 2015). Moving more inland (e.g., the Middle Palaeolithic site of Umm el Tlel, Syria), these bovids are recorded to have been accompanied by donkeys, horses, ostriches, and camels (Griggo 2004). The data suggest that also in the early Upper Palaeolithic at Ksâr ‘Akil faunal exploitation mainly took place in wooded areas probably on the seaward slopes of the Lebanon Mountains and perhaps on the coastal plain. Furthermore, the low frequency of open habitat arid species suggests that the highlands of the Beqaa Valley were less often targeted or that portions of hunted animals were not taken back to the site, although small-bodied arid species, such as gazelles, were exploited slightly more often in the Early Ahmarian. Thus, the Ksâr ‘Akil vertebrate fauna show a clear woodland signal, with Mesopotamic fallow deer and wild boar prominently represented. At the same time, although species representation is fairly similar, faunal composition does change, especially between the IUP and EUP layers where a shift to a more evenly distributed occurrence of various less-common small-bodied taxa occurs.

In chapters 5 and 6, another avenue of faunal exploitation at Ksâr ‘Akil, namely of invertebrates, is investigated. The data on the Ksâr ‘Akil vertebrate assemblages discussed above are used to contextualise these molluscan data to gain a broader view, albeit not complete, of IUP and EUP subsistence strategies.

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Chapter 3 ・ New chronology for Ksâr ‘Akil (Lebanon) supports Levantine route of modern human dispersal into Europe

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New chronology for Ksâr 'Akil (Lebanon) supports Levantine route of modern human dispersal into Europe

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Modern human dispersal into Europe is thought to have occurred with the start of the Upper Paleolithic around 50,000–40,000 y ago. The Levantine corridor hypothesis suggests that modern humans from Africa spread into Europe via the Levant. Ksâr 'Akil (Lebanon), with its deeply stratified Initial (IUP) and Early (EUP) Upper Paleolithic sequence containing modern human remains, has played an important part in the debate. The latest chronology for the site, based on AMS radiocarbon dates of shell ornaments, suggests that the appearance of the Levantine IUP is later than the start of the first Upper Paleolithic in Europe, thus questioning the Levantine corridor hypothesis. Here we report a series of AMS radiocarbon dates on the marine gastropod *Phorcus turbinatus* associated with modern human remains and IUP and EUP stone tools from Ksâr 'Akil. Our results, supported by an evaluation of individual sample integrity, place the EUP layer containing the skeleton known as "Egbert" between 43,200 and 42,900 cal B.P. and the IUP-associated modern human maxilla known as "Ethelruda" before ~45,900 cal B.P. This chronology is in line with those of other Levantine IUP and EUP sites and demonstrates that the presence of modern humans associated with Upper Paleolithic toolkits in the Levant predates all modern human fossils from Europe. The age of the IUP-associated Ethelruda fossil is significant for the spread of modern humans carrying the IUP into Europe and suggests a rapid initial colonization of Europe by our species.

modern human dispersal | Upper Paleolithic | Near East | chronology | zooarcheology

Fossil and genetic evidence suggest that anatomically modern humans (AMH) originated in Africa and colonized Europe between at least 50,000–40,000 calendar years ago (cal B.P.; i.e., calendar years relative to AD 1950) (1–6). The modern human fossil record for this time period is limited to only a few remains, including those found at Ksâr 'Akil (7) and Manot Cave (8) in the eastern Mediterranean region of southwestern Asia and Peştera cu Oase in Romania (2) (*SI Appendix*, Section 3). The interpretation of this scant record is affected by imprecise chronologies, and in some cases, by problematic stratigraphies or lack of contextual data (2, 8–10). The recently discovered fossil at Manot (Israel) places AMH in the Levant as early as 60,200–49,200 y ago (8). However, because the fossil was found on a natural shelf unconnected with the otherwise rich archeological deposits elsewhere in the cave, its affiliation to an archeological technocomplex is unclear. Based on the uranium–thorium dates, the authors suggest an attribution of the fossil to either a late Middle Paleolithic (MP) or Initial Upper Paleolithic (IUP) technocomplex. The lack of archeological association and contextual behavioral data limits our understanding of the fossil's relation to both the Levantine and the European record. Hence, there is very little information to study the dispersal trajectory of modern humans into Europe. However, bones of modern humans from the Levant (e.g., Üçağızlı I and Ksâr 'Akil) and Europe (e.g., Kostenki 1, 14, and 17) are found in archeological contexts and in association with Early UP (EUP) lithic technologies (7, 9, 11, 12). These lithic assemblages, therefore, can be used as a proxy for modern human dispersal (13) and links between several such Levantine and European technocomplexes have been documented (11, 12, 14–16). The archeological record suggests that modern human dispersal from Africa likely took place in several episodes rather than one large exodus (3, 6, 14, 17–19). This hypothesis is supported by genetic and fossil data (20).

AMH dispersal into Europe is broadly contemporaneous with the disappearance of Neanderthals and the beginning of the UP, as witnessed by changes in the archeological record including frequent use of red ochre, modified marine shells and perforated animal teeth as body ornaments, elaborate bone and antler technology, as well as changes in lithic technology (19). Most scholars (3, 6, 14, 19, 21, 22) advocate the importance of southwestern Asia, including the Levant, as a "gateway" to Eurasia for modern humans coming from Africa. This Levantine corridor hypothesis has recently been questioned, as it has been argued that the UP and modern behavior, evidenced by the presence of shell beads in the material culture, first appeared in Europe before their first occurrence in the Levant (23). This interpretation is based on a

Significance

Bayesian modeling of AMS radiocarbon dates on the marine mollusk *Phorcus turbinatus* from Ksâr 'Akil (Lebanon) indicates that the earliest presence of Upper Paleolithic (UP) modern humans in the Levant predates 45,900 cal B.P. Similarities in early UP lithic technology and material culture suggest population dispersals between the Levant and Europe around 50,000–40,000 cal B.P. Our data confirm the presence of modern humans carrying a UP toolkit in the Levant prior to any known European modern human fossils and allow rejection of recent claims that European UP modern humans predate those in the Levant. This result, in turn, suggests the Levant served as a corridor for the dispersal of modern humans out of Africa and into Eurasia.

Author contributions: M.D.B., M.A.M., and J.-J.H. designed research; M.D.B., M.A.M., A.L.P., B.D., S.M.T., L.N., and J.v.d.P. performed research; M.D.B., M.A.M., A.L.P., T.C.O., B.D., and J.v.d.P. analyzed data; and M.D.B., M.A.M., B.D., L.N., and J.-J.H. wrote the paper.

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combination of relatively old ages (around 39,900 cal B.P.) for Uluzzian ornamental shell in southern Italy (10) and strikingly young ages (around 36,300–37,400 cal B.P.) for shell ornaments from Üçağızlı I and Ksâr 'Akil in the Levant (23, 24). If the UP in Europe truly predates the Levantine evidence, as Douka et al. (24) suggest, it should be considered unlikely that its makers traveled from Africa through the Levant before arriving in Europe. Here, we provide a new chronology for Ksâr 'Akil and show that the earliest UP and its associated AMH remains predate any European evidence.

Ksâr 'Akil

Located on the Lebanese coast, Ksâr 'Akil is a key site for the region and is best known for its 23-m-long sequence, which includes rich IUP (Layers XXV–XXI) and EUP (Layers XX–XIV) deposits, both of which contain modern human remains (*SI Appendix*, Fig. S1.2). The site, about 10 km north of Beirut, lies about 3 km from the present day coast (*SI Appendix*, Section 1). Excavations conducted in the 1930s and 1940s (7, 25) exposed the entire sequence, whereas later investigations (26) did not reach the earliest UP deposits.

In Layer XXV, the lowermost part of the deposit attributed to the IUP, a maxillary fragment ("Ethelruda") was found accompanied by IUP lithics (7, 27). Ethelruda was initially interpreted as having "Neanderthaloid" features by the excavators (7), but reexamination of the fossil suggests that it falls within the range of modern human variation (28). In general, the IUP lithic assemblages are characterized by opposed platform blade cores with parallel edges and facetted platforms (29). Tool types include chamfered pieces, endscrapers, and burins (27, 29). *Dama mesopotamica* is the dominant vertebrate species throughout all IUP layers. Further, the IUP witnessed a shift in the vertebrate fauna, with a drop in the numbers of *Bos* sp. and *Sus scrofa* in favor of *Capra ibex*, *Capra aegagrus*, and *Capreolus capreolus*. Evidence for marine mollusk consumption is rare and first occurs in Layer XXII (*SI Appendix*, Section 1).

The EUP or Early Ahmarian is associated with the remains of an 8-y-old modern human ("Egbert") and possibly a second individual (25) in Layer XVII, both now lost. The classic Early Ahmarian (Layers XVIII–XVI) also features opposed platform cores with parallel edges, in this case with plain platforms and marginal flaking resulting in thinner blanks (29). Tool types include endscrapers, retouched blades, and bladelets including el-Wad points and *pointe à face plane*, whereas burins are virtually absent (29). *Dama mesopotamica* dominates the vertebrate fauna, but there is a shift to more evenly distributed numbers of *Cervus elaphus*, *Capra aegagrus*, *Capra ibex*, *Sus scrofa*, *Gazella* cf. *dorcas*, and *Testudo graeca* compared with the underlying IUP. In addition, marine intertidal gastropods increase in number and were a foodstuff consumed by the site's EUP occupants (*SI Appendix*, Section 1).

Results

The multidisciplinary approach adopted in this study included absolute dating (AMS radiocarbon), an attempt to attribute layers to climatic events (*SI Appendix*, Section 2) using oxygen isotope analysis as a paleotemperature proxy, the use of amino acid racemization (AAR) to verify the extent of intracrystalline protein diagenesis and thus to highlight potentially compromised samples, as well as in-depth zooarcheological and taphonomic analyses. A relatively large shell assemblage ($n > 3{,}500$) was recovered during the 1930s and 1940s excavations mainly from the UP layers (XXIV–I) (25, 30). The shells belong to marine, terrestrial, and freshwater species from a variety of habitats (*SI Appendix*, Table S1.2). Marine shells, collected empty from active beaches or fossil deposits, were used as tools (e.g., *Glycymeris* sp.) and ornaments (e.g., *Nassarius gibbosulus* and *Columbella rustica*) (30–32). Limpets (*Patella rustica*, *Patella caerulea*, and *Patella ulyssiponensis*) and topshells (*Phorcus turbinatus* and *Phorcus articulatus*) were live-collected for consumption and are the best-preserved taxa in the assemblage. Evidence for collection of live limpets and topshells includes the overall integrity of their shells, absence of bioerosion, and encrusting organisms on inner shell surfaces, as well as edge notches on limpet shells congruent with damage resulting from prying the animals off the rocks. Other subsistence-related anthropogenic modifications include the frequent intentional removal of the apices of *Phorcus turbinatus* to facilitate flesh extraction and occasional burning (*SI Appendix*, Section 1). By dating food remains, the "dated event" (i.e., incorporation of ^{14}C in the shell carbonate during growth) and "target event" (i.e., human foraging) directly follow each other (33). Therefore, dating *Phorcus turbinatus* shells captures a concise timeframe including mollusk collection and consumption and is thus a good proxy for site occupation. Individual shells of this species were selected based on their excellent preservation, by considering a combination of macroscopic and physicochemical characteristics (*SI Appendix*, Section 2).

Radiocarbon Dating. We obtained 16 AMS radiocarbon dates for the Ksâr 'Akil UP sequence (Layers XXII–V) (*SI Appendix*, Table S2.2). All age estimations are calibrated using the Marine13 curve (34) and are given at the 68.2% probability level (*SI Appendix*, Section 2). *Phorcus turbinatus* occurs in the IUP starting from Layer XXII, which is dated to 44,400–43,100 cal B.P. The 11 dates for the EUP (Layers XX–XVI) show a wide range of ages from 44,000–37,200 cal B.P., whereas the later UP (Layers XII, XI, and VI) dates to ∼40,700–31,700 cal B.P. The start of the Epipaleolithic or Proto-Kebaran (Layer V) can be placed at 30,400–29,500 cal B.P. Artifact associations made during the 1930s and 1940s were based on broad geological layers that potentially include several thinner archeological horizons (*SI Appendix*, Section 1). This limited detail in provenience could account for wide age ranges within a layer. The dates of samples XVII (1) and XVIII do not fit well in the overall sequence because they provided younger ages than overlying samples. These specimens could be intrusive from younger deposits or be subjected to contamination. In general, contamination of a sample of this age results in a younger estimate than the true age of the sample, because the effect of introducing modern carbon in highly ^{14}C-depleted samples is more pronounced than the effect of introducing radiocarbon-dead contaminants (35, 36). The fact that the dated material comes from an old excavation with inherent provenience limitations, and the problems of identifying and eliminating contaminants in shells, make it imperative to evaluate individual sample integrity. We have applied three independent methods to evaluate our chronological data and identify potential outliers: (*i*) modeling using Bayesian statistics (37), (*ii*) using AAR values as a proxy for diagenetic integrity of the shells, and (*iii*) analyzing the oxygen isotope composition of shell carbonates to evaluate whether all specimens from the same layer are likely to be contemporary and to compare paleotemperature estimates from these analyses with those documented for different climatic phases in the NGRIP curve (*SI Appendix*, Section 2).

Bayesian Modeling of the Radiocarbon Ages. Bayesian modeling (37) and outlier analysis resulted in a model with an agreement index (A_model) of 118.2% (Fig. 1; see *SI Appendix*, Section 2 for discussion of rejected alternative models). For six dates, high posterior outlier probabilities (indicative of outliers) were calculated at various stages of the modeling (*SI Appendix*, Table S2.4). The model identifies the older EUP dates as best reflecting the true ages. We used the OxCal "Date" function to calculate a probability distribution function (PDF) for the age of the human fossil-bearing archeological layers. The PDF for Egbert's layer results in an age of 43,200–42,900 cal B.P. Regarding the age of Ethelruda, a lack of datable material from its

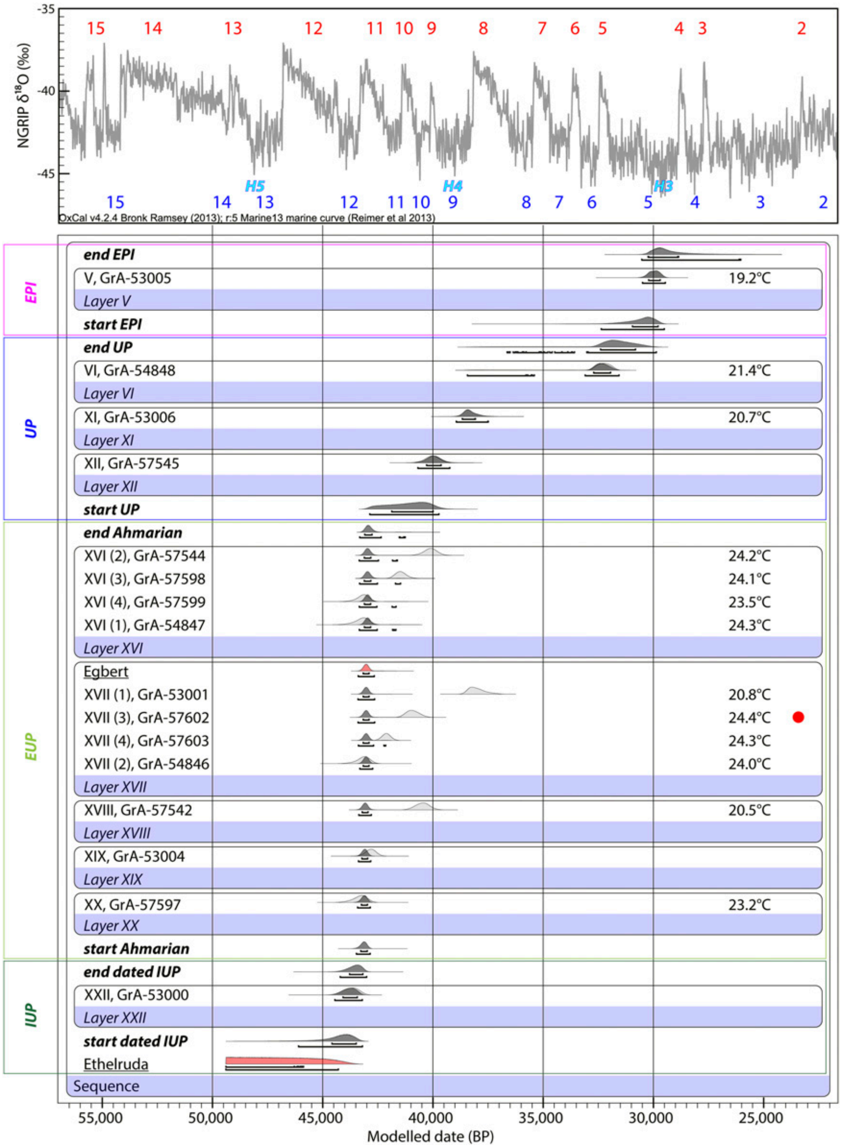

Fig. 1. Bayesian age model for the Ksâr ’Akil sequence produced using OxCal 4.2.4 (37). The radiocarbon dates are calibrated using the Marine13 dataset (34) ΔR value for the eastern Mediterranean (60). The individual radiocarbon likelihoods are shown in light gray, the posterior probability distributions are shown in dark gray, and PDFs for Ethelruda and Egbert’s layers are shown in red. The modeled data are compared with the NGRIP $\delta^{18}O$ curve (gray), Greenland Interstadials (GIS; red) and Stadials (GS; blue), and Heinrich Events (H3-5; light blue). Mean annual SSTs are given in degrees Celsius (°C). A red dot marks date XVII (3), as AAR analyses of the intracrystalline proteins showed that this sample displays some indication of open-system behavior.

associated Layer XXV, as well as from the layers directly above and underneath, hampers precise age estimation. Nevertheless, the date of the overlying IUP Layer XXII and the modeled start of the dated part of the IUP sequence provide termini ante quem for Ethelruda (i.e., >44,100 cal B.P. and >44,600 cal B.P., respectively). The PDF for Ethelruda’s layer extends beyond the range of the Marine13 calibration curve, and the upper limit of 45,900 cal B.P. can be used as a minimum age.

Amino Acid Racemization (AAR). The extent of racemization (D/L value) of 26 *Phorcus turbinatus* specimens, including 13 AMS dated samples, was evaluated. Both the total hydrolysable amino acids (THAA) and free amino acids (FAA) retained in an intracrystalline protein fraction (isolated by bleaching) of several amino acids were considered (*SI Appendix*, Section 2). Overall, intralayer variability of the D/L values was found to be comparable to the intrasite variability (*SI Appendix*, Fig. S2.7), and therefore D/Ls could not be used to resolve the relative chronology within the site. However, the covariance between FAA D/Ls and THAA D/Ls of different amino acids showed that the intracrystalline proteins in *Phorcus turbinatus* provide a robust fraction for AAR analyses (closed-system behavior). This result indicates that the shells had not been diagenetically compromised during their postdepositional history, supporting the results of the other geochemical methods and AMS dates (*SI Appendix*, Fig. S2.6). One exception is sample XVII (3), which shows some indication of open-system behavior, supporting the hypothesis that this date might be an outlier (Fig. 1).

Oxygen Isotope Analysis. $\delta^{18}O$ values of sequential carbonate samples from 13 specimens were converted to Sea Surface Temperatures (SST) and provided mean annual SST estimates (*SI Appendix*, Section 2). Observed fluctuations in mean annual SST, of 3–4 °C, are consistent with differences between warm Greenland Interstadials (GIS) and cooler Greenland Stadials (GS), including Heinrich events during Marine Isotope Stage 3 (MIS 3) (38). Oxygen isotope and SST data are consistent with the climatic phases inferred from tentative correlations of calibrated ages with the NGRIP data (Fig. 1). These tentative comparisons allow us to attribute samples with higher $\delta^{18}O_{shell}$ values [i.e., V, VI, XI, and XVII (1), and XVIII], corresponding to SST estimates between 19.2 °C and 21.4 °C, to cold events i.e., Heinrich 3, GS 5/6, GS 9, and GS 10, respectively. Samples with lower $\delta^{18}O_{shell}$ values, corresponding to temperatures ranging from 23.2 °C to 24.4 °C, could be attributed to GIS 11 [i.e., XVI (1), XVI (4), XVII (2), XVII (4), and XX] and GIS 10 [i.e., XVI (2, 3) and XVII (3)] (39). The colder annual SST estimate for sample XVII (1) is inconsistent with that of other Ahmarian samples, indicating that this specimen did not secrete its shell in the same temperature regime and is not contemporary with the others, which is also reflected by the younger AMS date. Provided the date is correct, this specimen is most likely intrusive from the later cold period GS 9.

Discussion

The chronological data reported above suggest that modern humans producing IUP and EUP assemblages were present at Ksâr 'Akil from before 45,900 cal B.P. and around 43,300–42,800 cal B.P., respectively. These age estimates have implications for (*i*) the chronology of the Levantine EUP and IUP, (*ii*) the age of UP modern human presence in the Levant, (*iii*) the spread of UP modern humans from the Levant into Eurasia, and (*iv*) the validity of the Levantine corridor hypothesis.

Ksâr 'Akil Chronology and Previous Dates. Our dates are in good agreement with conventional radiocarbon dates on charcoal (26, 40). They also overlap with the age estimates on shell by Douka et al. (24) for the upper part of the sequence, but are significantly older (3,000–4,000 y) for the IUP and EUP layers (*SI Appendix*, Section 2). The reasons behind the observed discrepancy are presently unresolved. Causes might include differences in (*i*) sample selection (i.e., shell preservation and its implications for time-averaging and diagenesis), (*ii*) sample pretreatment (e.g., potential incomplete elimination of contaminants by the CarDS method) (41), (*iii*) radiocarbon AMS laboratory (i.e., Groningen and Oxford), and (*iv*) the dated event based on taxa selection (i.e., collection of beached shells for ornaments or live mollusks for consumption; see *SI Appendix*, Section 2 for discussion).

Chronology in a Regional Context.

Levantine IUP chronology. The earliest IUP in the Levant is represented by Manot Cave and Boker Tachtit (both Israel), Üçağızlı I Cave (Turkey), and as inferred from Kebara Cave (Israel) (Fig. 2; *SI Appendix*, Section 3). For comparative purposes, radiocarbon dates were calibrated using IntCal/Marine13 (34) unless stated differently (*SI Appendix*, Section 3). A single AMS date from Unit 7 of Area C at Manot Cave of 48,700 ^{14}C B.P. is attributed to the IUP. It cannot be calibrated as it falls beyond the limits of the current calibration curve. The IUP lithics share features with Ksâr 'Akil IUP Layers XXV–XXI, but the unit also contains abundant EUP and scattered MP artifacts (8). Age calibration of conventional radiocarbon dates on charcoal suggests that the IUP at Boker Tachtit (Layers 1–4) dates to at least 50,000–40,000 cal B.P. (42), which should probably be considered a minimum estimate (43). The lithic assemblage of Layer 4 shows technological similarities with Ksâr 'Akil Layers XXII–XXI and is associated with a charcoal date of ~40,000 cal B.P., again a minimum age (42). The IUP at Üçağızlı I (Layers G–I) corresponds to Layer XXI of Ksâr 'Akil (31) and dates to 45,900–38,400 cal B.P. based on charcoal samples (9) and 40,800–37,800 cal B.P. based on shell ornaments (23). Kebara has a hiatus in the stratigraphy where the IUP would be expected to occur; based on age estimations for the Late Middle Paleolithic below and the EUP above, Rebollo et al. (44) assign a time window of 49,000–46,000 cal B.P. for the IUP. The estimated start of the IUP at Ksâr 'Akil, modeled to at least 45,900 cal B.P., is

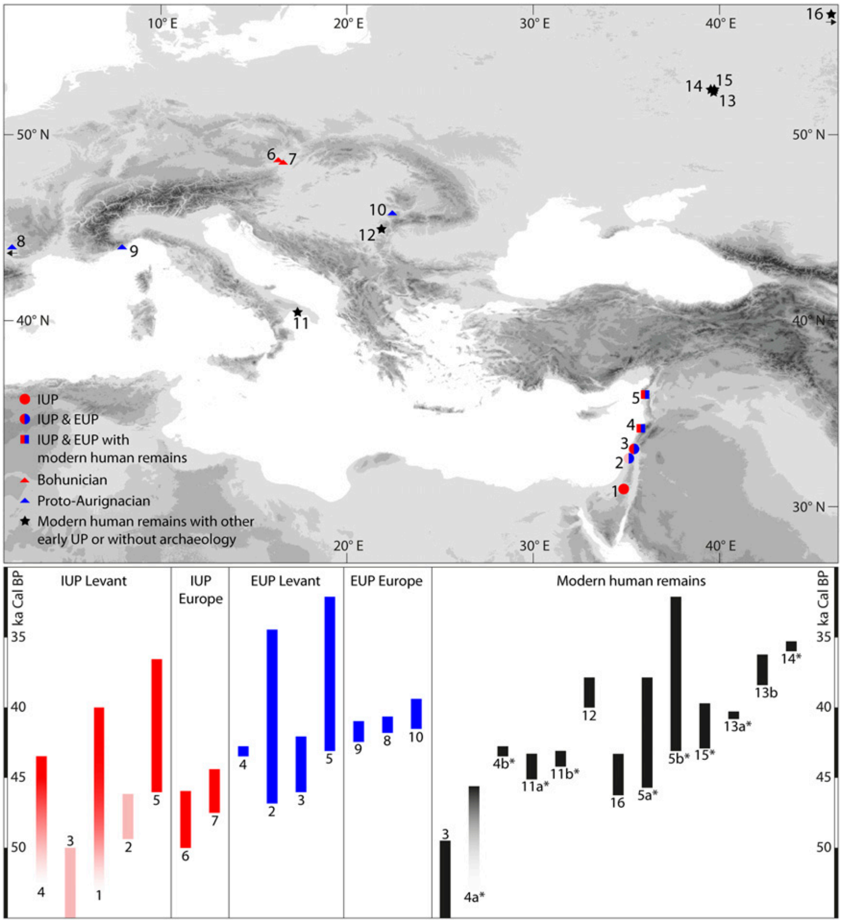

Fig. 2. Upper Paleolithic sites and human remains mentioned in the text (see also *SI Appendix*, Section 3). (*Upper*) Site location. (*Lower*) Age range (in 1,000 calendar ages before present) of sites and human remains (*: in association with UP). 1, Boker Tachtit; 2, Kebara Cave; 3, Manot Cave; 4, Ksâr 'Akil; 4a, Ethelruda; 4b, Egbert; 5, Üçağızlı I; 5a, Üçağızlı I IUP teeth; 5b, Üçağızlı I EUP teeth; 6, Brno-Bohunice 2002; 7, Brno-Kejbaly; 8, Isturitz; 9, Riparo Mochi; 10, Româneşti-Dumbrăviţa I; 11a Cavallo B; 11b, Cavallo C; 12, Peştera cu Oase; 13a, Kostenki 14 Layer IVb tooth; 13b, Kostenki 14 Burial; 14, Kostenki 1 Layer III; 15, Kostenki 17 Layer II; 16, Ust'-Ishim.

congruent with technological and chronological data from all four sites, of which the Manot IUP might be the most ancient.

Levantine EUP chronology. Our dates agree with established chronologies for other Levantine EUP or Early Ahmarian sites including Kebara, Manot, and Üçağızlı I. The Early Ahmarian at Kebara (Units III and IV) is dated between 46,000 and 34,000 cal B.P. and corresponds archeologically to Ksâr 'Akil Layers XIX–XV (44, 45). The Early Ahmarian component of Unit 7 (Area C) at Manot has been dated to 46,000–42,000 cal B.P. (46) and corresponds to Layers XX–XVI. The EUP Layers B to B4 at Üçağızlı I, dated to 39,800–32,200 cal, are similar in lithic technology but younger than Ksâr 'Akil Layers XVI–XVII (9, 31). Age estimates for the entire EUP sequence (Layers B–E) range between 42,800 and 32,200 cal B.P. (9) and 40,800 and 36,400 cal B.P. based on shell ornaments (23). The EUP of the four sites overlaps, although its start at both Manot and Kebara predates that of Üçağızlı I and Ksâr 'Akil by several millennia.

Implications for UP Modern Human Dispersals into Europe and the Levantine Corridor Hypothesis.

AMH remains. Ksâr 'Akil is one of the few sites with AMH fossils that are associated with IUP and EUP assemblages in Europe and the Levant. Our age estimations, placing Egbert's layer between 43,200 and 42,900 cal B.P., predate directly dated AMH remains from Europe, including those from Peştera cu Oase and Kostenki 14 (Russia) (Fig. 2 and *SI Appendix*, Section 3) (2, 11, 47), and overlap at 1σ with the modeled age for Cavallo C (Italy) (10). Further, this age is consistent with those for the AMH teeth from the EUP layers of Üçağızlı I (42,800–32,200 cal B.P.) (9). Our data also provide a minimum age of at least 45,900 cal B.P. for the archeological layer bearing the remains of Ethelruda and the start of the IUP in Layer XXV, placing the fossil well before the oldest European AMH fossil (i.e., Cavallo B dated to 45,000–43,400 cal B.P., *SI Appendix*, Table S3.2) (10). In contrast to the Ust'-Ishim femur (46,200–43,700 cal B.P.) (22), the Manot 1 skull (60,200–49,200 y ago) (8) might predate the IUP at Ksâr 'Akil. However, the uranium–thorium age of the latter is rather imprecise and none of these specimens was found in direct archeological context. It is therefore unclear what toolkit these humans carried. Within the Levant, the Ksâr 'Akil data are in rather good agreement with the age estimations for Üçağızlı I, where AMH teeth from the IUP date between 45,900 and 37,100 cal B.P. (9). Compared with European modern human remains associated with UP toolkits, the Ksâr 'Akil data predate the human remains from early UP contexts at Kostenki 14 Layer IVb between 41,500 and 40,900 cal B.P. (11, 48) and at Kostenki 17 Layer II dated to 42,800–39,600 cal B.P. (12) (*SI Appendix*, Section 3).

Archeological record. Similarities between Levantine and European early UP technocomplexes have been interpreted as evidence of several dispersal episodes (3, 6, 14, 18, 19). The earliest connection concerns the Levantine IUP/Emirian and Central European Bohunician and similar assemblages in Eastern Europe and North Asia (11, 14, 15, 21, 49). Similarities have also been documented between the Levantine Early Ahmarian (EUP) and the European Proto-Aurignacian (3, 16, 19, 50, 51). Therefore, identifying the first occurrence of technologically similar lithic industries in the Levant and Europe holds potential information about dispersal trajectories. In the case of the Levantine IUP and European Bohunician connection, the latter is generally placed in GIS 12 (21, 52) with its onset around 46,860 ± 956 b2k (i.e., calendar years before A.D. 2000) (39), or in GS 13 (53). The estimated start of the IUP at Ksâr 'Akil falls within GIS 12, but could also predate it. The dates of Boker Tachtit and Manot predate GIS 12, and could be as early as GIS 13 and GIS 14, respectively. The start of the Levantine EUP at Ksâr 'Akil, Kebara, and Manot predates the appearance of the Proto-Aurignacian in Europe around 42,700–39,100 cal B.P., i.e., at Isturitz (54), Riparo Mochi (55) and Românești-Dumbrăvița I (56), by several millennia (*SI Appendix*, Section 3).

Implications. On an interregional scale, similar UP lithic technocomplexes (e.g., IUP/Bohunician and Early Ahmarian/Proto-Aurignacian) first appear in the Levant. Our chronology for Ksâr 'Akil, corroborated by several lines of evidence, fits well with other early IUP and EUP Levantine sites. It is generally assumed that once there is a proven association between certain archeological assemblages and their makers, this could be extrapolated to the technocomplex as a whole (e.g., all Early Ahmarian is made by modern humans based on association of the Egbert fossil to the Ksâr 'Akil EUP). Although such extrapolations should be treated with caution especially when they are extended to other closely related assemblages over a large geographical area, the correlation of AMH associated technocomplexes with other closely related technocomplexes allows tracking of potential dispersal routes in the archeological record. Our data contribute to the debate on modern human dispersal patterns by providing age estimations for UP assemblages containing modern human fossils. Comparison of our age estimations with those of European AMH fossils place Eltheruda's layer before the first occurrence of modern humans in Europe. Similarly, Egbert's layer predates any known Aurignacian and other early UP modern humans in Europe. The antecedence of both UP lithic technocomplexes and modern human remains in the Levant, the latter also corroborated by Manot 1, indicates that modern humans carrying a UP toolkit were present in the Levant before arriving in Europe. This contradicts Douka et al.'s (24) hypothesis that shell beads, and by proxy UP modern humans, appeared first in Europe. Observed similarities in early UP lithic technology and other material culture of Levantine and European technocomplexes suggest a close interrelation that could well result from dispersal events. In turn, this implies that the Levant served as a corridor for modern humans dispersing out of Africa and into Europe rather than being a "cul-de-sac" where modern humans arrived after they dispersed into Europe.

That the first occurrence of the Levantine IUP and Bohunician takes place in a short time window suggests rapid dispersal events over large geographical areas (17), and the same is true for the first occurrence of the Proto-Aurignacian (13). The spread of modern humans and their material culture has implications for the replacement of Neanderthals by modern humans and acculturation debates, because current data suggest that at the time of these dispersals the former were still present in some parts of Europe (57–59). Changes in material culture of some of the last Neanderthals in Europe could therefore be related to contact and subsequent (stimulus) diffusion of modern human behaviors.

Materials and Methods

All analyses (AMS radiocarbon dating, AAR, and oxygen isotopes) have been conducted in conjunction on selected specimens to enable direct comparison and contextualization of the results of various datasets (*SI Appendix*, Section 2). We selected samples based on an evaluation of the shell preservation by using both macroscopic attributes and physicochemical characteristics (XRD, staining with Feigl and Mutvei solutions) (*SI Appendix*, Section 2). Radiocarbon dating at the Groningen radiocarbon laboratory consists of chemical cleaning of the outer surface using a 4% (wt/vol) HCl solution, followed by CO_2 development using concentrated H_3PO_4. All dates were calibrated using the Marine13 (34) calibration curve and the software OxCal 4.2.4 (37). Reservoir correction (R) was carried out taking into account a local ΔR of 53 ± 43 B.P. for the eastern Mediterranean (60). AAR was used as a test for diagenetic integrity after Demarchi et al. (61). Sampling for oxygen isotope analysis was adopted after Mannino et al. (62). Grossman and Ku's (63) equation with a correction for the conversion of VSMOW to VPDB (64) was used to calculate SST from $\delta^{18}O_{shell}$ values. Mean $\delta^{18}O_{water}$ is based on pore water estimations (65) and corrected for MIS 3 glacial conditions. For a full description of our sampling and analysis methods, see *SI Appendix*, Section 2.

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Supporting Information

New chronology for Ksâr ‘Akil (Lebanon) supports Levantine route of modern human dispersal into Europe

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Section 1: Ksâr ‘Akil

Site background

Location

Ksâr ‘Akil (KSA), which translates to “inaccessible or high place”, rockshelter is situated in the Antelias Valley (1–3), roughly 10 km northeast of Beirut (Lebanon). The valley is named after the town where the valley terminates in the Bay of St. George. About 2 km inland from this bay, the valley previously split into two smaller ones, which surrounded a limestone hill with a Semitic “high place” on top (1), probably lending its name to the rockshelter. This hill has been quarried away almost to the valley bottom (4). The Ksâr ‘Akil rockshelter itself, located on the northern slope of the valley, still survives, albeit filled with rubble from the quarrying activities (4).

In prehistoric times, the south-facing opening of the rockshelter would have been protected by the hill in the center of the valley. Fresh water supply would likely have come from the adjacent Antelias River running down the valley. Furthermore, the Ksâr ‘Akil occupants would have had access to the small coastal plain (sahil), the steep slopes of the Lebanon Mountains, and the open highlands of the El Beqaa Valley (Fig. S1.1).

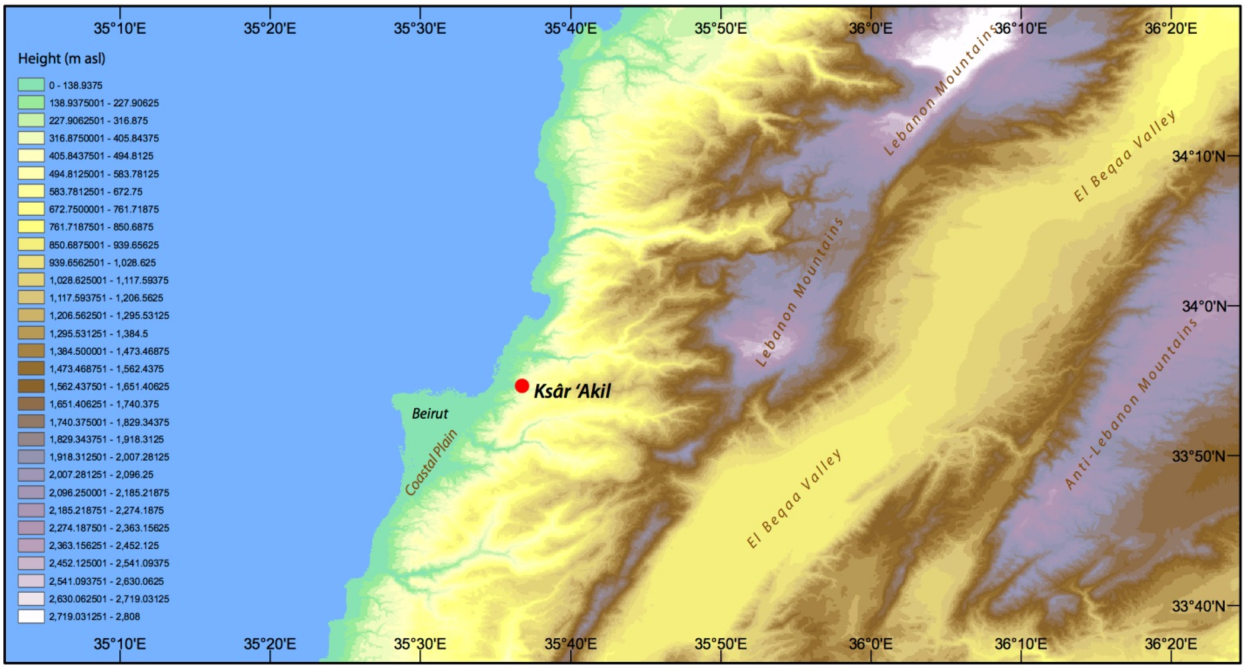


Figure S1.1. Geographical location of Ksâr ‘Akil, Lebanon. Digital elevation data based on NASA’s Shuttle Radar Topography Mission (SRTM) (downloaded from: https://lta.cr.usgs.gov/SRTM).

History

The site was discovered in 1922 when a treasure hunter bought Ksâr ‘Akil and started digging its deposits for gold (5). Professor E. Day, a geologist at the University of Beirut, learned of this activity and acquired some of the uncovered lithics and faunal material. The lithics were subsequently sent to Paris and London for identification where, among others, Abbé H. Breuil had the opportunity to study the materials. It was on his recommendation that a team led by Rev. J. G. Doherty from Boston

College go to Lebanon to conduct the first scientific excavations at the site in 1937 (1). In the first two seasons (1937 and 1938), deposits were excavated up to a depth of 19 m. After a break forced by World War II, Doherty and Ewing led the last excavation season (1947–1948) when bedrock was eventually reached at 23 m below datum (5). In 1969, J. Tixier reopened the site and continued excavations until 1975, reaching a depth of 9 m, when his team was forced to leave Lebanon due the outbreak of civil war (6, 7).

The 23-m sequence of Ksâr ʻAkil contains deeply-stratified deposits, spanning the Middle Paleolithic (MP) to the Epipaleolithic (EPI) (Fig. S1.2). The lowermost 7 m (16–23 m below datum) contain alluvial deposits with evidence of MP occupation (3, 5). During this period of deposition, Ksâr ʻAkil was likely occasionally flooded by the nearby stream depositing reddish alluvial sediments (3). Above 16 m, the sediments containing Upper Paleolithic (UP) artifacts are generally brown-greyish in color and intersected by complexes (e.g., at 16–17 m and 10–11 m) of red clay bands underlying a deposit of angular limestone blocks. Wright (3) suggests that the red clay, at least for the band at 10–11 m, is the result of *in situ* pedogenesis stemming from either an episode of non-habitation or a period of intensified weathering due to increased rainfall. Both Wright (3, 8) and Ewing (9) hypothesized that periods of clay formation coincided with humid climatic conditions, potentially representing pluvial sub-phases of the last glaciation.

The material under study here comes from the 1930s and 1940s excavations by Doherty, the only one to reach the Initial Upper Paleolithic (IUP) and Early Upper Paleolithic (EUP) layers. Although excavation techniques were not up to present-day standards, all sediments were dry sieved and special care was taken when excavating animal bones in anatomical association (10). Ewing (1, 2, 9) was responsible for curating the faunal (and human) remains in the field from 1938 onwards and made a preliminary, very detailed, and impressively accurate account of faunal distribution throughout the sequence. The envisioned fully-blown paleontological study was originally delegated to D. Bate, a specialist of Pleistocene Near Eastern faunas at the Natural History Museum in London, UK. However, she was not able to complete her study before her death in 1951. Therefore, the Ksâr ʻAkil fauna was subsequently sent to D. Hooijer at the Natural History Museum in Leiden, the Netherlands, who carried out a study of all vertebrates (11). During his investigations, Hooijer separated the vertebrates and invertebrates, and the latter were given to his colleague C. O. van Regteren-Altena for study (12). A. Kersten kindly provided us with lists based on notes from the original excavators that correlate depths per square to the layers assigned by Ewing and thus linking the material from the 1937-8 and 1947-8 excavations. Both faunal assemblages from Ksâr ʻAkil remain stored in the Naturalis Biodiversity Center in Leiden.

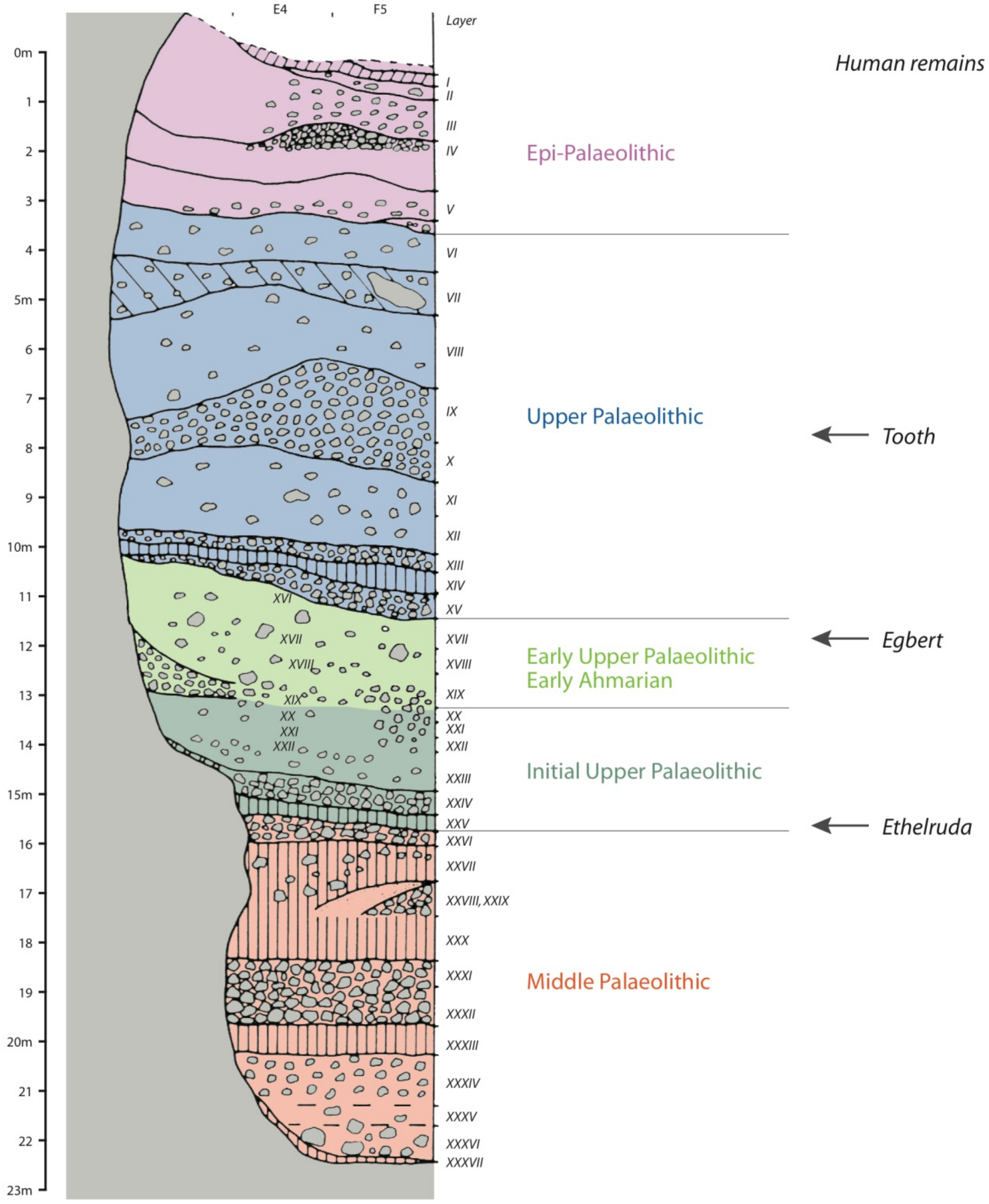


Figure S1.2. Ksâr 'Akil stratigraphic sequence (redrawn after (6) with reference to the major archeological divisions and human remains).

Over time, scholars have divided the Ksâr 'Akil sequence in several phases based either on changes in lithic technology (6, 13–15) or differences in faunal composition (11). In general, these divisions follow the same succession for the UP, i.e., from IUP/Emirian/transitional via EUP/Early Ahmarian and UP/Levantine Aurignacian to Epipaleolithic/proto-Kebaran deposits, although analogous packages are often labeled differently and individual layers are sometimes placed in different archeological phases (Table S1.1). Changes in faunal composition coincide with some, but not all, such boundaries. In this study, we generally follow the most recent division by Williams and Bergman (14), with the exception of grouping all named and unnamed UP assemblages into one UP (6). We have also sought to refer to individual layers so that the conclusions of our work may also be used within the frameworks proposed by other scholars.

Table S1.1. Division of the Upper Paleolithic sequence of Ksâr 'Akil phases based on lithic typology (6, 14, 15) and changes in faunal composition (11). Abbreviations: EPI: Epipaleolithic, UP: Upper Paleolithic, EUP: Early Upper Paleolithic, IUP: Initial Upper Paleolithic, Aur: Aurignacian.

Layer	Mellars & Tixier	Kuhn et al.	Williams & Bergman	Hooijer
I	EPI	early Kebaran	EPI (phase 7)	phase 6
II				
III				
IV				
V				
VI	UP		Atlian (phase 6)	phase 5
VII		late Levantine Aur	Levantine Aur (phase 5)	
VIII				
IX			Unnamed UP (phase 4)	
X				phase 4
XI		mid Levantine Aur	Unnamed UP (phase 3)	
XII		early Levantine Aur		
XIII				
XIV	Transitional phase B	UP II B		
XV				
XVI			Ahmarian (phase 2)	
XVII				
XVIII				
XIX		UP II A		phase 3
XX				
XXI	Transitional phase A	UP I	IUP (phase 1)	
XXII				
XXIII				
XXIV				
XXV				

Fauna

The IUP and EUP deposits at Ksâr 'Akil provided the bulk of both vertebrate and invertebrate faunal remains. In the framework of the doctoral research of the principle author, all invertebrate and vertebrate material of several selected IUP and EUP layers were subjected to a detailed zooarcheological study. The analysis of the UP vertebrates is still ongoing. Preliminary zooarcheological investigations indicate that the vertebrate remains are heavily fragmented (84%), albeit in reasonable condition (Fig. S1.3a). Bone weathering is commonly low (Fig. S1.3b), given that most specimens can be assigned to weathering stages 1–2 after Behrensmeyer (16). The bones were subjected to a mild form of acid treatment (soaked in 10% acetic acid solution overnight) to dissolve adhering sediment, after which any remaining reaction was stopped by a base-wash (10% sodium carbonate solution). After acid treatment, the cortical surface preservation is generally >50% (Fig. S1.3c). The majority of bones are not burned, but all burning stages, both carbonized (stages 1–3) and calcined (stages 4–6), after Stiner et al. (17), are present (Fig. S1.3d). Carnivore modifications are extremely rare (Fig. S1.4a) and human modifications in the form of cutmarks and impact fractures occur in about 11% of the assemblage (Fig. S1.4b).

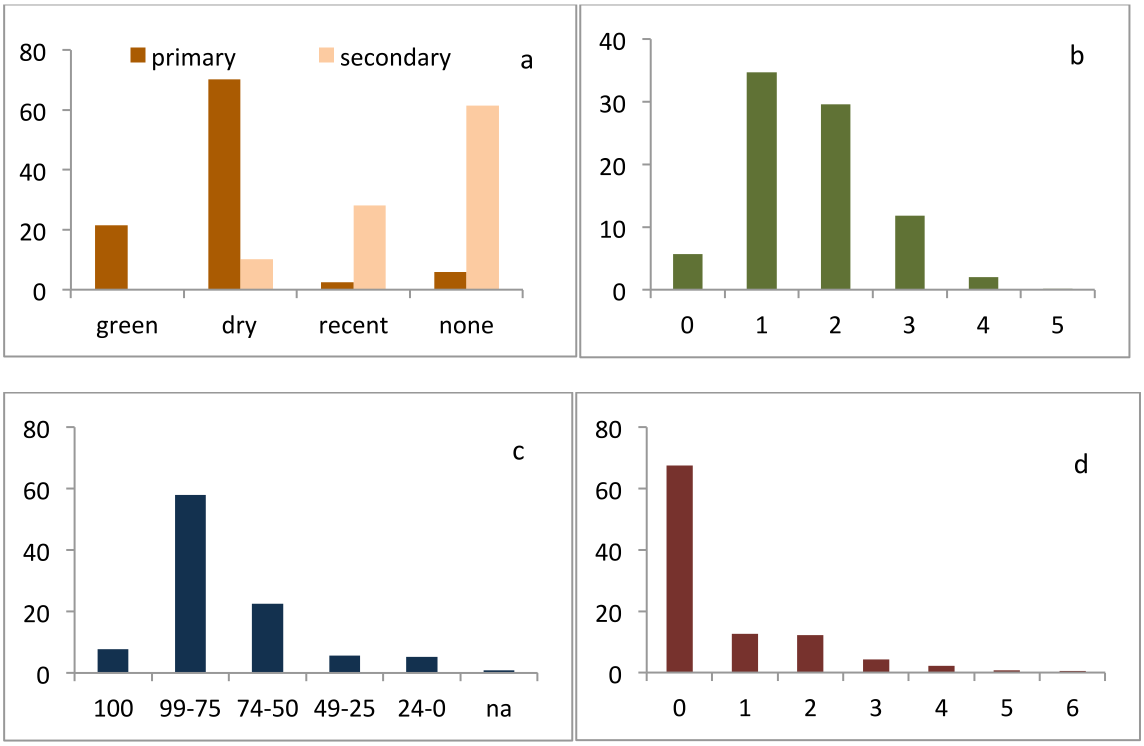
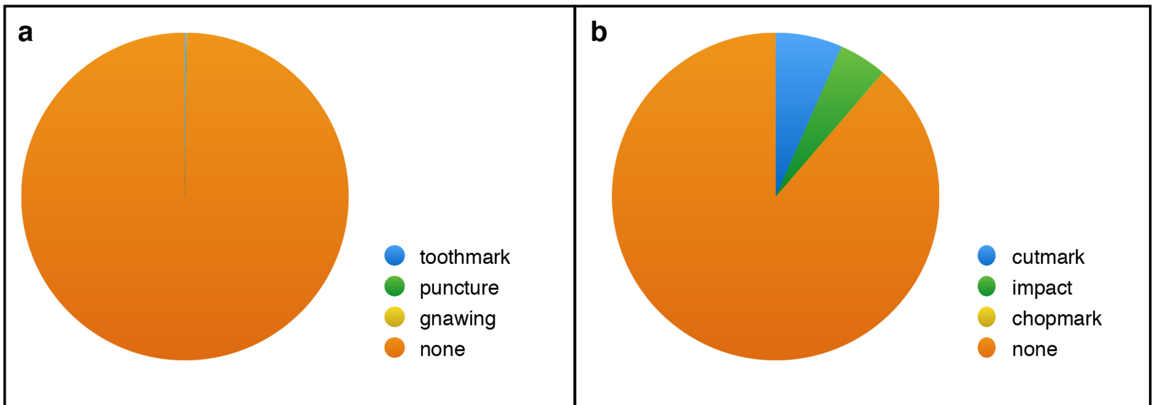


Figure S1.3. Bone preservation in the Upper Paleolithic at Ksâr ‘Akil. Percentage NISP of a) Primary and secondary bone breakage, b) Bone weathering stages after Behrensmeyer (16), c) Cortical bone preservation, and d) Bone burning stages after Stiner et al. (17).



modification type	n	%
toothmark	7	0.13
puncture	2	0.04
gnawing	1	0.02
none	5250	99.81

modification type	n	%
cutmark	347	6.59
impact	251	4.76
chopmark	1	0.02
none	4670	88.63

Figure S1.4. Bone modifications in the Upper Paleolithic at Ksâr ‘Akil. NISP and percentage NISP of a) carnivore modifications and b) human modifications.

IUP faunal exploitation

IUP Layers XXV and XXII were selected for detailed vertebrate faunal analysis. Preliminary investigations identified the following taxa: aurochs, ibex, wild goat, gazelle, red deer, Mesopotamic fallow deer, roe deer, wild boar, spur-thighed tortoise, hare, birds, and several carnivores (Fig. S1.5). During the IUP, faunal exploitation mainly took place in wooded areas, probably on the seaward slopes of the Lebanon Mountains, and partly on the coastal plain. The low frequency of open habitat arid species suggests that the highlands of the Beqaa Valley were less often targeted or that portions of hunted animals were not taken back to the site (Fig. S1.6). The main prey species include Mesopotamic fallow deer in combination with wild goat, wild boar, and aurochs (Fig. S1.5). Marine resources were exploited for consumption in low quantities, although empty shells were often collected to be used as tools or ornaments.

EUP faunal exploitation

Zooarcheological investigations were conducted for EUP Layers XVIII, XVI, and XIV. In our preliminary study, the same taxa were identified as those recovered in the IUP (Fig. S1.5). During the EUP or Early Ahmarian, the majority of terrestrial faunal remains are of woodland species, suggesting that hunting primarily took place in surrounding forested hills (Fig. S1.6). Small-bodied open habitat and arid species, such as gazelles, were exploited slightly more often than in the IUP. Overall, EUP faunal exploitation was more evenly distributed, i.e., taxa were hunted in more similar frequencies, than in the IUP. Mesopotamic fallow deer was still the dominant species, although red deer, aurochs, ibex, wild goat, gazelle, wild boar, and spur-thighed tortoise increased (Fig. S1.5). Among the invertebrate remains, edible species (i.e., intertidal gastropods) gained in importance relative to “non-food” species.

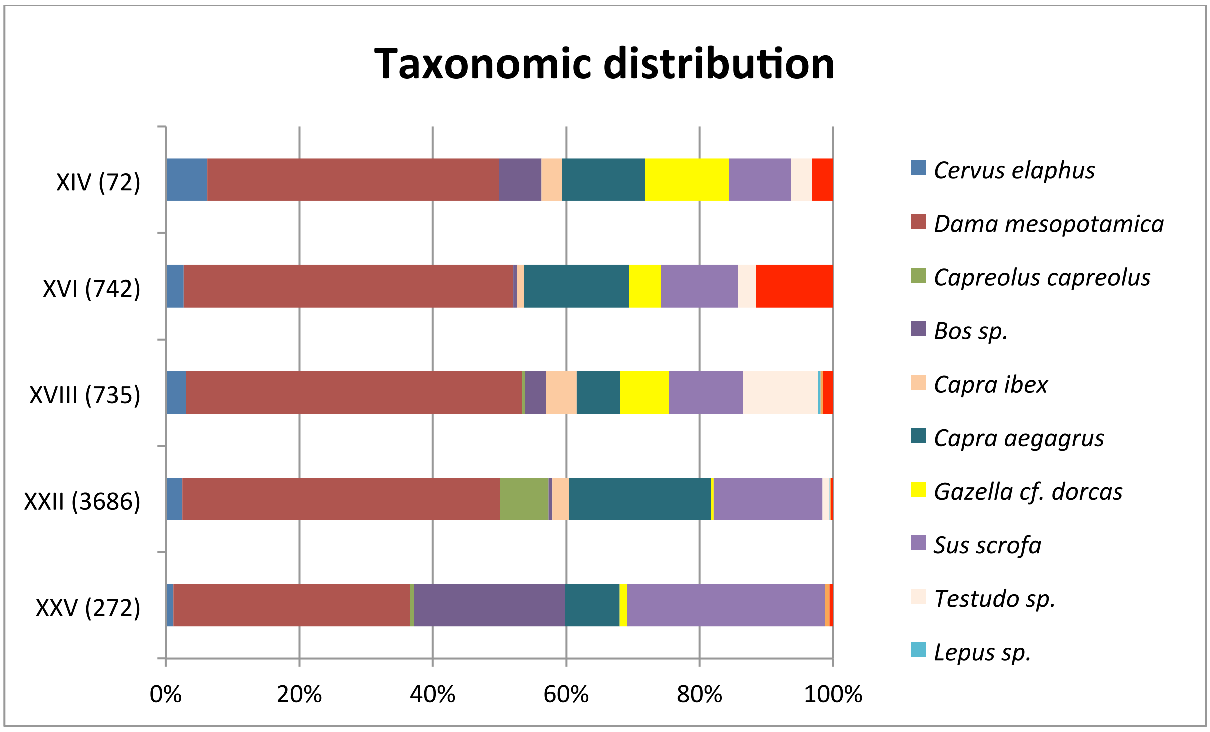


Figure S1.5. Taxonomic distribution. Percentages of exploited vertebrate faunal remains per studied layer (number of remains). Percentages are based on the number of identifiable specimens (NISP) per layer.

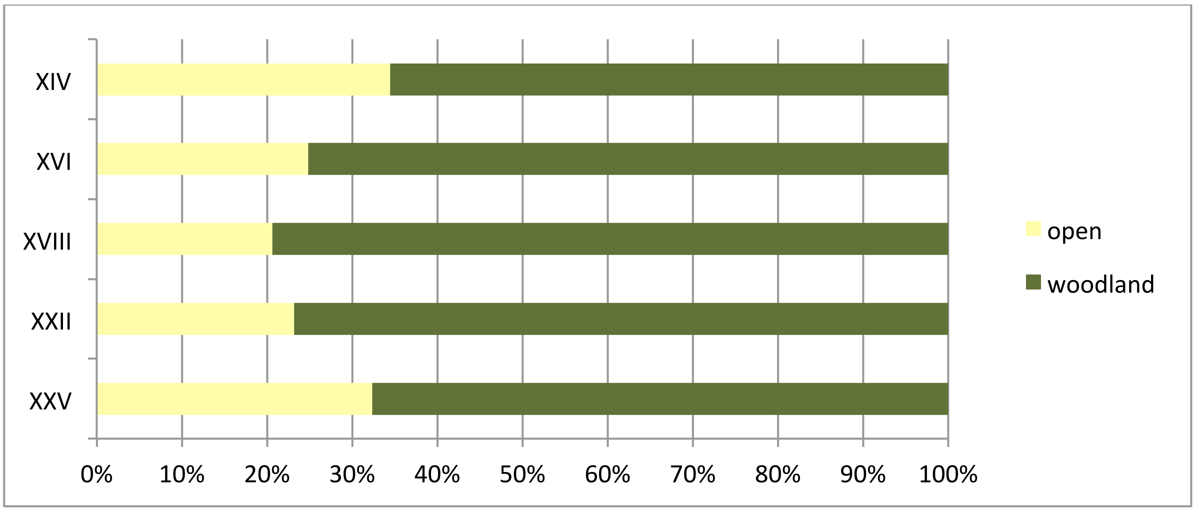


Figure S1.6. Frequency of habitat types of exploited terrestrial taxa. The frequency is based on the number of identifiable specimens (NISP) per layer. Division of woodland versus open/arid species is after Shea (18).

Invertebrate fauna

The invertebrate faunal assemblage studied here consists of 3571 specimens (n). The number of specimens that could be identified to species or family level (NISP) and for which a secure stratigraphic position could be ascertained on the basis of their labels is 3406 (see Table S1.2). We undertook a detailed archeomalacological study of the assemblage. Mollusks from Ksâr 'Akil include terrestrial, freshwater, and marine species. Most mollusk remains are from EUP and later UP deposits. Small amounts of mollusks were found in the Epipaleolithic layers and only a single specimen was found in the Middle Paleolithic deposits.

Table S1.2. Ksâr ‘Akil mollusks. Number of identified specimens (NISP) per layer.

Species	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XXI	XXII	XXIII	XXIV	XXVIIIA
marine gastropods																									
Patella caerulea		1			1	2	21	6	2	1	1					1	4								
Patella rustica	1	1	1		18	7	6	1	3	3						9	19								
Patella ulyssiponensis						2	2	2								1	1								
Patella sp.				1	1	2	7	1	3		1						11	2		1					
Trochidae											1						1								
Phorcus articulatus									1		8						2								
Phorcus turbinatus			14	5	120	25	34	13	19	21	43	7	7			37	71	6	7	2		1			
Phorcus sp.									3		60	3					10		1						
Bolma rugosa											3											2			
Cerithium vulgatum								1	2			1				10	5		4	5	4	13	2		
Naticarius hebraeus																		1				1			
Neverita josephinia											1						2		1			1			
Semicassis saburon		1																							
Euthria cornea																1	2								
Pisania striata									1		1														
Columbella rustica					3	2	20	16	132	37	5	4		1	1	31	115	4	10	4	2	19	2	1	
Tarantinaea lignarius																	2								
Nassarius gibbosulus				1	7	9	31	59	145	26	8	10	1			37	125	14	25	10	26	128	10	1	
Nassarius mutabilis									1												1				
Nassarius sp.																				1		1			
Bolinus brandaris																	2								
Hexaplex trunculus							2			2						2	5								
Murex sp.										1										1					
Mitra cornicula										1						1									
Conus ventricosus							3		4	1							5	2		3					
marine gastropod										2	13						5			2		1			
marine bivalves																									
Acanthocardia tuberculata		1						4	14	1	2					7	31	2				2	1		
Acanthocardia sp.								1			2														
Cerastoderma glaucum																	1								
Donax trunculus									1																
cf. *Callista chione*																	1	1							
Venus verrucosa																	1								
Anadara cf. *polii*									2																
Arca noae																	1								
Barbatia barbata																		1							
Glycymeris nummaria						1			2			1				10	7		1			1		1	
Glycymeris sp.		1		3	1		2	5	26	1	9	1			1	34	78	16	29	7	23	22	6	6	
Lima lima									4								2								
Ostrea edulis									1												1				2
Spondylus gaederopus											1	1											1		
Pinna nobilis					1						3														
marine scaphopods																									
Antalis dentalis									10																
Antalis vulgaris									13	1															
Antalis sp.								2	13																
freshwater gastropods																									
Theodoxus jordani									4										1						
Melanopsis praemorsa							1		2										1						
freshwater bivalves																									
Unionacea						1		2	1																
Potomida littoralis									1																

Table S1.2. continued

Species	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XXI	XXII	XXIII	XXIV	XXVIIIA
terrestrial gastropods																									
Pomatias elegans																	1			1					
Pomatias olivieri					2	1	7	7	6	4	1	2	2			10	10	13	6	1		1			
Buliminus labrosus							2	1			1							2							
Pene syriacus								1											1						
Cristataria porrecta												1													
Oxychilus syriacus					3	1	1	4		2							2	1	1						
Helicidae											69						3		5	5					
Helix engadensis	1	1	13	12	80	42	125	64	21	9	21	4	1	2		16	44	2	8		2				
Sphincterochila cariosa					1																				
Metafructicola berytensis					2	5	5	4	2	3						13	12	4	10	1		2			
Monacha nummus																		1			1				
Monacha syriaca					2	3	4	1	7	1							6		4			2			
terrestrial gastropod										2	211	16					46		62	2					
total NISP	2	6	28	22	242	103	273	195	446	119	465	51	11	3	2	220	633	72	177	46	60	197	22	9	2

Taphonomic investigations reveal marked differences between marine species from different habitats (Table S1.3). Rocky shore intertidal gastropods were generally not exposed to marine taphonomic processes and were likely live-collected. Other marine gastropods, bivalves, and scaphopods show heavy marine alterations in the form of beach-wear and bioerosion and were collected empty probably from active or fossil beach deposits. The collection of empty shells took place for various purposes, for instance to use them as tools (19) or body ornaments (15, 20). Intertidal rocky shore gastropods were likely exploited for subsistence purposes. Human collection of these species is evident from edge damage on *Patella* spp. This is consistent with damage resulting from prying the limpets off the rocks. Other human modifications include the removal of the apex of *Phorcus* spp., probably to facilitate flesh extraction (Fig. S1.7). This evidence, together with the fact that they were collected live, strongly suggests that these species were used as food. Occasional burning (n=667) resulting in a combination of heat cracks, discoloration, and decalcification was observed in the assemblage. This burning damage might either result from indirect (while buried) or direct (while on the surface) exposure to heat. Indirect exposure to heat might have occurred by lighting a fire on top of deposits containing shell and, therefore, was not necessarily deliberate (17).

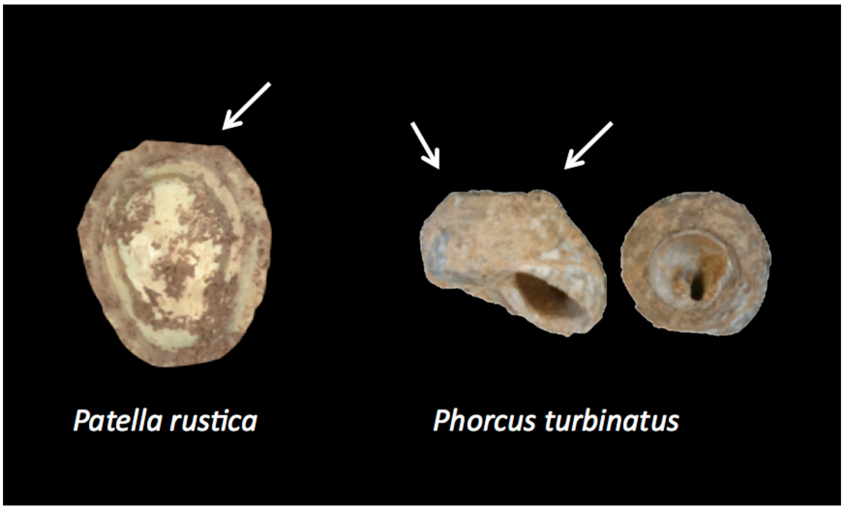


Figure S1.7. Examples (marked by arrows) of human modifications on intertidal rocky shore gastropods. Edge damage on *Patella rustica* (left) congruent with damage resulting from forcing live specimens loose from the rocks they live on and the removal of the apex of *Phorcus turbinatus* (right) to aid flesh extraction.

Table S1.3. Marine taphonomic alterations. n: number; %: percentage relative to the total marine mollusk assemblage. “Food:” numbers of marine alterations for species collected for consumption (i.e., rocky shore intertidal gastropods: *Phorcus turbinatus, Phorcus articulatis, Patella rustica, Patella caerulea* and *Patella ulyssiponensis)*; “Non-food:” numbers of marine alterations for marine mollusk species transported to the site for purposes other than consumption (e.g., used as tools and ornaments). Note: shells may show more than one type of taphonomic alteration. Therefore, the total number of marine taphonomic altered shells (last row) is less than the sum of all individual marine taphonomic alterations.

Marine taphonomic alterations	**n**	**%**	**Food**	**Non-food**
Bioerosion	38	1.59	0	38
epizootic encrustation	4	0.17	0	4
reducing atmosphere	36	1.51	0	36
beach washed	867	36.38	1	866
gastropod damage	50	2.10	0	50
crab damage	72	3.02	1	71
boring sponge damage	263	11.04	0	263
total marine alterations	**989**	**41.50**	**2**	**987**

Section 2: Geochemical methods

Introduction

We applied an array of zooarcheological, geochronological, and geochemical techniques on the shells of the rocky shore intertidal gastropod *P. turbinatus*. By dating a species of shellfish gathered for consumption, the objective of this study was to reconstruct when UP humans were present at the site and exploiting marine resources. The species *P. turbinatus* was selected because it is the most abundant taxon exploited as food and, thus, representative of past environments and behaviors pertaining to the occupation of Ksâr 'Akil. Previous studies have shown that the oxygen isotope composition of *P. turbinatus* is an accurate record of sea surface temperature (SST) (21, 22) and that this species can be used to obtain reliable AMS radiocarbon dates (23, 24). AMS radiocarbon dating on *P. turbinatus* specimens has allowed us to refine the chronology of the site and episodes of mollusk collection. AAR analyses were used to provide an independent estimate of the diagenetic integrity of the intra-crystalline proteins trapped in the shells. Dated shells were also sampled for oxygen isotope analyses to reconstruct SSTs. Moreover, all analyses were conducted in conjunction on selected specimens (Fig. S2.1; Table S2.1) allowing correlation of the results from the different lines of investigation (25).

Sample selection

Zooarcheological and specifically taphonomic investigations have shown that intertidal rocky shore species collected for consumption were the best-preserved species in the assemblage (see SI section 1). Individual *P. turbinatus* specimens were selected for study based on their excellent preservation, as determined by a set of macroscopic and chemical characteristics. Shells were initially selected if they had visible mother-of-pearl layers (i.e., inside the aperture) and, preferentially, when these were translucent, as in living specimens. Care was also taken to avoid shells with ante mortem damage and visible growth-stops parallel to the aperture edge. *P. turbinatus* shells are bimineralic and consist of an aragonitic inner nacreous layer and an outer prismatic layer of calcite (23, 26). Diagenetic alterations are more easily detectable in the aragonitic part of the shell than the calcitic part because aragonite is a less stable crystal phase than calcite (26) (but see (27)). We conducted X-ray diffraction analysis of the inner nacreous layer to confirm that the aragonite was still pristine and had not recrystallized into calcite. A portion of the dated shells (n=5) was also sectioned along the periphery of the outer whorl (perpendicular to the axis of growth) with a Buehler Isomet 1000 precision saw, set in resin, ground, and polished to inspect microgrowth increments. These sections were initially stained with Mutvei solution (28), a blue substance that etches microgrowth-structures, allowing them to be examined. Intact microstructures suggest no recrystallization of carbonate occurred after death and, thereby, that the primary aragonitic structure of the shell is intact. The Mutvei solution was later removed by successively grinding with 400, 800, and 1200 µm powder and Feigl solution (see Fig. S2.5 D–E) applied to differentiate calcite from aragonite within the shell (29). Aragonite reacts faster to Feigl solution (after roughly 20 min) than calcite (after approximately a day) making it possible to detect diagenetic substitutions of primary aragonite with secondary calcite in the nacreous layer (30). Well-preserved *P. turbinatus* shells were then sampled to obtain sequences of oxygen isotope values for SST reconstruction. The top part of the shell (i.e., the apex or directly below in instances where the apex had already been cut off by the Paleolithic inhabitants of Ksâr 'Akil) was mechanically cleaned of adhering sediment and sent to the Centre for Isotope Research of the University of Groningen for AMS radiocarbon dating. The basal part of the shell (including part of the lip) was sent to the NEaar laboratory of the University of York for amino acid racemization analyses.

Table S2.1. List of samples showing layer, square, and laboratory numbers for oxygen isotope analysis (Oxygen), amino acid racemization (NEaar) and AMS radiocarbon dating. RGM-nr: museum inventory number (Naturalis Biodiversity Center, Leiden). Note: all specimens of one species with identical provenience (i.e., layer, square, depth below datum) were combined and given a single RGM-number and, therefore, we have assigned a unique sample ID (KSA nr) to all specimens under study and refer to this number in the SI text. To ease interpretation, radiocarbon dated samples are referred to by only their layer or with a sub-number (e.g., XVI (1)) when more dates are available.

KSA nr (Oxygen)	RGM-nr	layer (ref in text)	Square	NEaar lab ID (AAR)	GrA nr (^{14}C)
KSASV04	606336	V	F3-6	8700	-
KSASV03	606336	V	F3-6	8701	-
KSASV02	606338	V	E4-6	8702	-
KSASV01	606338	V	E4-6	8703	-
KSAS01V	606338	V	E4-6	8704	53005
KSASVI04	606337	VI	E4,FG3-4	8695	-
KSASVI03	606337	VI	E4,FG3-4	8696	-
KSASVI02	606337	VI	E4,FG3-4	8697	-
KSASVI01	606337	VI	E4,FG3-4	8698	-
KSAS08VI	606337	VI	E4,FG3-4	8699	54848
KSASXI02	606317	XI	E5	8692	-
KSASXI01	606317	XI	E5	8693	-
KSAS02XI	606317	XI	E5	8694	53006
KSAS11XII	606921	XII	E4	9344, 9345	57545
KSAS07XVI	606334	XVI (1)	E5	8691	54847
KSAS10XVI	606310	XVI (2)	F3	9346, 9347	57544
KSASXVI02	606334	XVI (3)	E5	8689	57598
KSASXVI03	606334	XVI (4)	E5	8688	57599
KSASXVI04	606334	XVI	E5	8687	-
KSASXVI01	606334	XVI	E5	8690	-
KSAS03XVII	606306	XVII (1)	F4	8686	53001
KSAS06XVII	606306	XVII (2)	F4	8685	54846
KSASXVII01	606309	XVII (3)	E4	8684	57602
KSASXVII02	606309	XVII (4)	E4	8683	57603
KSASXVII03	606306	XVII	F4	8682	-
KSAS09XVIII	606308	XVIII	E4	9348, 9349	57542
KSAS04XIX	639387	XIX	F4	-	53004
KSAS12XX	606294	XX	F4	-	57597
KSAS05XXII	606420	XXII	F4	-	53000

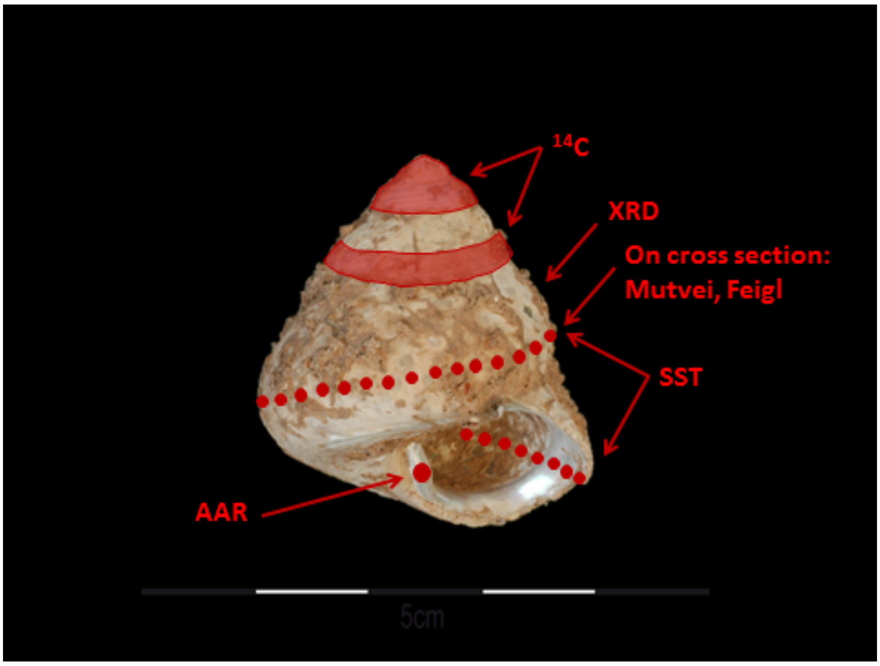


Figure S2.1. *Phorcus turbinatus* with sampling spots for the different analyses. ^{14}C: AMS radiocarbon dating, XRD: X-ray diffraction, Mutvei: Mutvei solution (28), Feigl: Feigl solution (29), SST: Sequences (all small red dots) of oxygen isotope samples for sea surface temperature reconstruction, AAR: amino acid racemization. Scale bar in cm.

Radiocarbon dating

Samples

We sampled 16 *Phorcus turbinatus* shells from the Upper Paleolithic part of the sequence for AMS radiocarbon dating (Table S2.2). The selected species allowed us to date the antiquity of shellfish exploitation and estimate the timing of IUP and EUP occupation at Ksâr ʻAkil. Dating well-preserved specimens of a taxon collected for consumption allows us to attain accurate dates for human occupation linked to this behavior, because like other mollusks, *P. turbinatus* needs to be consumed fresh. Thus, its death coincides with the time of human collection, consumption, and discard.

Table S2.2. AMS radiocarbon samples. BP: uncalibrated radiocarbon years before present; +/-: Error at one sigma level; cal BP: calendar years before 1950. Calibration conducted using the Marine13 calibration curve (31) and OxCal 4.2.4 software (32). Dates were corrected for the global mean reservoir age (R: i.e., 400 years) with a local correction or ΔR of 53 ± 43 (33). Calibrated ages are shown at 68.2% and 95.4% probability.

KSA nr	Layer	Laboratory nr	Date BP	+/-	age cal BP (68.2%)	age cal BP (95.4%)
KSAS01V	V	GrA-53005	26,210	130/120	30,210–29,700	30,430–29,500
KSAS08VI	VI	GrA-54848	28,810	130/130	32,550–31,930	32,790–31,690
KSAS02XI	XI	GrA-53006	34,310	230/210	38,660–38,090	38,890–37,590
KSAS11XII	XII	GrA-57545	35,880	260/230	40,340–39,690	40,710–39,360
KSAS07XVI	XVI (1)	GrA-54847	39,910	370/320	43,470–42,850	43,930–42,620
KSAS10XVI	XVI (2)	GrA-57544	35,960	230/210	40,390–39,800	40,730–39,520
KSASXV102	XVI (3)	GrA-57598	37,320	270/240	41,730–41,230	41,950–40,930
KSASXV103	XVI (4)	GrA-57599	39,890	310/280	43,400–42,870	43,770–42,650
KSAS03XVII	XVII (1)	GrA-53001	34,090	220/200	38,460–37,770	38,640–37,200
KSAS06XVII	XVII (2)	GrA-54846	39,850	340/310	43,390–42,830	43,800–42,600
KSASXVII01	XVII (3)	GrA-57602	36,730	240/220	41,240–40,650	41,460–40,340
KSASXVII02	XVII (4)	GrA-57603	38,260	260/240	42,310–41,920	42,510–41,720
KSAS09XVIII	XVIII	GrA-57542	36,290	240/220	40,780–40,160	41,100–39,880
KSAS04XIX	XIX	GrA-53004	39,390	330/290	43,050–42,570	43,330–42,340
KSAS12XX	XX	GrA-57597	40,040	340/300	43,560–42,950	43,990–42,730
KSAS05XXII	XXII	GrA-53000	40,550	350/310	44,060–43,340	44,430–43,070

Dates

The 16 AMS radiocarbon dates were obtained from the Centre for Isotope Research of the University of Groningen (Table S2.2) and are consistent with the stratigraphic division. Our data show that the earliest shellfish exploitation in the IUP Layer XXII dates to 40,550 +350/-310 BP. The start of the Early Ahmarian (*sensu lato*; Layer XX) dates to 40,040 +340/-300 BP. A shell fragment from Layer XIX dates to 39,390 +330/-290 BP. There are nine dates for Layers XVIII–XVI considered by most scholars to belong to the "classic" Early Ahmarian (34) showing a wide range of age estimations from 39,910 +370/-320 to 34,090 +220/-200 BP. The dates of 36,290 +240/-220 BP obtained for Layer XVIII and 34,090 +220/-200 BP for layer XVII are unexpectedly young relative to other dates obtained from the same layer or subsequent, overlying layers. The Upper Paleolithic Layers XII, XI, and VI (also named Atlian) were dated to 35,880 +260/-230 BP, 34,310 +230/-210 BP, and 28,810 ± 130 BP, respectively. The start of the Epipaleolithic or Proto-Kebaran (Layer V) was dated to 26,210 +130/-120 BP. The latter two dates are slightly older than expected for Atlian and Proto-Kebaran lithic industries (35), but fit well with the dates on charcoal obtained by Mellars and Tixier (6) (Table S2.3).

Two conventional dates were obtained decades ago by Vogel and Waterbolk (36) on land snails (GrN-2195) and on charred material (GrN-2579). GrN-2195 was made on shells collected between 6 and 7.5 m below datum (Layers VII–IX). GrN-2579 with a date of 43,750 ± 1500 BP is probably a minimum age due to uncertainty as to the type of the dated material (i.e., charcoal as suggested by Wright (3) or a dark clay band containing organic material or charred bone (see (36)). It has erroneously been reported as Gro-2574-75 by Wright (3).This date has been variously placed in

Layer XXVI or XXVII (37, 38). However, based on the original descriptions of the stratigraphy as it was known at the time, it more likely comes from layer XXV or the boundary between XXV–XXVI. Vogel and Waterbolk (36) describe the provenience of the sample as "a dark clay band at 16 m level 1 m below the top of the Upper Levalloisian-Mousterian" and provide references (1) for further details. Wright (3) describes two red clay layers at 16 and 17 m below datum that are associated with (overlying) layers of angular stones, although in his stratigraphic drawing (3) they appear to be at 15 and 16 m depth. He further notes that the partly alluvial deposits stop at 16 m below datum (3). Ewing (1) describes the same two angular stone/clay complexes (Complex 3 and 4), but places them at 15 and 16 m depth. Complex 3 is made up of a layer of angular stones (XXIV) and a layer of red clay (XXV). Complex 4 is composed in a similar way (i.e., Layer XXVI angular stones and layer XXVII red clay). In Ewing's (5) drawing of the stratigraphy, a depth of 16 m coincides with the boundary between stone complexes 3 and 4, which is 1 m below the start of the Upper Levalloiso-Mousterian layers. It also coincides with a significant faunal change including the disappearance of rhinoceros (which we ascertained can be placed in Layer XXV; see SI section 1). Thus, sample GrN-2579 probably comes from the boundary between Layers XXVI and XXV, perhaps more likely from the upper Layer XXV, as both Wright (3) and Vogel and Waterbolk (36) describe it originating from a clay substrate. Considered a minimum age, the date corresponds well with our minimum age estimation for Layer XXV, where the human fossil of Ethelruda was found (Tables S2.3, S2.5).

Table S2.3. List of all previous radiocarbon dates for Ksâr 'Akil. Layers after Ewing (5); dates in uncalibrated radiocarbon years. Note: the two dates in pink are the same date, but reported differently by different scholars.

Layer	Laboratory nr.	Date	+/-	Sample material	Reference
III	MC-410	24,400	900	Land snail	(38)
III	OxA-1791	23,170	400	Charcoal	(6)
III	OxA-1792	22,850	400	Charcoal	(6)
III	OxA-1793	22,020	360	Charcoal	(6)
III	OxA-1794	22,480	380	Charcoal	(6)
III	OxA-1795	22,850	380	Charcoal	(6)
V–VI	MC-1191	26,500	900	Charcoal	(6)
V–VI	OxA-1796	21,100	500	Charcoal	(6)
V–VI	OxA-1797	26,900	600	Charcoal	(6)
V–VI	OxA-1798	29,300	800	Charcoal	(6)
VII	OxA-1803	30,250	850	Charcoal	(6)
VII	OxA-19194	30,250	170	Charcoal	(37)
VIII	OxA-20875	30,640	160	*Nassarius gibbosulus*	(37)
VII–IX	GrN-2195	28,840	380	Shell	(36)
IX	OxA-1804	31,200	1300	Charcoal	(6)
IX	OxA-1805	32,400	1100	Charcoal	(6)
IX	OxA-20022	37,210	230	*Glycymeris* sp.	(37)
IX	OxA-20023	30,360	140	*Nassarius gibbosulus*	(37)
X	MC-1192	32,000	1500	Charcoal	(6)
X	OxA-25585	34,550	250	*Nassarius gibbosulus*	(37)

Table S2.3. Continued

Layer	Laboratory nr.	Date	+/-	Sample material	Reference
XII	OxA-20024	35,520	200	*Nassarius gibbosulus*	(37)
XV	OxA-20876	35,020	240	*Nassarius gibbosulus*	(37)
XVI	OxA-22665	36,040	240	*Nassarius gibbosulus*	(37)
XVII	OxA-X-2342-57	28,130	110	*Columbella rustica*	(37)
XVII	OxA-20877	36,270	240	*Glycymeris* sp.	(37)
XVII	OxA-22269	35,390	250	*Acanthocardia* sp.	(37)
XVII	OxA-20487	33,930	220	*Nassarius gibbosulus*	(37)
XVII	OxA-25652	33,300	230	*Columbella rustica*	(37)
XVII	OxA-20486	35,780	240	*Nassarius gibbosulus*	(37)
XVIII	OxA-X-2338-8	33,760	210	*Columbella rustica*	(37)
XVIII	OxA-25653	34,830	240	*Nassarius gibbosulus*	(37)
XVIII	OxA-20488	34,230	210	*Nassarius gibbosulus*	(37)
XIX	OxA-22664	35,510	240	*Nassarius gibbosulus*	(37)
XIX	OxA-X-2361-14	32,960	160	*Columbella rustica*	(37)
XX	OxA-20879	35,010	240	*Nassarius gibbosulus*	(37)
XXI	OxA-20025	36,390	210	*Nassarius gibbosulus*	(37)
XXII	OxA-25655	30,890	160	*Columbella rustica*	(37)
XXII	OxA-20880	34,940	200	*Nassarius gibbosulus*	(37)
XXII	OxA-22667	34,320	190	*Nassarius gibbosulus*	(37)
XXIII	OxA-20489	36,790	270	*Nassarius gibbosulus*	(39)
XXIII	OxA-20490	37,430	320	*Nassarius gibbosulus*	(39)
16 m	Gro-2574-75	44,400		Charcoal	(3)
XXV/(XXVI)	GrN-2579	43,750	1500	dark clay band	(36)
XXVIII	OxA-X-2361-17	33,810	180	*Ostrea* sp.	(37)
XXVIII	OxA-X-2361-23	35,900	400	*Ostrea* sp.	(37)
XXVIII	OxA-20491	39,310	330	*Ostrea* sp.	(37)
XXVIII A	OxA-25656	39,530	330	*Ostrea* sp.	(37)

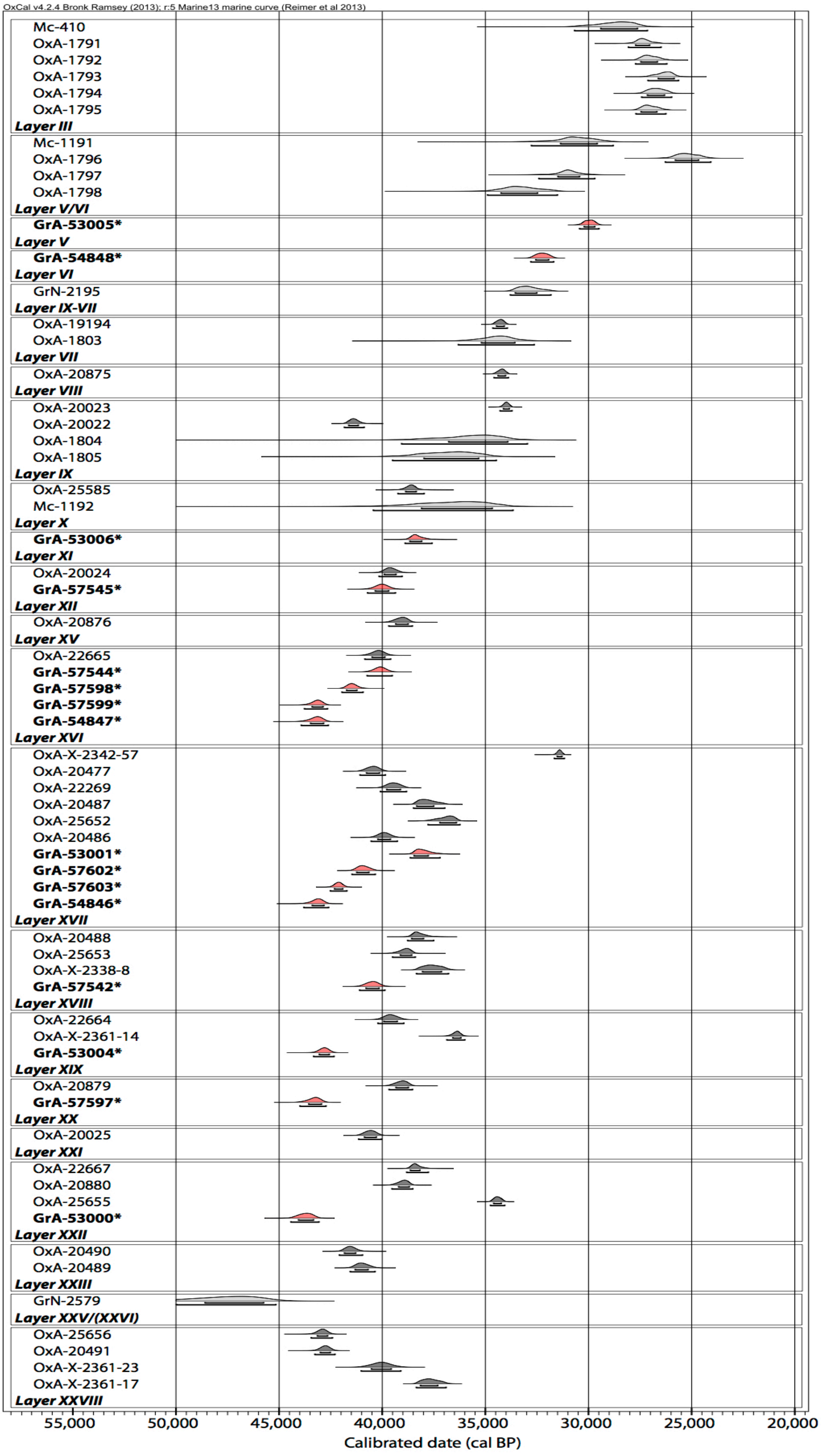


Figure S2.2. All age estimations for Ksâr 'Akil calibrated with OxCal 4.2.4 (32), dates of terrestrial samples with IntCal13 and those of marine samples with Marine13 calibration curve (31) using a delta R of 53 ± 43 for the eastern Mediterranean (33). Light grey: dates by Mellars & Tixier (6) and Vogel & Waterbolk (36); Dark grey: dates by Douka et al. (37, 39); Red: dates reported in this paper. Note: For date GrN-2195 on land snails of unknown species it was impossible to calculate an accurate reservoir effect and was calibrated with IntCal13 (100% atmospheric). It is displayed only for completeness, but the calibrated age should be treated with caution.

Bayesian modeling

Calibration and Bayesian modeling of the AMS radiocarbon dates on *P. turbinatus* shell carbonates was conducted using the Marine13 calibration curve (31) and the OxCal 4.2.4 software package (32). Our samples were corrected for reservoir age, which is the offset between the atmospheric and the ocean carbon ratio that results of the upwelling of old carbon from deep oceanic water. The pre-industrial global mean reservoir correction (R) is about 400 years. Additionally, local fluctuations in upwelling intensity (ΔR) are used to fine-tune marine calibration corrections. We used a ΔR value of 53 ± 43 as an estimation for the Eastern Mediterranean by Reimer & McCormac (33).

Several Bayesian models were constructed using prior information regarding the provenience of the samples within the general stratigraphy. In the first model, all samples of a layer were placed in a phase. Boundaries were inserted at points where changes in lithic technology were observed (6, 14), allowing for the potential time elapsed between these technologically distinct periods. In general, the OxCal agreement index (A_model) of the resulting model should have a similar value as the agreement indices of individual measurements and should in any case not be below 60% (31). An outlier analysis was carried out as described by Bronk Ramsey (40). Initially, all measurements were given a prior outlier probability of 0.05. In subsequent steps, dates that were in poor agreement with the model resulting from the previous step were given increasingly higher prior outlier probabilities until the resulting Bayesian model and individual measurements had acceptable agreement indices (i.e., A_model and A_ind >60). The resulting model (hereafter model 1) has an agreement index A_model of 118.2% and has identified samples XVI (2–3), XVII (1, 3–4) and XVIII as outliers (see main text Fig. 1 for the model; Fig. S2.3 for the model configuration; Table S2.4 for the outliers; Table S2.5 for the calibrated and modeled age ranges). To test the robustness of our model we ran several variants of the outlier analysis (i.e., varying the prior outlier probabilities) all resulting in similar outcomes. In an alternative model, we considered that the young age of sample XVIII might indicate a gap in time between layers XIX and XVIII and separated the EUP in two phases. Kuhn et al. (14) identified a change in lithic technology (see Table S1.1) at this point in the sequence, between what they call UPII A (Layers XX-XIX) and UPII B (XVIII-XIV). Similarly, Hoojier (11) described a shift in fauna, between his Phase 3 (Layers XXV-XIX) and phase 4 (Layers XVIII-X). The resulting model (hereafter model 2; Fig. S2.4; Table S2.6) has the same amount of outliers (i.e., 6 namely samples: XVI (1, 3–4), XVII (1–2, and 4)) as model 1, but it shows a lower overall agreement index (A_model) of 83.5%. The main difference between these two models is the duration of the EUP (or UP IIA-B) and the modeled age for layer XVII, in which Egbert was found. The implications of these differences and a more detailed evaluation of models 1 and 2 are discussed below.

```
Plot()
 {
  Outlier_Model("General",T(5),U(0,4),"t");
  Sequence()
  {
   Curve("Marine13","Marine13.14c");
   Delta_R("LocalMarine",53,43);
   Date("Ethelruda");
   Boundary("start dated IUP");
   Phase("Layer XXII")
   {
    R_Date("GrA-53000", 40550, 350);
    {
     Outlier(0.05);
    };
   };
   Boundary("end dated IUP");
   Boundary("start Ahmarian");
   Phase("Layer XX")
   {
    R_Date("GrA-57597", 40040, 340);
    {
     Outlier(0.05);
    };
   };
   Phase("Layer XIX")
   {
    R_Date("GrA-53004", 39390, 330);
    {
     Outlier(0.05);
    };
   };
   Phase("Layer XVIII")
   {
    R_Date("GrA-57542", 36290, 240);
    {
     Outlier(1.00);
    };
   };
   Phase("Layer XVII")
   {
    R_Date("GrA-54846", 39850, 340);
    {
     Outlier(0.05);
    };
    R_Date("GrA-57603", 38260, 260);
    {
     Outlier(0.50);
    };
    R_Date("GrA-57602", 36730, 240);
    {
     Outlier(0.50);
    };
    R_Date("GrA-53001", 34090, 220);
    {
     Outlier(1.00);
    };
    Date("Egbert");
   };
   Phase("Layer XVI")
   {
    R_Date("GrA-54847", 39910, 370);
```

```
   {
    Outlier(0.20);
   };
   R_Date("GrA-57599", 39890, 310);
   {
    Outlier(0.20);
   };
   R_Date("GrA-57598", 37320, 270);
   {
    Outlier(0.50);
   };
   R_Date("GrA-57544", 35960, 230);
   {
    Outlier(0.50);
   };
  };
  Boundary("end Ahmarian");
  Boundary("start UP");
  Phase("Layer XII")
  {
   R_Date("GrA-57545", 35880, 260);
   {
    Outlier(0.05);
   };
  };
  Phase("Layer XI")
  {
   R_Date("GrA-53006", 34310, 230);
   {
    Outlier(0.05);
   };
  };
  Phase("Layer VI")
  {
   R_Date("GrA-54848", 28810, 130);
   {
    Outlier(0.05);
   };
  };
  Boundary("end UP");
  Boundary("start EPI");
  Phase("Layer V")
  {
   R_Date("GrA-53005", 26210, 130);
   {
    Outlier(0.05);
   };
  };
  Boundary("end EPI");
 };
};
```

Figure S2.3. Configuration (CQL code) of the Bayesian model presented in the main text (model 1).

Table S2.4. Prior and Posterior Outlier Probabilities results (model 1).

Element	Prior Outlier Probability	Posterior Outlier Probability	Model	Type
GrA-53000; 40550, 350	5	2	General	T
GrA-57597; 40040, 340	5	1	General	T
GrA-53004; 39390, 330	5	1	General	T
GrA-57542; 36290, 240	100	100	General	T
GrA-54846; 39850, 340	5	1	General	T
GrA-57603; 38260, 260	50	96	General	T
GrA-57602; 36730, 240	50	100	General	T
GrA-53001; 34090, 220	100	100	General	T
GrA-54847; 39910, 370	20	9	General	T
GrA-57599; 39890, 310	20	9	General	T
GrA-57598; 37320, 270	50	96	General	T
GrA-57544; 35960, 230	50	100	General	T
GrA-53006; 34310, 230	5	3	General	T
GrA-53006; 34310, 230	5	3	General	T
GrA-54848; 28810, 130	5	16	General	T
GrA-53005; 26210, 130	5	3	General	T

Table S2.5. Calibrated age ranges and results of age modeling for the Ksâr ʻAkil sequence (model 1).

Indices **A_{model}=118.2** **$A_{overall}$=115.4**	**Unmodelled age range (cal BP) 68.2%**		**Unmodelled age range (cal BP) 95.4%**		**Modelled range (cal BP) 68.2%**		**Modelled range (cal BP) 95.4%**		**Individual Agree-ment**	**Conver gence**
	from	**To**	**From**	**to**	**from**	**to**	**from**	**to**		
end EPI Boundary					**30236**	**28853**	**30521**	**26032**		**98.7**
GrA-53005; 26210, 130	30205	29697	30430	29495	30213	29688	30490	29455	101.9	99.8
Phase Layer V										
start EPI Boundary					**30944**	**29783**	**32361**	**29500**		**99.2**
end UP Boundary					**32392**	**30809**	**36634**	**29866**		**96.2**
GrA-54848; 28810, 130	32553	31933	32794	31690	32706	31936	38432	31557	88.4	96.7
Phase Layer VI										
GrA-53006; 34310, 230	38658	38090	38888	37587	38665	38069	38938	37488	102.3	99.6
Phase Layer XI										
GrA-57545; 35880, 260	40336	39690	40710	39363	40285	39626	40681	39234	101.9	99.7
Phase Layer XII										
start UP Boundary					**41865**	**39988**	**42862**	**39726**		**99.4**
end Ahmarian Boundary					**43092**	**42760**	**43318**	**41253**		**99.3**
GrA-57544; 35960, 230	40391	39802	40731	39519	43112	42816	43342	41611	99.3	99.7
GrA-57598; 37320, 270	41725	41231	41950	40931	43111	42815	43322	41467	100	99.6
GrA-57599; 39890, 310	43397	42871	43770	42654	43107	42821	43337	41672	117.4	99.7
GrA-54847; 39910, 370	43471	42846	43925	42615	43107	42821	43337	41677	121.5	99.7
Phase Layer XVI										
Egbert					43162	42896	43383	42658		99.7
GrA-53001; 34090, 220	38455	37770	38635	37202	43162	42896	43395	42642	103	99.7
GrA-57602; 36730, 240	41236	40650	41464	40338	43163	42896	43393	42641	99.9	99.7
GrA-57603; 38260, 260	42310	41916	42514	41716	43164	42895	43378	42143	99.7	99.5
GrA-54846; 39850, 340	43390	42829	43798	42601	43157	42900	43314	42731	130.4	99.5
Phase Layer XVII										
GrA-57542; 36290, 240	40782	40157	41095	39875	43205	42943	43359	42794	99.4	99.6
Phase Layer XVIII										
GrA-53004; 39390, 330	43049	42569	43325	42339	43221	42956	43374	42820	75.8	99.7
Phase Layer XIX										
GrA-57597; 40040, 340	43561	42949	43986	42728	43244	42969	43415	42841	125.6	99.9
Phase Layer XX										
start Ahmarian Boundary					**43270**	**42975**	**43467**	**42843**		**99.7**
end dated IUP Boundary					**43781**	**43177**	**44205**	**43003**		**99.9**
GrA-53000; 40550, 350	44056	43336	44426	43071	44075	43428	44444	43204	107.9	99.9
Phase Layer XXII										
start dated IUP Boundary					**44578**	**43477**	**46094**	**43195**		**99.4**
Ethelruda					49386	45866	49390	44289		99.6

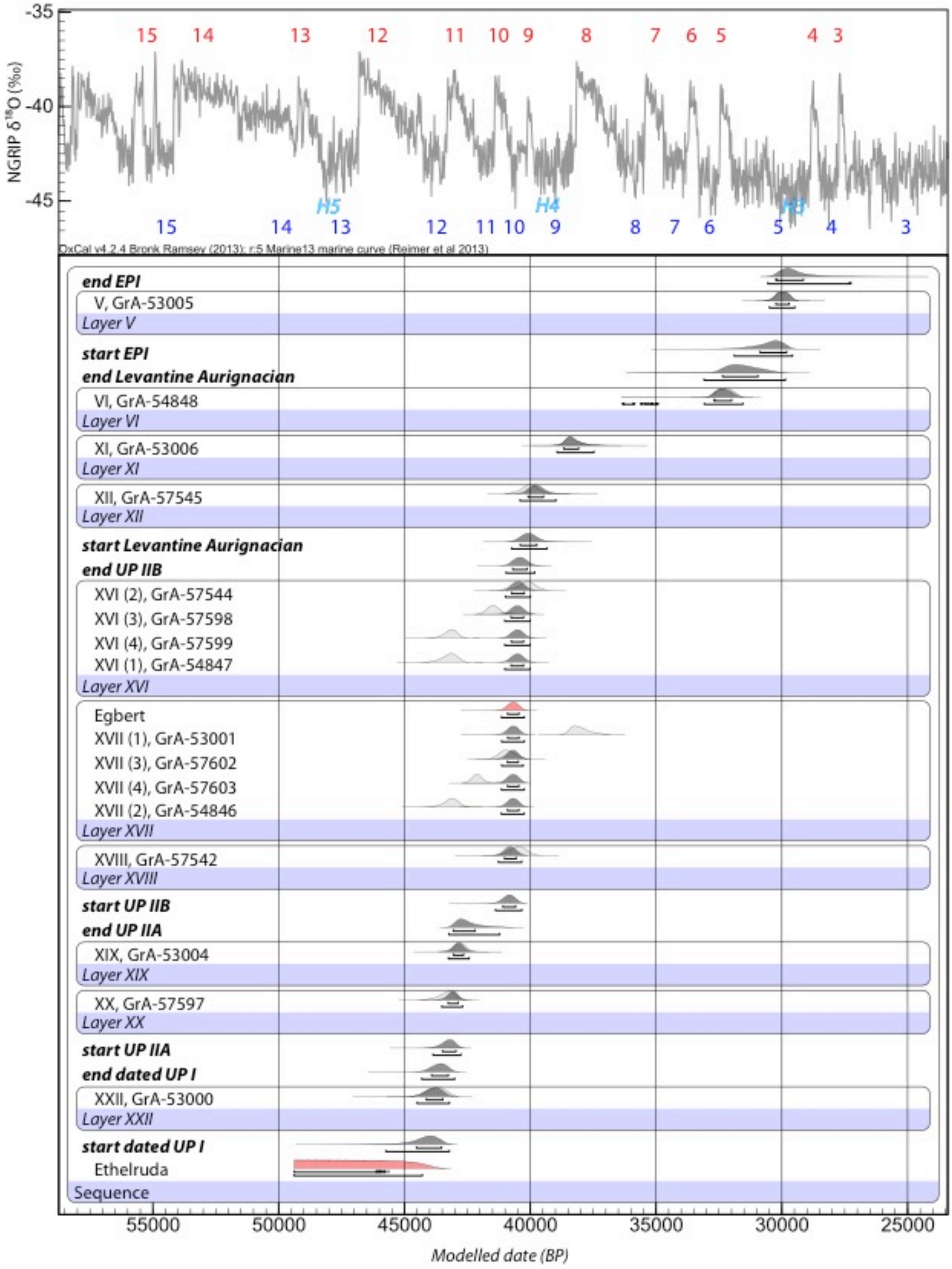


Figure S2.4. Bayesian age model 2 for the Ksâr 'Akil sequence using OxCal 4.2.4 (32). The radiocarbon dates are calibrated using the Marine13 dataset (31) and ΔR value for the eastern Mediterranean (33). Light grey: individual radiocarbon likelihoods, dark grey: posterior probability distributions, red: PDFs for Ethelruda and Egbert's layers. The modeled data is compared with the NGRIP $\delta^{18}O$ curve (grey), Greenland Interstadials (GIS; red) and Stadials (GS; blue) and Heinrich Events (H3-5; light blue).

Table S2.6. Calibrated age ranges and results of age modeling for the Ksâr 'Akil sequence (model 2).

Indices **A_{model}=84.2** **$A_{overall}$=88.1**	**Unmodelled age range (cal BP) 68.2%**		**Unmodelled age range (cal BP) 95.4%**		**Modelled range (cal BP) 68.2%**		**Modelled range (cal BP) 95.4%**		**Individual Agreement**	**Convergence**
	from	**To**	**From**	**to**	**from**	**to**	**from**	**to**		
end EPI Boundary					**30232**	**29143**	**30557**	**27254**		**98.5**
GrA-53005; 26210, 130	30205	29697	30430	29495	30235	29714	30495	29485	101.9	99.8
Phase Layer V										
start EPI Boundary					**30867**	**29813**	**31890**	**29579**		**99.7**
end Levantine Aurignacian Boundary					**32355**	**30949**	**33093**	**29854**		**99.3**
GrA-54848; 28810, 130	32553	31933	32794	31690	32687	31997	36335	31550	95	99.1
Phase Layer VI										
GrA-53006; 34310, 230	38658	38090	38888	37587	38668	38075	38933	37468	101.6	99.6
Phase Layer XI										
GrA-57545; 35880, 260	40336	39690	40710	39363	40083	39475	40408	38979	89.8	99.7
Phase Layer XII										
start Levantine Aurignacian Boundary					**40397**	**39742**	**40743**	**39331**		**99.8**
end UP IIB Boundary					**40696**	**40127**	**40960**	**39822**		**99.5**
GrA-57544; 35960, 230	40391	39802	40731	39519	40737	40239	40986	39996	67.9	99.6
GrA-57598; 37320, 270	41725	41231	41950	40931	40764	40264	41015	40004	88.7	99.6
GrA-57599; 39890, 310	43397	42871	43770	42654	40757	40265	41012	40008	101.2	99.7
GrA-54847; 39910, 370	43471	42846	43925	42615	40761	40267	41012	40010	101.6	99.7
Phase Layer XVI										
Egbert					40901	40449	41147	40237		99.7
GrA-53001; 34090, 220	38455	37770	38635	37202	40898	40446	41140	40235	103.3	99.7
GrA-57602; 36730, 240	41236	40650	41464	40338	40910	40475	41135	40281	95.4	99.7
GrA-57603; 38260, 260	42310	41916	42514	41716	40904	40450	41149	40237	100.1	99.7
GrA-54846; 39850, 340	43390	42829	43798	42601	40905	40451	41154	40241	101.5	99.7
Phase Layer XVII										
GrA-57542; 36290, 240	40782	40157	41095	39875	41024	40559	41271	40338	82.4	99.7
Phase Layer XVIII										
start UP IIB Boundary					**41085**	**40583**	**41383**	**40334**		**99.1**
end UP IIA Boundary					**43056**	**42197**	**43231**	**41213**		**99.6**
GrA-53004; 39390, 330	43049	42569	43325	42339	43054	42649	43253	42428	112	99.9
Phase Layer XIX										
GrA-57597; 40040, 340	43561	42949	43986	42728	43266	42869	43515	42690	109.2	99.9
Phase Layer XX										
Start UP IIA Boundary					**43486**	**42955**	**43864**	**42756**		**99.9**
end dated UP I Boundary					**43923**	**43257**	**44312**	**43003**		**99.8**
GrA-53000; 40550, 350	44056	43336	44426	43071	44134	43478	44497	43213	105	99.8
Phase Layer XXII										
start dated UP I Boundary					**44520**	**43529**	**45741**	**43216**		**99.2**

Ethelruda	49386	45634	49390	44287	99.6

Wide age ranges, as seen in Ksâr 'Akil Layers XVI and XVIII, are often encountered in organic samples dating to the Levantine IUP and EUP, even when up-to-date pre-treatment methods have been used (37, 41). This complicates the construction of chronologies for these types of sites, especially the ones like Ksâr 'Akil where the dated material comes from a museum collection rather than a freshly excavated sequence. This is evident from the high number of outliers in both considered Bayesian models (and also visible in the work of Douka et al. (37)). To determine which of the models is more accurate it is imperative to evaluate the integrity of individual dated samples. In general, the occurrence of outliers may result from 1) unsuccessful removal of contaminants in the sample, 2) post-depositional relocation (e.g., bioturbation), 3) burning, 4) excavation and/or curation errors, or 5) measurement errors. We have tried to avoid contamination by only using well-preserved and unburned specimens. We have also looked for potential markers of bioturbation or other forms of post-depositional, excavation, and curation errors like differential color and structure of adhering sediment in comparison to other specimens of the layer. Despite these efforts a small possibility always remains that intrusive material was wrongly included (e.g., perhaps sample XVII (1)). Wide age ranges might further be caused by (a) a long duration, of, e.g., the Early Ahmarian as suggested by model 2, (b) a disturbance of the later EUP (i.e., UP IIB; Layers XVIII-XIV) deposits by the occupants, or (c) an erosional event related to complex 2 (Layers XV-XIV; see SI section 1) resulting in extensive time-averaging of layer XVI specifically.

Regarding the age of the Early Ahmarian and its associated AMH fossil known as Egbert, our data suggest a time window of 43,400–37,800 cal BP or more likely 43,400–40,700 cal BP (excluding the XVII (1) date). The main difference between the two Bayesian models is the duration of the EUP (or UP IIA-B) between 43,300–43,100 cal BP (model 1) and between 43,500–40,100 cal BP (model 2), which also affects the estimated age for the Egbert fossil. Based on solely the output of the models it is hard to argue for/against either model. We therefore, investigated the integrity and taphonomic history of all individual samples through a study of intra-crystalline protein diagenesis and oxygen isotope analysis (see below).

Model 1 has a higher agreement index and is therefore probably more likely than model 2, but both models have the same number of outliers. While models are built on different prior information (e.g., different division in phases), both models consider samples XVII (1), XVII (4) and XVI (3) outliers. The age-estimation for the EUP in model 1 relies most on samples XX, XIX, XVII (2), XVI (1) and (4), whereas the UP IIB of model 2 draws heavily on samples XVIII, XVII (3), and XVI (2). Regarding sample XVIII, mean annual $\delta^{18}O_{shell}$ values (see below) indicate that the mollusk did not secrete its shell in the same temperature regime, and therefore did not live at the same time, as the other Ahmarian samples (with the exception of XVII (1), that is considered to be an outlier by both models). We therefore doubt that sample XVIII is indicative for the Ahmarian as a whole. As the corresponding AMS date is younger than most of the other Ahmarian samples coming from the layers above XVIII this date is more likely intrusive from higher up in the sequence rather than being residual from an older colder climatic phase. Further, sample XVII (3) does not fall entirely in the same diagenetic trajectory as the other samples (especially visible in the distribution of the amino-acid valine (THAA vs FAA; see discussion below and Fig. S2.6). This is an indication of open system behavior, and therefore the diagenetic integrity of this sample can be questioned.

We therefore argue that model 2, relying on two problematic dates (XVIII and XVII (3)), should be considered highly unlikely. This, in turn, implies that the Ahmarian at Ksâr ‘Akil falls between 43,300 cal BP and 42,800 cal BP. The remains of Egbert are most likely from Layer XVII, as reported by the original excavator (1, 9). However, attempts to reconstruct Egbert’s provenience from excavation notes and drawings have variously argued for an origin of the fossil from Layers XVI to XVIII (43), placing Egbert anywhere in these Early Ahmarian deposits. These uncertainties do not affect the modeled age for Egbert significantly due to the overall short time window modeled for the Early Ahmarian Layers XVI to XVIII in our model 1 (i.e., 43,200–42,800 cal BP).

During the Bayesian modeling, we used the “Date” function in OxCal to calculate probability distribution functions (PDF) for the age of the human fossils. In model 1, the date function provides a PDF of 43,200–42,900 cal BP (68.2% probability) for Egbert. Regarding the most likely age of Layer XXV’s AMH human remains, known as Ethelruda, the lack of datable material from this layer and those directly above and below hampers precise age estimation. The date of the overlying IUP Layer XXII (i.e., > 44,100 cal BP) and the modeled start of the dated IUP (which has consistently been modeled to 44,600–43,500 cal BP in both models), nevertheless, provide *termini ante quem* for Ethelruda. The PDF for Ethelruda’s layer provided by the “Date” function of OxCal extends beyond the end of the Marine13 calibration curve, but its upper limit of 45,900 cal BP provides a minimum age for the fossil. This minimum age fits well with the conventional radiocarbon date GrN-2579, probably from Layer XXV or the boundary of Layers XXV and XXVI (see discussion above).

Discussion of the dating approach in relation to other chronologies of Ksâr ‘Akil

The largest discrepancies between our attempt to date the human occupation of Ksâr ‘Akil and those of others occur in the lower part of the chronology and are provided by Douka et al. (38). They obtained AMS dates for 26 beach-collected shells of the taxa *Ostrea edulis, Glycymeris* sp., *Acanthocardia* sp., *Nassarius gibbosulus,* and *Columbella rustica.* They provided two Bayesian models, one similar to our approach assigning phases to individual layers (with 11 outliers) and one with the dates grouped per broader archeological phase (9 outliers). Similar to our set of radiocarbon dates, those of Douka et al. also have wide age ranges for the EUP/Ahmarian layers (36,000–28,000 BP) and for the IUP layers (i.e., 37,000–31,000 BP) (38). However, our age determinations are up to 4000 years older for the IUP and up to 3000 years older for the EUP (Fig. S2.2). These discrepancies in age estimations heavily influence any conclusions drawn regarding the start and duration of the IUP and EUP at Ksâr ‘Akil, the first occurrence of modern humans in the Levant in relation to their first arrival in Europe, and the validity of the Levantine corridor hypothesis. The reasons behind the observed dissimilarity are currently unclear and further investigations are needed. The two studies used shells of different taxa that were used for different purposes by humans and that have different taphonomic histories. In addition, the samples were subjected to different pretreatment protocols and were dated in different radiocarbon laboratories. In the following text, we describe the potential effects of both approaches on the radiocarbon results in an effort to ascertain the causes of observed discrepancies.

Sample selection: Rationale

Our study selected *P. turbinatus,* which was gathered alive to be eaten by Paleolithic humans, while the species selected by Douka et al. (37) were collected empty from active or fossil beach deposits to be used as tools and ornaments. Exposure to different taphonomic environments could explain the observed divergence between our dates and those published by Douka et al. (37). Active beach deposits are known for the temporal mixing or time-averaging effect they have on mollusk shell death assemblages (43–45). Shells might have undergone several burial and exhumation cycles in active beach deposits before they were picked up by humans. This process can continue for several thousands of years (44–46). Additionally, species that burrow in sandy substrates, like Glycymeridae, Acantocardidae, and Nassariidae, might be buried in sub-littoral sediments for periods of hundreds to thousands of years before they are washed ashore and are incorporated in active beach deposits (47). Therefore, individual shells from beached death assemblages or thanatocoenoses could have died thousands of years apart. These time-averaging processes would result in identical or older ages for beach-collected shells in relation to live-collected specimens and, although using beached specimens introduces a considerable uncertainty, this does not explain the inconsistency in age-estimations observed.

Post-mortem beach-collected shells would have additionally been exposed to a series of marine taphonomic processes, such as beach erosion or bioerosion (e.g., boring sponge damage). These taphonomic processes can heavily impact shell preservation and may have altered shell structure or made it more liable to post-depositional diagenesis. Abrasion and bioerosion result in pitting and fragmentation, which in turn enhance surface weathering (e.g., smoothing and decalcification). Decalcification is characteristic of shells subjected to diagenesis and also occurs in shells damaged by heat exposure. In the Ksâr ʻAkil mollusk assemblage, decalcification that cannot be attributed to heating (i.e., no evidence of discoloration and/or heat cracks) is evident in 23.8% (n=355) of the beach collected species, but only in 0.2% (n=1) of *P. turbinatus* used in this study (Table S2.7). Therefore, *P. turbinatus* was likely less affected by diagenetic alterations than beach collected taxa.

Table S2.7. Decalcification observed macroscopically in species used for radiocarbon dating. Note: decalcification attributed to damage by heat exposure (i.e., that was accompanied by traces of discoloration, heat cracks and/or potlids) is excluded.

Species	NISP	n decalcified	% decalcified
Phorcus turbinatus	452	1	0.2
Acanthocardia tuberculata	66	7	10.6
Columbella rustica	429	80	18.7
Glycymeris sp.	299	99	33.1
Nassarius gibbosulus	696	169	24.3
total beach collected	1490	355	23.8

Post-mortem carbonate recrystallization is known to be the main cause for the introduction of younger carbon resulting in younger radiocarbon ages (39, 48, 49). Generally, this diagenesis results in the replacement of the more soluble aragonite by the more stable calcite. Busschers et al. (27) have demonstrated that, under saline conditions, microbial activity can also result in aragonite-to-aragonite substitutions. They further suggest that this phenomenon and the inherent introduction of young ^{14}C in the shells explain the recent (MIS 3) radiocarbon dates they obtained for Eemian (MIS 5e) North Sea mollusks. Eliminating contamination in shell carbonates is therefore problematic.

Ante-mortem incorporation of old carbon in shell carbonates is normally caused by mixing of sea surface waters with older oceanic carbon brought up by upwelling currents. The divergence between atmospheric and marine ^{14}C, known as reservoir effect (R), has been measured and modeled (50) and can be corrected for. Local fluctuations in old carbon mixing occur and ΔR values for the Mediterranean Sea have been estimated to fine-tune the correction method (33, 51, 52). Hogg and Higham (53) have suggested that some intertidal marine species have enriched ^{14}C values compared to those of subtidal taxa. They argue that this is due to the intertidal species being exposed to the air (and atmospheric carbon) at low tides. If one corrects for a full marine environment in such cases, dates will be too young. However, shell growth does generally not occur when mollusks are out of the water (54). Minor growth lines that represent daily periods of non-growth are visible in the inner nacreous layer (Fig. S2.5 A–C) (55). This makes it unlikely that incorporation of atmospheric carbon is a significant source of contamination. Moreover, for the eastern Mediterranean, Boaretto et al. (51) see no relation between reservoir age and water depth or species (see also (56)). Precipitation of old carbon on rocky shore species by exposure to freshwater input from rivers in limestone or calcareous geological settings is another potential source of contamination (57). Limestone substrates do occur in the Lebanese coast and hinterland where Ksâr 'Akil is located. *P. turbinatus* is less tolerant to temperature and salinity changes than other species of the genus living in the Eastern Mediterranean (58, 59). As a result, it lives relatively low in the intertidal zone and is only found in rock pools that are regularly flushed out by seawater (21, 22, 59), avoiding localities where freshwater rivers or streams flow into the sea (59). We therefore assume that so-called hard-water effects do not have a major influence on the carbonate composition of *P. turbinatus.* Precipitation of old carbon onto shells after deposition in the rock shelter sediments could also occur and would result in a superficial diagenetic alterations and/or a carbonate crust adhering to the shells surface. Both the Oxford and Groningen pre-treatment protocols chemically etch the outer surface of the samples to remove these potential secondary carbonates.

In addition, it has been suggested that mollusks that graze on rocky shores may incorporate old carbon from the substrate while foraging (60–62). Small rock particles including old carbon can be abraded by the radulae of mollusks and are subsequently ingested with its food. This phenomenon may have affected radiocarbon dates on *Patella* spp. from the Iberian Peninsula, making them older that their true age (61). The radulae of the species used in our study, *Phorcus* sp., however, are described as "as soft as a brush" (i.e., Moh's scale 2.0–2.5), while radulae of *Patella* sp. are harder "like a shovel" (i.e., Moh's scale 4.0–4.5) (60, 63). Therefore, using *P. turbinatus* for dating reduces to a minimum the likelihood of obtaining older ages due to potential uptake of old carbon. Furthermore, fluctuations in ΔR values for intertidal rocky shore taxa measured in the eastern Mediterranean (i.e., *Patella caerulea* and *Phorcus* (*Osilinus*) *turbinatus*) are small, i.e., in the order of 200 years (33, 51). Calibration of our radiocarbon dates using either extreme ΔR value resulted in identical age estimations. As mentioned above, Boaretto et al. (51) found no correlation between $\delta^{13}C$ or ΔR values and water depth or shell environment, which would be observable when any of these potential ante-mortem contaminants played a significant role in carbonate biomineralization.

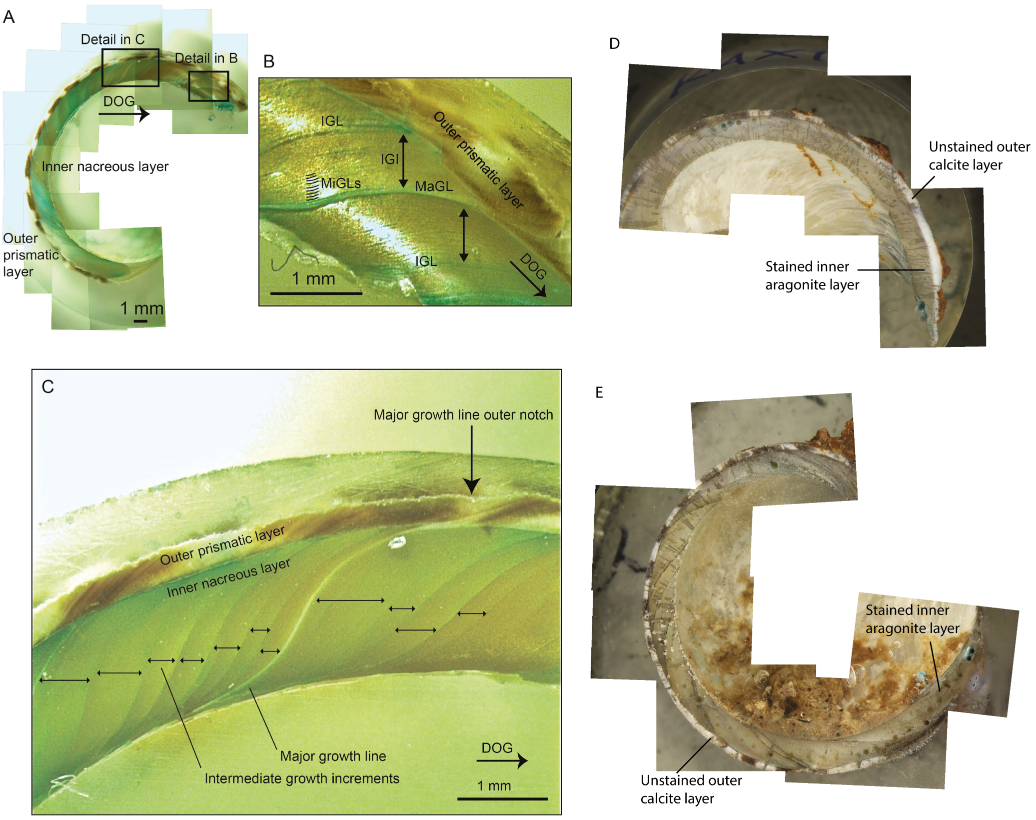


Figure S2.5. The microstructure of *Phorcus turbinatus* shell in cross section. The section is cut parallel to the direction of growth (DOG): A: Shell stained with Mutvei's solution to enhance visibility of growth increments. The whole outer whorl with outer prismatic later and inner nacreous layer is visible. B: Detail showing minor growth lines (MiGLs) deposited daily, intermediate growth increments (IGI) and intermediate growth lines (IGL) at fortnightly resolution, and a major growth line (MaGL) indicating an annual growth increment. C: Detail showing major growth line in the nacreous layer corresponding to major growth line outer notch in the prismatic layer. D and E: Shells from layer XI and XVII (1) respectively immersed in Feigl's solution for 20 minutes. The inner layers are stained grey indicating that they are aragonite whilst the outer layers remain unstained indicating that they are calcitic.

Pre-treatment method

In Groningen, the samples were cleaned in a 4% HCl bath, removing the outer surface chemically so that possible secondary carbonate is removed. From this pretreated shell fraction, CO$_2$ gas is produced using concentrated H$_3$PO$_4$ (64). Douka et al. (37) used the CarDS (39, 57) pretreatment protocol to eliminate potential contamination. The CarDS (carbonate density separation) method is aimed at separating the aragonitic and calcitic carbonate components of the shell using organic liquids (i.e., Bromoform by Russo et al. (57) or polytungstates by Douka et al. (39)). The method is based on the assumption that diagenetic alterations mainly result in the recrystallization of secondary calcite and that high magnesium calcite and aragonite are mainly in primary state. Only the aragonitic fraction is used for radiocarbon dating. It is expected that non-pretreated samples will give younger ages rather than older ones (but see (57)). For Ksâr 'Akil, Douka et al. (39) obtained two dates on sample number Ka 51 (Layer XXIII), one date without CarDS pretreatment (OxA-20489: 36,790 ± 270 BP) and one with CarDS (OxA-20490: 37,430 ± 320). The CarDS method effectively separated most calcite from the aragonite; the original sample had 80% calcite and the CarDS sample 7%. The pretreatment method in this case results in a slightly older age, but overlaps with the non-pretreated sample at the 2σ level (see Table S2.3) (39). The non-pretreated sample is still ~4000 radiocarbon years younger than our date of Layer XXII (36,790 ± 270 years BP and 40,550 +350/-310 years BP, respectively). It is therefore unlikely that the CarDS pretreatment method causes these age discrepancies.

AMS radiocarbon laboratory

Both studies dated marine shells, but at different radiocarbon laboratories. The standard graphitization process and AMS protocols in both laboratories are practically identical. The CO_2 is reduced to C (graphite powder) by H_2 gas using Fe powder as a catalyst (65). The graphite powder is pressed into targets, which were placed in the sample carousel of the ion source of the AMS. The AMS system measured the isotopic ratios $^{14}C/^{12}C$ and $^{13}C/^{12}C$ of the graphite (66).

The dated event

The approach followed by both studies is similar in that it aims to date evidence of human activities as proxies for site occupation. Douka et al. (37) obtained their dates from ornamental shells with the objective of dating site occupation and “symbolically mediated” behavior (*sensu* (67)). We used *P. turbinatus,* brought to the site for consumption, to date shellfish exploitation and site occupation. However, our approaches differ when it comes to the time elapsed between the dated event and the so-called “target” event (68). The dated event is in both cases the time at which the ^{14}C was incorporated in the carbonate structure of the shell. Excepting post-mortem diagenetic changes, this occurs during shell growth i.e., during the life of the mollusk. The target event is what we want to date: the site occupation. With shell ornaments and tools, the mollusk may have been dead for a few years up to several millennia before the empty shell was collected by humans, whereas for consumed shellfish, death occurred at the site where the mollusk was eaten at the time of occupation. In addition, the “use-life” is also quite different. Given that the shells of *P. turbinatus* were likely discarded immediately after the mollusk had been consumed, their “use-life” would have been short and penecontemporaneous to site occupation. Empty shells, transformed into tools and ornaments, could have potentially been used for a relatively long time. By dating food remains, the dated event and target event are nearly identical, while in the case of shells used for utilitarian purposes, a gap of unknown duration exists between the death of the mollusk and its collection, as well as between its initial use and final deposition. Thus, we argue that dating molluskan species collected for consumption offers a more precise chronological estimate of site occupation. It also avoids dating shells that were subject to a marine taphonomic environment and inherent diagenetic changes as observed in macroscopic traces of decalcification of beached shells that were virtually absent in live-gathered taxa.

In summary, when radiocarbon dating shell carbonates, potential contamination with foreign carbon cannot be excluded. The main sources of contamination and the hardest to eliminate are post-mortem diagenetic processes that alter the mineral structure of shells. Methods for detecting diagenesis (e.g., macroscopic observations, Feigl solution, XRD), however useful, do not reveal potential carbon contamination by secondary aragonite, nor does the CarDS pretreatment method eliminate it. The effect of contamination by admixture with younger carbon increases with sample age and has a greater impact on AMS dates than on conventional dates (69). Therefore, it is preferable to date other organic materials (i.e., bone or charcoal) if available. In instances where such material is not available or poorly preserved, we argue it is essential to date the best-preserved shells and taxa with the least evidence and/or likelihood of taphonomic alterations. In addition, dating species collected for consumption reduces the time elapsed between the life of the mollusk (i.e., the dated event) and the time of deposition (i.e., target event) and thereby provides us with a more precise chronological estimate of human presence at the site. In this study, we used a range of methods for assessing the diagenetic integrity of the samples, including XRD, staining with Feigl solution (see Fig. S2.5 D and E for examples), and biomolecular techniques (AAR) for evaluating closed-system behavior of the intra-crystalline proteins retained in the shell. The reasons for the discrepancies between the Douka et al. (37) chronology are currently unresolved, however the graphitization and AMS measurement methods at Groningen and Oxford are nearly identical and it is unlikely that either of those causes the differences observed. Ante-mortem incorporation of old carbon during grazing is unlikely due to the softness of *P. turbinatus* radulae, as is incorporation of atmospheric carbon while it is out of the water due to the species' behavior in these stressful periods. Local fluctuations of the reservoir effect in the eastern Mediterranean and the range of ΔR values for various intertidal rocky shore taxa are small and do not seem to influence the calibration results. Both the Groningen and Oxford pretreatment protocol use chemical cleaning to remove potential contamination by secondary carbonates. Post-mortem alterations generally make shell seem younger as they record the time of δ^{14}C substitution. We used best preserved shell displaying the least evidence for diagenetic alterations, whereas Douka et al. (37) used shell with macroscopically visible diagenetic alterations (38). Diagenetic processes are not fully understood and in the light of the recently proposed aragonite – aragonite substitutions (27) it seems plausible that the CarDS method did not successfully eliminate all contaminants. We therefore argue that our older radiocarbon dates provide more accurate estimates of the true sample ages.

Intra-crystalline protein diagenesis (Amino Acid Racemization, AAR)

Introduction

Mollusk shells are biocomposites containing a fraction of proteins and other organics that play a role in the biomineralization process during the organism's life (70). Protein diagenesis is a complex network of breakdown reactions that occur after death: these include peptide bond hydrolysis, racemization, and amino acid decomposition (e.g., dehydration of serine to alanine). The rate of diagenesis is temperature- and time-dependent and provided that the effect of other environmental and taphonomic factors can be excluded or accounted for, the extent of breakdown can be used as a proxy for estimating relative age since death. Historically, the main diagenesis reaction used for geochronological purposes has been amino acid racemization (AAR), the interconversion between the L- and D- enantiomers of an amino acid, yielding a D/L value between 0 (in live organisms) and 1 (when the reaction has reached equilibrium in old fossil shells).

Recent advances in the method (71) emphasized that the isolation of an intra-crystalline fraction of proteins by strong oxidation (bleaching) offers a more robust system for geochronological applications, as this intra-crystalline fraction is shown to behave as a "closed system" in a range of biominerals, including some species of mollusk shells (71–75). Protein geochronology has its main application over the Quaternary, due to lack of resolution over younger timescales (e.g., compared to radiocarbon). However, a big advantage of the new methodology is that the analysis of multiple amino acids and two different fractions of amino acids (Total Hydrolysable Amino Acids, THAA, and Free Amino Acids, FAA) allows identification of potentially compromised samples (75–77).

Method

Phorcus turbinatus samples were prepared and analyzed at the NEaar (North East Amino Acid Racemization) facility at the University of York (UK). Bleaching and leaching (high-temperature) experiments to test the suitability of *P. turbinatus* for the new method of AAR dating were undertaken as part of a larger study and confirmed that *P. turbinatus* retains a stable fraction of intra-crystalline proteins, which behaves as a closed system under artificial diagenesis conditions. Sample preparation for this study followed a standard protocol, which includes a 48-h bleaching step to isolate the intra-crystalline fraction, as detailed for other mollusk taxa (71, 74). Amino acid analyses were performed by liquid chromatography (RP-HPLC) following the method of Penkman et al. (71). This allows the detection of the L- and D- enantiomers of 10 amino acids. Here, we focus on the amino acids Asx (aspartic acid/asparagine), Glx (glutamic acid/glutamine), Ala (alanine), and Val (valine).

AAR analyses were undertaken on 26 *P. turbinatus* shell specimens, of which 13 had been dated by radiocarbon. A single AAR sample was taken from 23 specimens, and 2 samples (biological replicates) were obtained from 3 specimens (KSAS11XII, KSAS10XVI and KSAS09XVIII), for a total of 29 individual AAR samples (NEaar ID, Table S2.8). Each AAR sample was split into two subsamples for the analysis of the THAA and FAA fractions (71), and each subsample was analyzed twice by RP-HPLC (analytical replicates). Procedural blanks and standard amino acid mixtures of known D/L and concentration were interspersed during each analytical run.

Results

Table S2.8. D/L values of hydrolyzed (THAA) and free (FAA) amino acids. Results are presented as the average and standard deviation of two analytical replicates for each sample. KSA ID is the reference number for the current study. NEaar ID is the reference number for the amino acid racemization analysis at the NEaar laboratory (University of York).

KSA ID	NEaar ID	Fraction	Asx D/L		Glx D/L		Ala D/L		Val D/L	
			Av	σ	av	σ	Av	σ	Av	σ
KSASV04	8700bF	FAA	0.633	0.003	0.515	0.001	0.670	0.002	0.256	0.011
KSASV04	8700bH*	THAA	0.440	0.004	0.300	0.002	0.435	0.005	0.129	0.006
KSASV03	8701bF	FAA	0.687	0.004	0.573	0.098	0.713	0.007	0.256	0.013
KSASV03	8701bH*	THAA	0.516	0.002	0.292	0.004	0.503	0.002	0.143	0.001
KSASV02	8702bF	FAA	0.640	0.000	0.661	0.010	0.667	0.001	0.289	0.003
KSASV02	8702bH*	THAA	0.417	0.001	0.299	0.024	0.405	0.001	0.124	0.006
KSASV01	8703bF	FAA	0.670	0.011	0.546	0.049	0.700	0.003	0.237	0.006
KSASV01	8703bH*	THAA	0.483	0.012	0.311	0.028	0.514	0.008	0.132	0.007
KSAS01V	8704bF	FAA	0.686	0.001	0.604	0.005	0.708	0.001	0.248	0.001
KSAS01V	8704bH*	THAA	0.495	0.006	0.292	0.045	0.513	0.002	0.135	0.005
KSASVI04	8695bF	FAA	0.754	0.002	0.586	0.015	0.784	0.000	0.240	0.001
KSASVI04	8695bH*	THAA	0.591	0.000	0.353	0.002	0.664	0.010	0.167	0.001
KSASVI03	8696bF	FAA	0.681	0.001	0.623	0.078	0.674	0.006	0.248	0.002
KSASVI03	8696bH*	THAA	0.488	0.001	0.273	0.004	0.480	0.003	0.144	0.002
KSASVI02	8697bF	FAA	0.586	0.003	0.782	0.010	0.793	0.002	0.819	0.030
KSASVI02	8697bH*	THAA	0.406	0.000	0.408	0.003	0.532	0.012	0.241	0.007
KSASVI01	8698bF	FAA	0.644	0.007	0.565	0.030	0.687	0.009	0.251	0.013
KSASVI01	8698bH*	THAA	0.477	0.005	0.278	0.002	0.485	0.004	0.132	0.001
KSAS08VI	8699bF	FAA	0.614	0.011	0.611	0.156	0.641	0.002	0.249	0.011
KSAS08VI	8699bH*	THAA	0.446	0.007	0.267	0.029	0.441	0.003	0.118	0.000
KSASXI02	8692bF	FAA	0.734	0.014	0.576	0.026	0.789	0.003	0.254	0.009
KSASXI02	8692bH*	THAA	0.552	0.005	0.362	0.011	0.662	0.002	0.173	0.006
KSASXI01	8693bF	FAA	0.681	0.005	0.519	0.008	0.717	0.008	0.226	0.025
KSASXI01	8693bH*	THAA	0.494	0.000	0.291	0.009	0.529	0.009	0.135	0.001
KSAS02XI	8694bF	FAA	0.660	0.011	0.580	0.088	0.696	0.007	0.268	0.013
KSAS02XI	8694bH*	THAA	0.474	0.005	0.302	0.026	0.504	0.005	0.141	0.007
KSAS11XII	9344bF	FAA	0.631	0.001	0.456	0.003	0.712	0.000	0.251	0.002
KSAS11XII	9344bH*	THAA	0.479	0.001	0.271	0.001	0.511	0.001	0.139	0.000

Table S2.8. continued

KSA ID	NEaar ID	Fraction	Asx D/L		Glx D/L		Ala D/L		Val D/L	
			Av	σ	av	σ	Av	σ	Av	σ
KSAS11XII	9345bF	FAA	0.652	0.009	0.450	0.010	0.718	0.006	0.247	0.001
KSAS11XII	9345bH*	THAA	0.488	0.001	0.277	0.002	0.531	0.001	0.144	0.001
KSASXVI04	8687bF	FAA	0.729	0.003	0.559	0.052	0.815	0.005	0.224	0.015
KSASXVI04	8687bH*	THAA	0.572	0.000	0.355	0.009	0.704	0.016	0.190	0.013
KSASXVI03	8688bF	FAA	0.693	0.002	0.508	0.049	0.705	0.017	0.262	0.021
KSASXVI03	8688bH*	THAA	0.505	0.005	0.297	0.027	0.544	0.002	0.146	0.006
KSASXVI02	8689bF	FAA	0.719	0.010	0.531	0.020	0.734	0.014	0.272	0.021
KSASXVI02	8689bH*	THAA	0.532	0.002	0.335	0.004	0.578	0.002	0.181	0.022
KSASXVI01	8690bF	FAA	0.710	0.013	0.502	0.048	0.769	0.001	0.253	0.001
KSASXVI01	8690bH*	THAA	0.555	0.003	0.341	0.001	0.631	0.001	0.173	0.001
KSAS07XVI	8691bF	FAA	0.728	0.012	0.535	0.042	0.753	0.008	0.245	0.009
KSAS07XVI	8691bH*	THAA	0.571	0.006	0.342	0.012	0.663	0.010	0.179	0.006
KSAS10XVI	9346bF	FAA	0.599	0.001	0.451	0.003	0.663	0.000	0.270	0.003
KSAS10XVI	9346bH*	THAA	0.459	0.001	0.235	0.000	0.427	0.000	0.123	0.000
KSAS10XVI	9347bF	FAA	0.604	0.000	0.444	0.016	0.669	0.001	0.273	0.006
KSAS10XVI	9347bH*	THAA	0.462	0.001	0.241	0.001	0.448	0.002	0.131	0.004
KSASXVII03	8682bF	FAA	0.714	0.000	0.470	0.001	0.750	0.008	0.241	0.010
KSASXVII03	8682bH*	THAA	0.542	0.008	0.321	0.002	0.608	0.005	0.169	0.007
KSASXVII02	8683bF	FAA	0.665	0.005	0.348	0.005	0.697	0.000	0.262	0.011
KSASXVII02	8683bH*	THAA	0.480	0.001	0.240	0.007	0.498	0.015	0.147	0.010
KSASXVII01	8684bF	FAA	0.564	0.001	0.512	0.084	0.639	0.009	0.373	0.003
KSASXVII01	8684bH*	THAA	0.390	0.001	0.240	0.000	0.385	0.004	0.103	0.004
KSAS06XVII	8685bF	FAA	0.670	0.004	0.346	0.012	0.744	0.004	0.270	0.019
KSAS06XVII	8685bH*	THAA	0.486	0.004	0.276	0.004	0.594	0.017	0.158	0.000
KSAS03XVII	8686bF	FAA	0.694	0.001	0.439	0.004	0.701	0.004	0.223	0.005
KSAS03XVII	8686bH*	THAA	0.487	0.000	0.276	0.002	0.536	0.000	0.141	0.001
KSAS09XVIII	9348bF	FAA	0.667	0.000	0.455	0.005	0.705	0.001	0.241	0.003
KSAS09XVIII	9348bH*	THAA	0.514	0.000	0.288	0.000	0.541	0.003	0.159	0.001
KSAS09XVIII	9349bF	FAA	0.624	0.010	0.457	0.001	0.695	0.000	0.243	0.001
KSAS09XVIII	9349bH*	THAA	0.492	0.001	0.275	0.002	0.516	0.000	0.137	0.001

Closed-system behavior

Plots of THAA D/L versus FAA D/L values and THAA D/L versus THAA D/L values were used to assess the closed-system behavior of the samples analyzed. If the proteins analyzed (and their degradation products) are endogenous and have been undergoing diagenesis in a closed-system environment, then the two independent measures should be highly correlated, with compromised samples falling outside the trajectory of covariance (75, 77, 78). Typically, compromised samples are those where recrystallization of the mineral phase has occurred during diagenesis, and thus the intra-crystalline (closed) system might have incorporated exogenous amino acids or, more generally, the proteins might have been affected by local fluctuations of pH or other environmental factors (open-system behavior).

P. turbinatus samples from Ksâr 'Akil showed excellent closed-system behavior (Fig. S2.6, A–D: covariance between THAA and FAA fractions of the same amino acid; Fig. S2.6, E–F: covariance between THAA D/Ls of two different amino acids). Glx FAA D/Ls are variable due to the difficulty of detecting FAA Glx, as this amino acid is preferentially released as stable lactam. One exception is represented by sample NEaar 8697, which falls outside the main trajectory of diagenesis for all amino acids except Asx, thus suggesting open-system behavior for this sample (Fig. S2.6). However, this shell was not analyzed for AMS dating (Table S2.1) and therefore this result does not affect the interpretation of the radiocarbon chronology of the site.

Sample NEaar 8684 taken from *Phorcus turbinatus* specimen XVII (3) corresponds to ^{14}C date GrA-57602, a potential outlier (see section on AMS dates). Although not as clear an outlier as sample NEaar 8697, it falls at the lower boundary of the D/L distribution for Asx and Ala (Fig. S2.6 A,C,E,F) and outside the main distribution on a Val THAA versus FAA plot, although variable FAA Val D/L values are to be expected as the result of low FAA concentrations of the D-enantiomer (74).

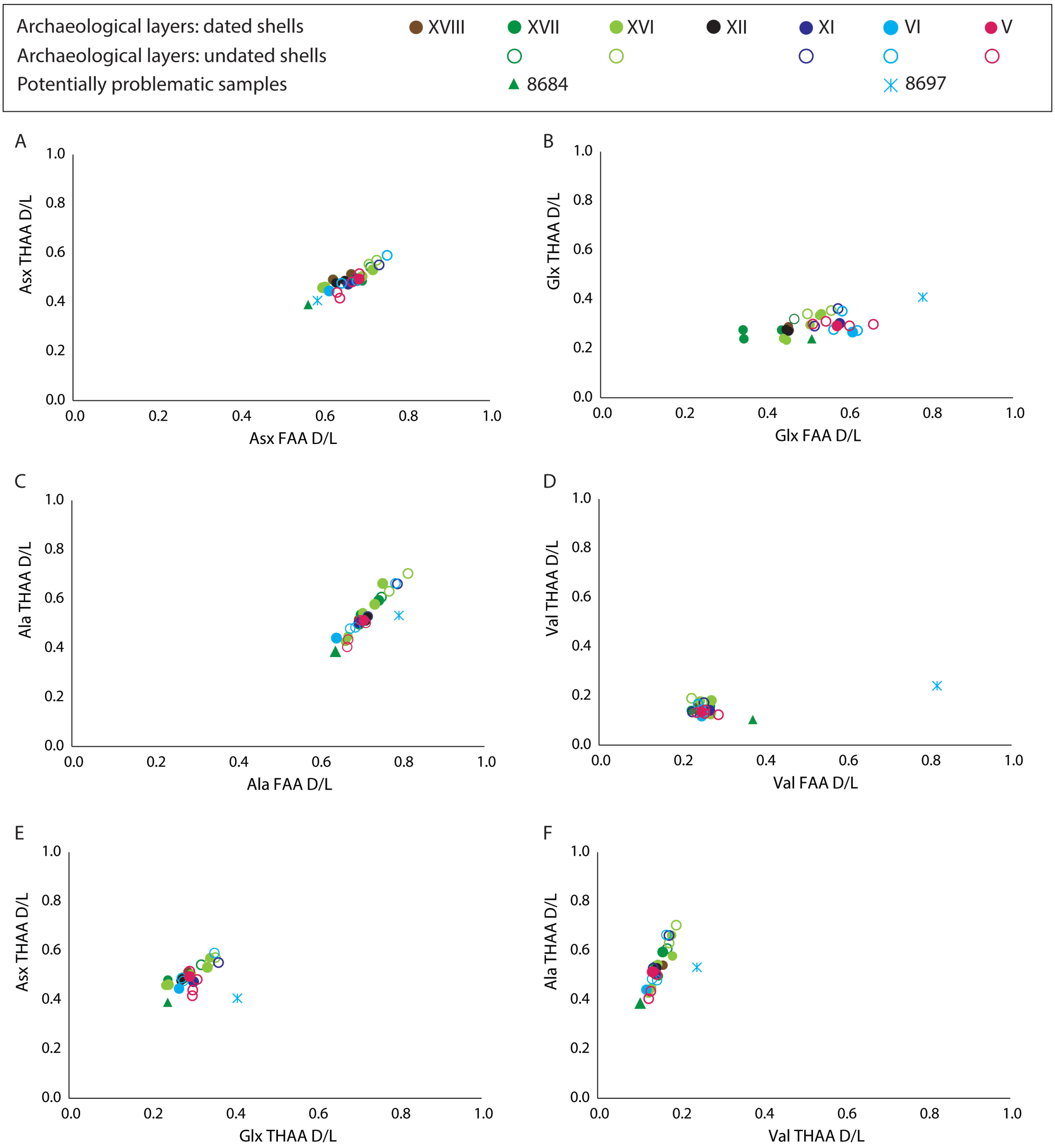


Figure S2.6. THAA vs FAA D/L plots for Asx (A), Glx (B), Ala (C), Val (D) and THAA vs THAA D/L plot for Asx vs Glx (E) and Ala vs Val (F). Note that most samples fall within a clearly defined trajectory of diagenesis, while sample 8697 is clearly highlighted as an outlier.

Natural variability

THAA D/L values for Asx, Glx, Ala, and Val show that the intra-layer variability (calculated as coefficient of variation, CV) is comparable to the overall site variability (Fig. S2.7). CVs of ~20% may be expected at site level, as recently found on a study on the intra-crystalline diagenesis of *Glycymeris* sp. in Mediterranean Last Interglacial raised beaches (75). Consequently, the resolution level of the method at this timescale (layers V–XVII, ca. 30–43 ka BP) is not sufficient to differentiate archeological layers and we did not attempt to use D/L values to resolve within-site ages.

Overall, the consistency of the AAR dataset supports no or very limited diagenetic post-depositional alteration for the shells analyzed in this study and used for radiocarbon and isotope analyses.

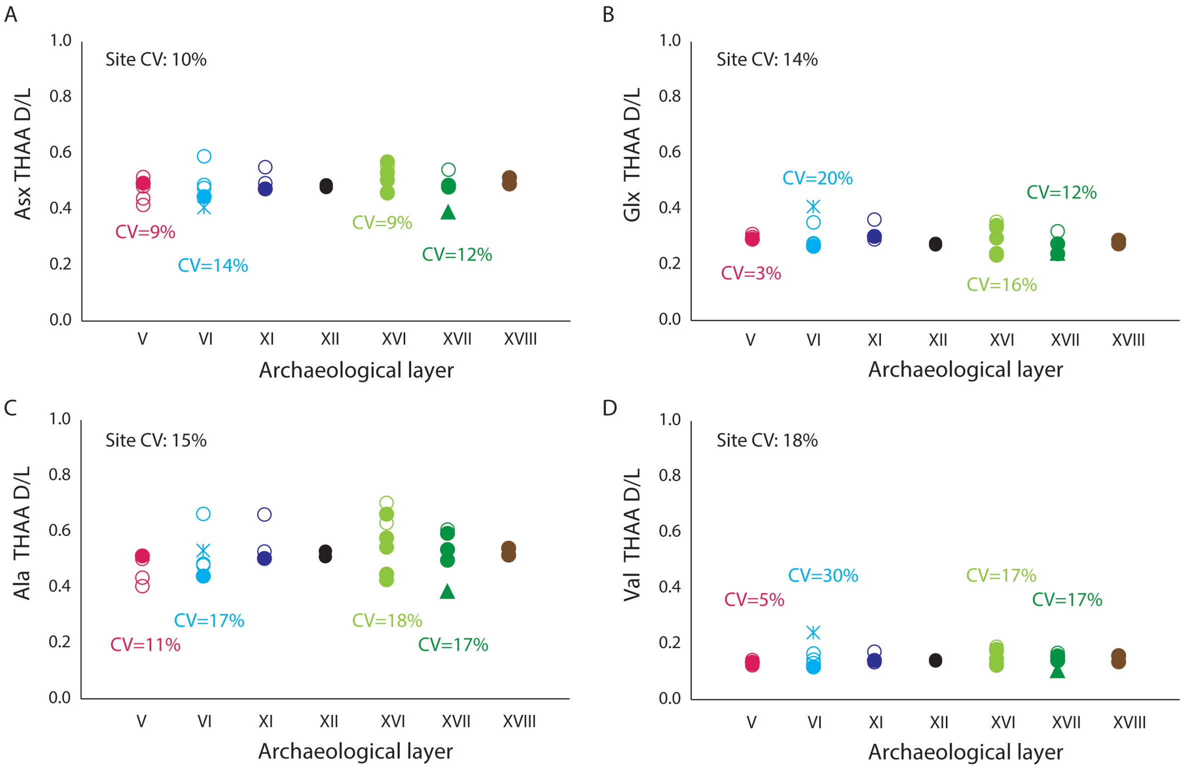


Figure S2.7. THAA D/L values for Asx (A), Glx (B), Ala (C) and Val (D) for each of the archeological layers considered in the AAR study. Radiocarbon-dated samples are represented by full circles. Potentially compromised samples are shown as triangle and cross. Note that the CVs for layers where the number of samples (n) is >5 is comparable to the CVs for the site, thus hampering resolution between layers.

Oxygen isotope analysis

Method

Oxygen isotope analysis was conducted on 13 specimens that were also dated with AMS radiocarbon and analyzed for AAR. Sampling was carried out at the Max Planck Institute for Evolutionary Anthropology. The sampling method was adopted after Mannino et al. (21) for *P. turbinatus*. A sequence of up to 40 samples was taken starting from the edge of the aperture along the periphery of the shell to obtain a full annual range of δ^{18}O values (Fig. S2.8). Sequential samples were taken from the midpoint of the aperture, because here the growth rate is highest and growth increments largest, thereby resulting in the least time-averaged results (21). The inner nacreous layer was sampled for oxygen isotope analyses, to avoid potential diagenesis, which is likely to have been most extensive in the outer prismatic layer, and because diagenetic alterations are more easily detectable in the aragonitic part of the shell (26). Therefore, the outer calcareous layer of the shell was initially removed with a hand drill along the periphery of the body whorl exposing the translucent nacreous layer. Then samples of carbonate powder (approximately 100 µg) were taken from the groove using a 0.5 mm drill bit. Care was taken to sample at equal depth at roughly 0.8-mm intervals starting at the midpoint of the aperture and continuing along the body whorl. Oxygen isotope analyses were undertaken at the Godwin Laboratory for Palaeoclimatic Research, University of Cambridge. Carbonate samples were transferred to exetainer vials and sealed with silicone rubber septa using a screw cap. The samples were flushed with CP grade helium, then acidified, left to react for 1 h at 70°C and then analyzed using a Thermo Gasbench preparation system attached to a Thermo MAT 253 mass spectrometer in continuous flow mode. Each run of samples was accompanied by 10 reference carbonates (Carrara Z) and two control samples (Fletton Clay). Carrara Z has been calibrated to the Vienna Pee Dee Belemite (VPDB) using the international standard NBS19. Results are reported in delta units (δ) in parts per mil (‰) with reference to the international VPDB standard and the precision is better than ± 0.10 ‰ for $\delta^{18}O$.

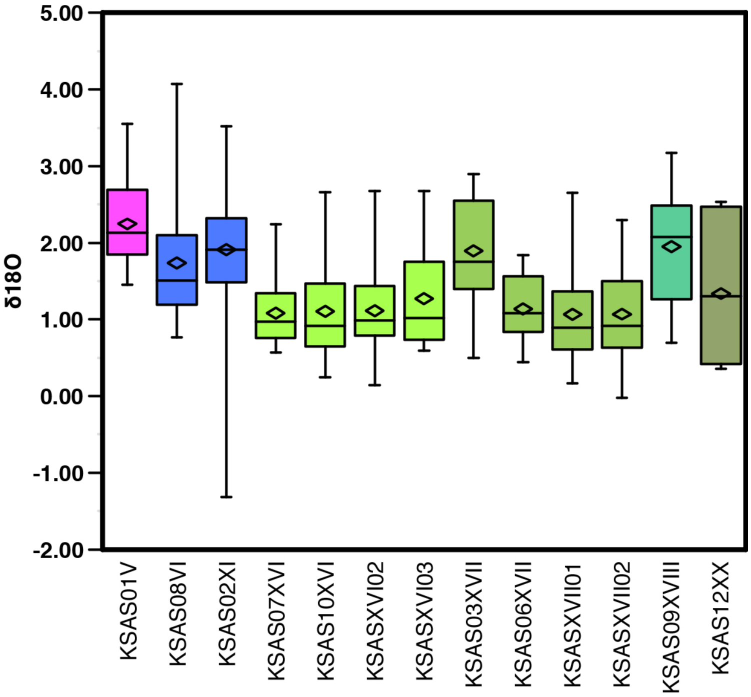


Figure S2.8. Boxplots showing ranges of $\delta^{18}O$ values in per mil (‰) for *P. turbinatus* per selected specimen. Early Upper Paleolithic (EUP): green, Upper Paleolithic (UP): blue, Epipaleolithic (EPI): pink. Boxes show the range of data points between the 25th and 75th percentile. Whiskers include extreme data points. Also shown are the median (horizontal bar) and mean (diamond) values.

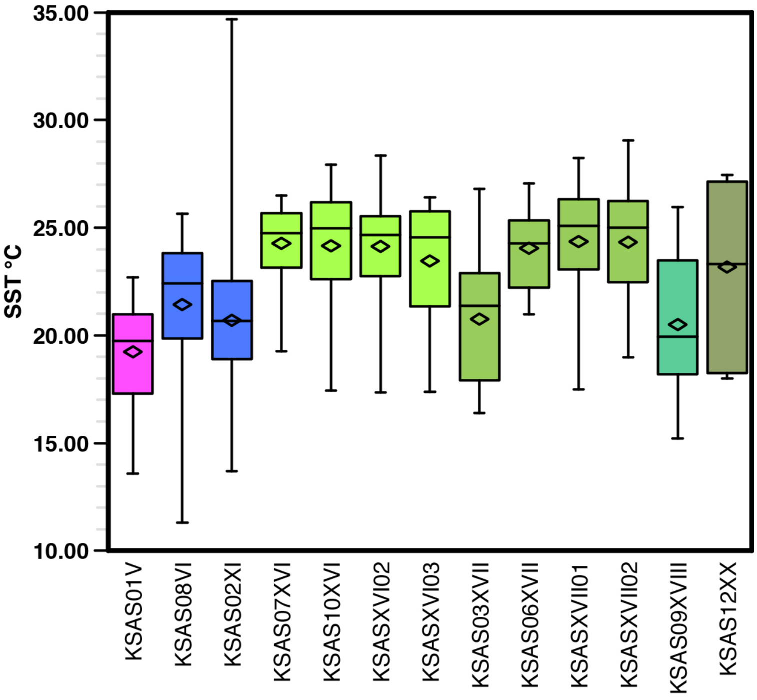


Figure S2.9 Boxplots showing ranges of sea surface temperature (SST) values in degrees Celsius (°C) for *P. turbinatus* per selected specimen. Early Upper Paleolithic (EUP): green, Upper Paleolithic (UP): blue, Epipaleolithic (EPI): pink. Boxes show the range of data points between the 25th and 75th percentile. Whiskers include extreme data points. Also shown are the median (horizontal bar) and mean (diamond) values.

The obtained $\delta^{18}O$ values were used to calculate SST estimates using the established aragonite-temperature equations of Grossman and Ku (79) with a conversion of VSMOW (used for $\delta^{18}O_{water}$ values) to VPDB by Dettman et al. (80) (Table S2.9; Fig. S2.9). Mollusk shell $\delta^{18}O$ is a function of the $\delta^{18}O$ of ambient water ($\delta^{18}O_{water}$) and temperature (80). For paleotemperature reconstruction an estimation of paleo $\delta^{18}O_{water}$ must be incorporated in the equation. Here, we used measured mean annual $\delta^{18}O_{water}$ values of 1.2‰ from a modern calibration study in Libya and incorporated an estimated correction for the glacial conditions during MIS 3. Paul et al. (81) showed that Mediterranean sea $\delta^{18}O_{water}$ was higher by 1.2‰ during the last glacial based on $\delta^{18}O$ pore water of Mediterranean marine sediment cores. The fact that the Ksâr 'Akil shells do not date to the height of the LGM introduces some unknown error into the SST calculations, as $\delta^{18}O_{water}$ fluctuated quite substantially during MIS 3. However, at this stage no other independent paleothermometers exist to compare with the $\delta^{18}O_{shell}$ analysis to provide a better understanding of local and temporal $\delta^{18}O_{water}$ fluctuations. Here, we used an approximation of sea $\delta^{18}O$ during MIS 3 of 1.0‰. This resulted in the following equation: SST°C = 20.6–4.34 ($\delta^{18}O_{shell\ (VPDB)}$ – (2.2–0.27)). Although the SST estimates might not be entirely accurate, our approximation allows evaluation of the relative differences in SST between shells and between archeological layers.

Table S2.9. Oxygen isotope analysis and Sea Surface Temperature estimates. KSA nr: sample ID; n: number of sequential samples; min: minimum $\delta^{18}O_{shell}$ value; max: maximum $\delta^{18}O_{shell}$ value; mean: mean $\delta^{18}O_{shell}$; SD: Standard deviation; range: range of $\delta^{18}O_{shell}$ values; SST rec: Paleo Sea Surface Temperature estimates in °C using the equation mentioned in the text (79–81).

KSA nr	**n of samples**	**Min** ($\delta^{18}O_{shell}$)	**Max** ($\delta^{18}O_{shell}$)	**Mean** ($\delta^{18}O_{shell}$)	**SD** ($\delta^{18}O_{shell}$)	**Range** ($\delta^{18}O_{shell}$)	**SST rec** **(°C)**
KSAS01V	40	1.45	3.55	2.25	0.57	2.10	19.2
KSAS08VI	40	0.77	4.07	1.74	0.80	3.30	21.4
KSAS02XI	40	0.51	3.52	1.91	0.84	3.01	20.7
KSAS07XVI	32	0.57	2.24	1.08	0.39	1.67	24.3
KSAS10XVI	35	0.24	2.66	1.11	0.60	2.42	24.2
KSASXVI02	40	0.15	2.68	1.11	0.56	2.53	24.1
KSASXVI03	30	0.59	2.67	1.27	0.62	2.08	23.5
KSAS03XVII	36	0.50	2.90	1.90	0.80	2.40	20.8
KSAS06XVII	30	0.44	1.84	1.14	0.42	1.40	24.0
KSASXVII01	30	0.17	2.65	1.07	0.59	2.48	24.4
KSASXVII02	40	0.29	2.30	1.07	0.56	2.01	24.3
KSAS09XVIII	40	0.70	3.17	1.95	0.67	2.47	20.5
KSAS12XX	15	0.35	2.53	1.34	0.86	2.18	23.2

These SST estimates were compared to present-day conditions (~23°C from AVHRR data for offshore Lebanon (82) and temperature estimations for Marine Isotope Stage 3 (83, 84)). Samples V, VI, XI, and XVII (1), and XVIII show comparably low mean annual SST values, ranging from 19.2°C to 21.4°C, and represent cooler phases throughout the Ksâr ‘Akil sequence. Warmer mean annual SSTs ranging between 23.2–24.4°C are represented by samples XVI (1–4), XVII (2–4), and XX.

Section 3: Comparison with early UP sites and human fossils

Early Upper Paleolithic sites

Table S3.1. Early Upper Paleolithic sites in Europe and the Levant mentioned in the text. IUP = Initial Upper Paleolithic; EUP = Early Upper Paleolithic; Proto-Aur = Proto-Aurignacian. Calibrated radiocarbon dates given at 68.2% probability level, * = weighted mean for TL dates (in years ago). ' = calibrated/modeled with Marine13; " = calibrated with IntCal13 (charcoal) and Marine13 (shell); ^ = calibrated with IntCal13; ~ = calibrated/modeled with Marine09. IntCal/Marine13 (31); IntCal/Marine09 (85).

site [country]	technocomplex	layer	Method	date cal BP (68.2%)	reference
Ksâr 'Akil	IUP	XXII	^{14}C	44,580–43,180'	this paper
Boker Tachtit [Israel]	IUP	1–4	^{14}C	>50,000–40,000	(86)
Üçağızlı I [Turkey]	IUP	I–F	^{14}C	45,890–37,060"	(15)
Manot [Israel]	IUP	area C Unit 7	^{14}C	>50,000	(87)
Üçağızlı I [Turkey]	EUP	E–B	^{14}C	42,840–32,180"	(15)
Ksâr 'Akil	EUP	XX–XIV	^{14}C	43,270–42,760'	this paper
Kebara Cave [Israel]	EUP	Units III–IV	^{14}C	46,000–34,000	(88)
Manot Cave [Israel]	EUP	area C Unit 7	^{14}C	46,000–42,000	(89)
Isturitz [France]	Proto-Aur	C4c4	^{14}C	42,300–41,700^	(90)
Riparo Mochi [Italy]	Proto-Aur	G	^{14}C	42,700–41,600~	(91)
Româneşti-Dumbrăviţa I [Romania]	Proto-Aur	GH3	TL	42,100–39,100*	(92)
Brno-Kejbaly [Czech Republic]	Bohunician	base Bohunice soil	^{14}C	47,410–44,420	(93)
Brno-Bohunice 2002 [Czech Republic]	Bohunician	Bohunice soil	TL	50,000–46,300*	(94)

Human fossils

Table S3.2. Human fossil remains mentioned in the text. IUP = Initial Upper Paleolithic. Method: laboratory number indicates a direct date; range: range of dates for the layer(s) from which the fossil(s) originate; PDF = modeled date for specimen. Calibrated dates given at 68.2% probability level. ‘ = calibrated /modeled with Marine13; ~ = calibrated/modeled with Marine09; * = average corrected age (arithmetic mean ±2σ), " = Calibrated with a combination of IntCal13/Marine13; ^ = Calibrated with IntCal13. IntCal/Marine13 (31); IntCal/Marine09 (84).

site [fossil]	**layer**	**technocomplex**	**method**	**date cal BP (68.2%)**	**reference**
Ksâr ‘Akil [Egbert]	XVII	Ahmarian	^{14}C (PDF)	43,270–42,760'	this paper
Ksâr ‘Akil [Ethelruda]	XXV	IUP	^{14}C (PDF)	> 45,870'	this paper
Cavallo [C]	E II–I	Uluzian	^{14}C (PDF)	44,000–43,000~	(95)
Cavallo [B]	E III	Uluzian	^{14}C (PDF)	45,010–43,380~	(95)
Manot [1]	na	no archeology	uranium-thorium	60,200–49,200*	(87)
Peştera cu Oase [1]	na	no archeology	^{14}C (GrA-22810)	40,040–37,610"	(96)
Üçağızlı I [6 teeth]	B–E	Ahmarian	^{14}C (range)	42,840–32,180"	(41, 97, 98)
Üçağızlı I [3 teeth]	F	IUP	^{14}C (range)	40,360–37,060"	(42, 97, 98)
Üçağızlı I [1 tooth]	H–I	IUP	^{14}C (range)	45,890–37,800"	(42, 97, 98)
Kostenki 14 [tooth]	IVb	unnamed IUP	^{14}C (GrA-15961)	41,490–40,920^	(99, 100)
Kostenki 14 [skeleton]	burial	no archeology	^{14}C (OxA-X-2395-15)	38,210–36,820^	(101)
Kostenki 1 [tibia & fibula]	III	Aurignacian	^{14}C (OxA-15055)	36,200–35,760^	(102, 103)
Kostenki 17 [tooth]	II	Spitsynian	^{14}C (GrN-12596)	42,800–39,700^	(104)
Ust’-Ishim [femur]	na	no archeology	^{14}C (range)	46,200–43,600^	(105)

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Chapter 4 • The Ksâr 'Akil chronology questioned

The paper that forms Chapter 3 (Bosch et al. 2015a) has been criticized by Douka et al. (2015). This chapter presents a short summary of their critiques and our published reply (Bosch et al. 2015b) as well as some additional remarks and suggestions as to how to move forward the debate on the chronology of Ksâr 'Akil.

4.1. Summary of Douka et al.'s critiques

Douka et al.'s (2015) criticisms revolve around two main points: (1) the way in which the Bayesian model was constructed; namely, they argue that it lacks consistent boundaries between phases and that we used incompatible approaches to determine the robustness of the model (i.e., using both agreement indices and outlier detection; and (2) they believe that our knowledge of the stratigraphy was inadequate.

The argumentation by Douka et al. (2015) is partly based on an inaccurate representation of our data set. For example, Douka et al. claim we did not build adequate boundaries into our model. Our boundaries in fact represent the archaeological layers and phases of the sequence as defined by the excavators (e.g., Ewing 1947) and by scholars who subsequently studied the material (for a summary, see Bergman and Goring-Morris 1987). However, excluding the lower boundary issue, to which is discussed below, the two models for the Ksâr 'Akil chronology presented by Douka et al. (2013) used the same amount of boundaries, especially in the lower part of the model where our age estimates diverge the most (Fig. 4.1). In other cases, they used even fewer, as their preferred model uses broader phases (e.g., MP, IUP) conflating—and mixing—the dates from different layers within a phase.

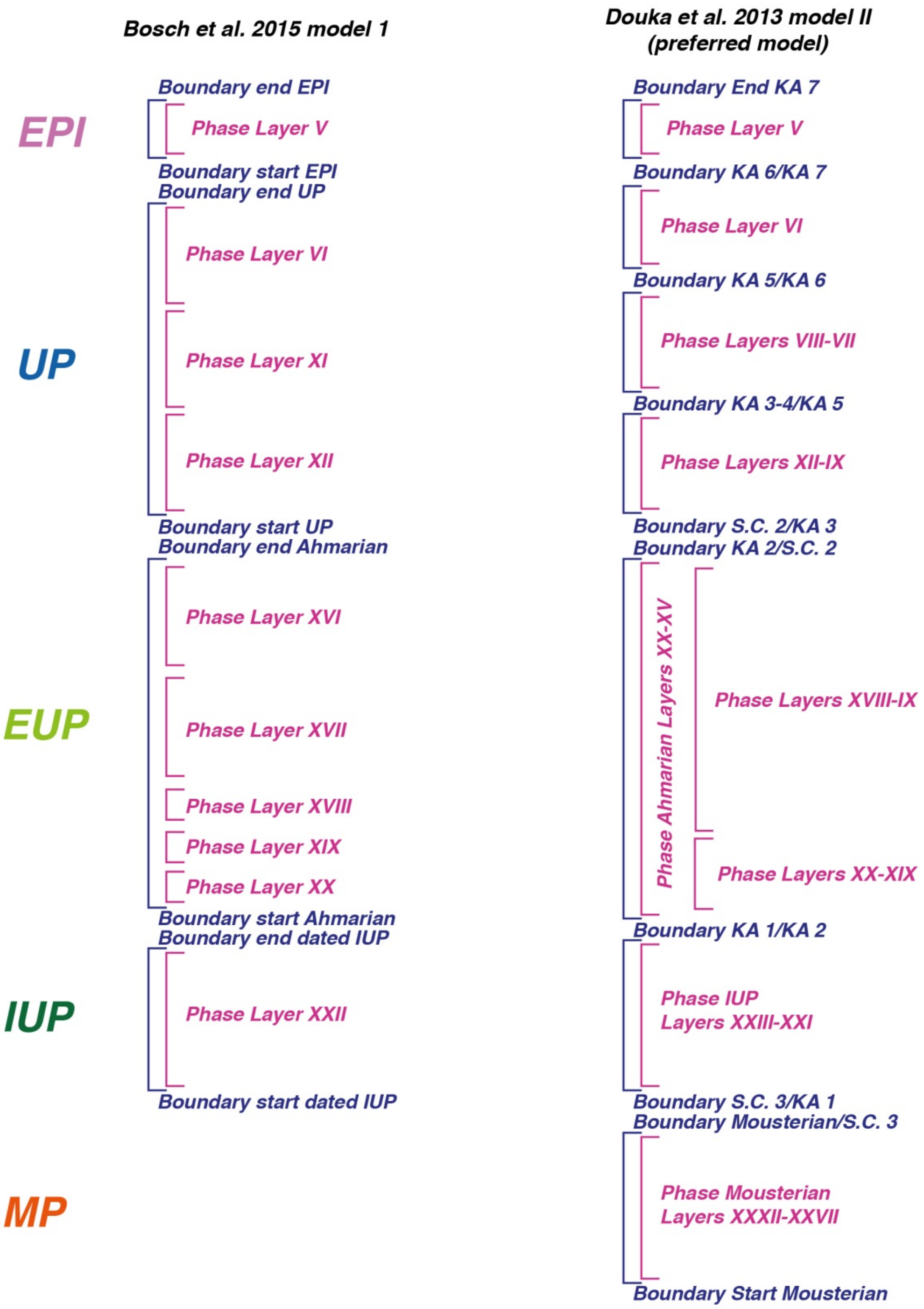

Figure 4.1: Schematic of the Bayesian models of Bosch et al. (2015a) and Douka et al. (2013) showing the placement of boundaries (blue) and phases (pink). The models used are Bosch et al.'s (2015a) Model 1 and Douka et al.'s (2013) preferred Bayesian Model II. Left column shows technocomplexes at Ksâr 'Akil as used by Bosch et al. (2015a). Abbreviations: MP: Middle Palaeolithic, IUP: Initial Upper Palaeolithic, EUP: Early Upper Palaeolithic (Early Ahmarian), UP: Upper Palaeolithic, EPI: Epipalaeolithic. Abbreviations used in Boundary and Phase labels after Bosch et al. (2015a) and Douka et al. (2013).

Douka et al. (2015) further state that we did not take into account the difficulties of correlating the material from the 1930s and 1940s excavations, even though we clearly state in the supplementary material (Chapter 3) that we did do so on the basis of unpublished lists made by the original excavators that have been used in several publications dealing with the Ksâr 'Akil fauna (e.g., Hooijer 1962; Kersten 1991). Moreover, Douka et al. state that six of our twelve dates between Layers XVIII and XVI are 100% outliers, where in fact there are only two. In addition, they ignore the fact that these specific dates were deemed as potentially compromised through other, independent types of analyses, namely amino acid racemization and oxygen isotope analyses. Importantly, they claim that if their critiques are taken into consideration the model would show significantly different results. However, newly created models taking Douka et al.'s critiques into consideration (i.e., one using only outlier detection, one using only the agreement indexes, and both with and without the dates from the 1940s) provide similar age estimations as in our original publication (Bosch et al. 2015a), especially for the IUP. These results, therefore, have reinforced our original conclusions rather than rejected them.

Another issue is the lower-boundary reference, which requires some explanation. Douka et al. have argued that the 'date call' for the Ethelruda fossil, which coincides with the start of the IUP, should have been constrained with a so-called lower boundary and that the lack of this lower boundary skews the oldest possible age of the fossil back in time, which is evident from Figure 1 of our paper (Bosch et al. 2015a). However, as there are no dates for the lowest part of the IUP, there are no chronological data that can back up placing such a boundary. Higham and Douka have argued that we should have either (1) placed a virtual boundary, i.e., a 'start of the undated IUP' boundary, or (2) taken into consideration available dates for the underlying Middle Palaeolithic part of the sequence. However, as we pointed out in our reply (Bosch et al. 2015b), the outcome of placing a virtual lower boundary not substantiated by chronological data would be an artefact of the modelling rather than representing the actual chronology. The second option would be to use dates from the underlying Middle Palaeolithic part of the sequence as practiced by Douka et al. (2013). Such an approach is questionable, as it uses of dates of uncertain provenience (i.e., unclear position in the stratigraphy) and/or dates obtained from potentially compromised samples (e.g., layers of brown sediment possibly of organic origin) (Vogel and Waterbolk 1963; Mellars and Tixier 1989). Further at our disposal are U-series dates that were reported to be potentially subject to open system behaviour (van der Plicht et al. 1989) and radiocarbon ages on highly diagenetically altered shells (Douka et al 2013a), which are by some deemed unreliable (Stutz et al. 2015). Therefore, neither of these 'solutions' is without problems.

Instead, we had chosen to place a boundary (our lowest) just below the lowermost IUP layer for which we have a date (i.e., Layer XXII) and place the 'date call' for the start of the IUP and Ethelruda below this boundary. To ensure that the lack of a lower constraint does not influence the actual model, we ran several versions with and without this 'date call' and found no effective difference in the rest of the model. In our opinion, the 'date call' with its unconstrained start reflects what we know: (1) the fossil should be older than the date for Layer XXII and (2) with currently available dates, we have no way of assessing a lower age constraint. Because of the assumptions underlying this type of Bayesian model, the calculated upper boundary for the Ethelruda fossil is placed two standard deviations from the age estimation of the modelled 'start of the dated IUP' (i.e., our lowermost boundary) (see Bronk Ramsey 2000; Steier and Rom 2000). This assumed time lapse between the two events seems plausible, as there are several layers culminating in roughly a metre of deposits that divide them. Moreover, because these data are solely used as a *terminus ante quem* in our paper—we claim that the start of the IUP should be prior to 45.9 ka cal B.P.—the lack of lower constraint does not alter our interpretations. So although it is true, as Douka et al. point out, that if the model is configured in this way, Bayesian statistics cannot resolve the lower end of the 'date call', it does not change our conclusions.

4.2 Reply to Douka et al.: Critical evaluation of the Ksâr 'Akil chronologies[1]

Our paper (Bosch et al. 2015a) proposes a new chronology for Ksâr 'Akil based on 16 accelerator mass spectrometry (AMS) determinations on shells. To minimize the possibility of dating diagenetically compromised samples, we conducted amino acid racemization analyses on the intracrystalline proteins, oxygen isotope analysis, and geochemical characterization of all dated shells. Our calibrated radiocarbon ages fit well with existing Levantine chronologies, but are up to 4,000 y older than Douka et al.'s (2013). Our paper explores several possibilities for this difference, whereas Douka et al. (2015) provide alternative explanations. They accept our radiocarbon ages as correct but question our sample selection and Bayesian modelling. Douka et al. (2015) question both the inclusion of samples from the 1940s excavations and our

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combined outlier analysis. Excluding the 1940s samples and running a manual outlier analysis (using 0.05 prior outlier probabilities without manual down-weighting) (Bronk Ramsey 2009) results in age ranges of 42.7–40.9 ka cal B.P. for the Egbert fossil and 44.9–43.6 ka cal B.P. for the start of the dated Initial Upper Paleolithic (IUP; Layer XXII). Thus, Egbert's age estimation is slightly younger than in our paper (Bosch et al. 2015a), but the age estimations for the IUP do not change, and they support our original conclusions. The date for the Ethelruda fossil found in Layer XXV was modelled without a lower constraint, thus generating an age estimate that may be skewed backward in time. As suggested by Douka et al. (2015), placing start and end boundaries for the undated IUP allows the model to constrain the lower boundary of Ethelruda's age range. We would not dispute that, but setting a lower constraint is problematic. Currently, there are no dates for the start of the IUP; thus, placing boundaries cannot be substantiated by any chronological data. Nonetheless, incorporating these boundaries in our model provides an age estimate for Ethelruda of 49.9–44.1 ka cal B.P., making it older than all European human fossils except Cavallo B [the context of which has been questioned (Zilhão et al. 2015)]. Douka et al. (2015) also propose including dates from lower in the sequence. We rejected this option, as all available dates are of uncertain provenience and/or obtained on compromised samples (Bosch et al. 2015a). Stutz et al. (2015) independently raised doubts on the Middle Paleolithic AMS dates by Douka et al. (2013), concluding that chemical diagenesis resulted in minimum ages. Moreover, excluding both the date function for Ethelruda and the constraining boundaries, the start of the dated IUP is 44.9–43.6 ka cal B.P., both with and without the 1940s samples. This provides a minimum age estimate for the underlying undated IUP deposits containing Ethelruda at their base. In conclusion, differences in the Bayesian models used do not appear to explain the divergence between our dates and those reported by Douka et al. (2013). Our data provide reliable estimates for modern humans and the IUP at Ksâr 'Akil and support our initial conclusions for an early chronology for modern humans in the Levant. This is in line with other Levantine datasets and is compatible with the Levantine corridor hypothesis.

4.3 Ways to move forward

At this point, it is important to also realise that a chronology based on Bayesian modelling is just that: a model. It gives a representation of the most parsimonious chronological interpretation and should be treated as a hypothesis not the ultimate truth. Attempts should be made, as we have done, to develop multimethod approaches using independent data sets to evaluate the probability that a model (Bayesian or otherwise) is correct rather than relying solely on approaches inherent to the modelling, e.g., outlier analyses or agreement indices.

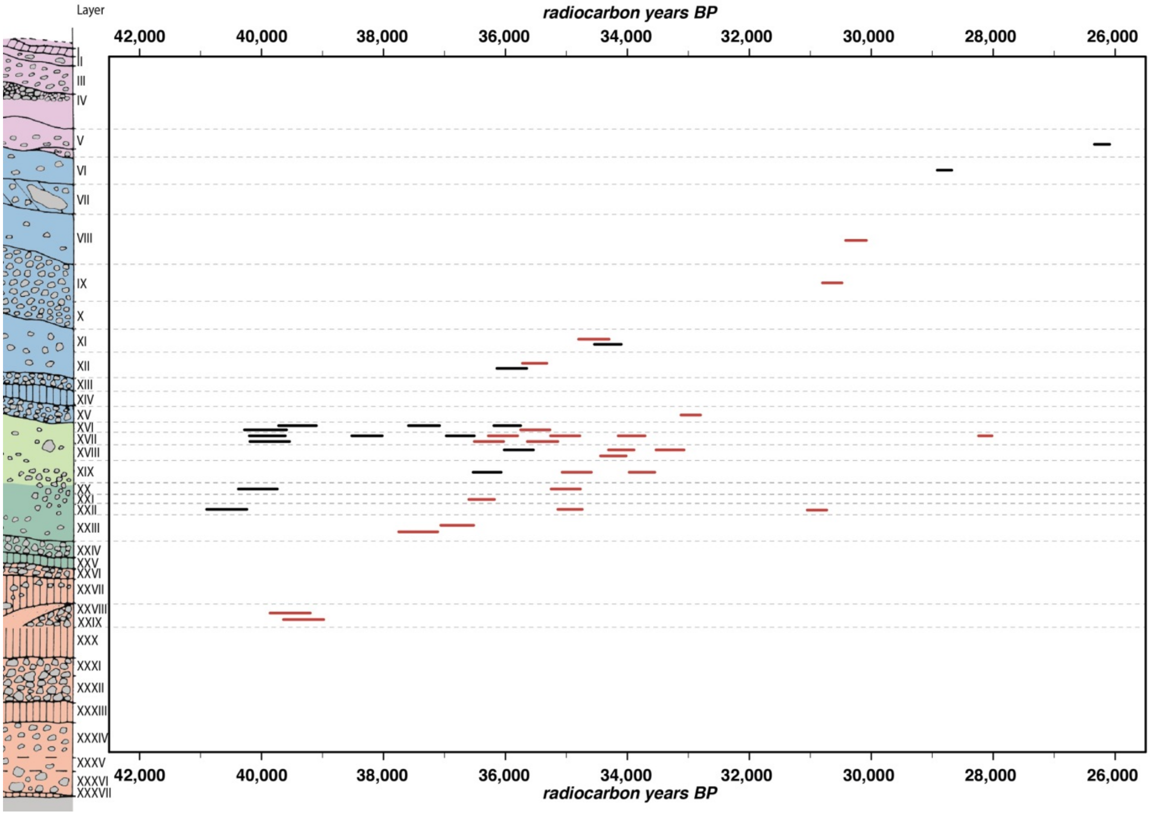

Figure 4.2: Radiocarbon determinations by Douka et al. 2013 (red) and Bosch et al. 2015a (black) for Ksâr 'Akil sorted by layer. Results show a one-sigma range (uncal BP).

The more important issue at hand, namely the substantial differences in radiocarbon determinations between the two published chronologies (Table 4.1; Fig. 4.2), remains unresolved. Our drastically different radiocarbon determinations, especially in the lower part of the sequence where our ages are up to 4000 radiocarbon years older, show that different pre-treatment and dating methods may hugely alter the results. Moreover, shell dates have been proven problematic in other studies. For example, at Üçağızlı I (Turkey) radiocarbon dates on shell are generally much younger than dates on charcoal (Kuhn et al. 2009; see also Mangerud 1972; Hogg and Higham 1998; Douka et al. 2010). In their reply, Douka et al. (2015) state that they deem our radiocarbon ages to be accurate; obviously, they think theirs are too, so why then do our chronologies diverge more and more the further back in time we go? After careful consideration of all steps of both our analyses, we concluded that differences between the two chronologies most likely have their origins in the pre-treatment methods and sample selection strategies (Table 4.2; see also Chapter 3 and Bosch et al. 2015a, Supplementary Information section 2). Specifically, we have reason to believe that the so-called CarDS method (Douka et al. 2010; Russo et al. 2010), which uses a heavy liquid to divide the to-be-dated aragonite from potentially intrusive (recrystallized) calcite in an effort to purify diagenetically compromised samples, might not be adequate to extract all contaminants (e.g., Busschers et al. 2014).

Furthermore, shells that are used as ornaments are usually collected from active beaches or fossilized beaches and have been exposed to marine taphonomic processes that damaged the shells and left them subject to diagenetic alterations. At present, we do not fully understand what is causing the divide in age estimations; therefore, at least for now, it might be best to avoid dating visibly taphonomically altered shells. The ways forward to resolve issues with dating shell, are (1) to further tease apart details in the pre-treatment methods and sampling strategies to better understand what is causing the different age estimates and ultimately overcome our methodological issues; (2) to determine what it is we want to date (i.e., the target event) and which selection strategy or dated event provides the closed approximation of the target event (Dean 1978); and 3) to develop methods to detect diagenetically compromised samples, for example, using amino acid racemization (e.g., Demarchi et al. 2013) and identifying carbonate substitution pathways under various post-depositional conditions (e.g., Busschers et al. 2014). It would also be valuable to explore the effects of burning on archaeological shells (e.g., Milano et al. 2016), as this process can potentially damage samples.

Table 4.1: Radiocarbon determinations for Ksâr 'Akil used by Douka et al. (2013) and Bosch et al. (2015a). Radiocarbon determinations are provided per layer and with laboratory reference number. * U-series dates from van der Plicht et al. (1989), ~ dates on the same shell, † dates from Mellars and Tixier (1989), ‡ dates from Vogel and Waterbolk (1963), § date from Wright (1962), ** dates by Douka et al. (2010).

Layer	Douka et al. 2013	Bosch et al.2015
V	26,500 ± 900 (MC-1191†)	26,210 ± 130 (GrA-53005)
	26,900 ± 600 (OxA-1797†)	
VI	29,300 ± 800 (OxA-1798†)	28,810 ± 130 (GrA-54848)
VII	30,250 ± 170 (OxA-19194) 30,250 ± 850 (OxA-1803†)	
VIII	30,640 ± 160 (OxA-20875)	
IX	30,360 ± 140 (OxA-20023) 31,200 ± 1300 (OxA-1804†) 32,400 ± 1100 (OxA-1805†)	
VII-IX	28,840 ± 380 (GrN-2195‡)	
X	32,000 ± 1500 (MC-1192†) 34,550 ± 250 (OxA-25585)	
XI		34,310 ± 230 (GrA-53006)
XII	35,520 ± 200 (OxA-20024)	35,880 ± 260 (GrA-57545)
XV	35,020 ± 240 (OxA-20876)	
XVI	36,040 ± 240 (OxA-22665)	35,960 ± 230 (GrA-57544) 37,320 ± 270 (GrA-57598) 39,890 ± 310 (GrA-57599) 39,910 ± 370 (GrA-54847)
XVII	28,130 ± 110 (OxA-X-2342-57) 33,300 ± 240 (OxA-20486) 33,930 ± 220 (OxA-20487) 35,390 ± 250 (OxA-22269) 36,270 ± 240 (OxA-20877)	34,090 ± 220 (GrA-53001) 36,730 ± 240 (GrA-57602) 38,260 ± 260 (GrA-57603) 39,850 ± 340 (GrA-54846)
XVIII	33,760 ± 210 (OxA-X-2338-8) 34,230 ± 210 (OxA-20488) 34,830 ± 240 (OxA-25653)	36,290 ± 240 (GrA-57542)
XIX	35510 ± 240 (OxA-22664) 32,960 ± 160 (OxA-X-2361-14)	39,390 ± 330 (GrA-53004)
XX	35,010 ± 240 (OxA-20879)	40,040 ± 340 (GrA-57597)
XXI	36,390 ± 210 (OxA-20025)	
XXII	30,890 ± 160 (OxA-25665) 34,940 ± 200 (OxA-20880)	40,550 ± 350 (GrA-53000)
XXIII	36,790 ± 270 (OxA-20489**) 37,430 ± 320 (OxA-20490**)	
XXV / (XXVI)	43,750 ± 1500 (GrN-2579‡)	
16 m	44,400 ± ? (Gro-2574-75§)	
XXVI B	47,000 ± 9000 (G-88174*)	
XXVIII (A)	39,310 ± 330 (OxA-20491~) 39,530 ± 330 (OxA-25656~)	
XXXII	51,000 ± 4000 (G-88177*)	

Table 4.2: Summary of potential factors that could influence radiocarbon determinations on the shells of Ksâr 'Akil, including the implication for our chronology and an assessment and rationale of the likelihood of its occurrence. For more detailed descriptions of the factors and rationale, please see Chapter 3 and Bosch et al. (2015a), Supplementary Information Section 2.

Factor	Implication	Assessment	Rationale
Sample selection			
Dating of beached shells I: Time elapse between the 'target-event' or human activity and 'dated event' or time of shell death	Younger	Unlikely	This does not fit the pattern seen (our dates would be younger than Douka et al.'s dates)
Dating of beached shells II: Increased liability of postmortem diagenesis due to increased incidence of damage due to taphonomic processes in active marine environments	Older	Likely	The incidence of damage due to taphonomic alterations is high in beached specimens and virtually absent in live-collected ones
Archaeological use life: Shell ornaments and tools are used for a longer amount of time than shellfish of which the shell is discarded after consumption	Younger	Unlikely	This does not fit the pattern seen (our dates would be younger that Douka et al.'s dates)
Ante-mortem: Over-compensation of reservoir effect in intertidal species	Older	Unlikely	*Phorcus turbinatus* does not grow its shell while out of the water at low tide due to stress, hence the discernable growth increments
Ante-mortem: Hard-water effect: due to precipitation of old carbon on shells by exposure to fresh water from a limestone environment	Older	Unlikely	*Phorcus turbinatus* has a limited tolerance for temperature and salinity changes and lives in the lower intertidal zone avoiding locations with fresh-water input
Ante-mortem: introduction of old carbon while foraging	Older	Unlikely	*Phorcus turbinatus* radulae are soft (Moh's scale: 2) and do not leave substantial damage on the rocks during foraging
Postmortem: Hard-water effect: due to precipitation of old carbon on shells by exposure to fresh water from a limestone environment	Older	Unlikely	Both the Groningen and Oxford sample cleaning protocols are sufficient to eliminate this source of contamination
Sample pre-treatment			
CarDS pre-treatment method does not eliminate all sources of diagenesis	Older	Likely	CarDS does not eliminate contamination in the aragonite fraction, e.g., aragonite-aragonite substitutions, which can occur in saline conditions
Radiocarbon measurement			
Groningen vs Oxford	Unknown	Unlikely	Measurement protocols at both laboratories are nearly identical

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Chapter 5 ・ The Ksâr 'Akil (Lebanon) mollusc assemblage: Zooarchaeological and taphonomic investigations

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The Ksâr ’Akil (Lebanon) mollusc assemblage: Zooarchaeological and taphonomic investigations

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ABSTRACT

Shells of marine molluscs exploited by prehistoric humans constitute archives of palaeoecological and palaeoclimatic data, as well as of human behaviour in coastal settings. Here we present our investigations on the mollusc assemblage from Ksâr ’Akil (Lebanon), a key site in southwestern Asia occupied during the Middle and Upper Palaeolithic. The site plays an important role in understanding modern human dispersals into Eurasia. Taxa from intertidal rocky shore, subtidal soft bottom, and rocky littoral habitats dominate the marine component of the invertebrate assemblage. Terrestrial snails indicate wooded and open half shaded habitats in the vicinity of the site. Species composition suggests that these habitats were present throughout the Upper Palaeolithic. Humans transported marine molluscs to the rockshelter as ‘food packages’ for dietary purposes (e.g., *Patella caerulea*, *Patella rustica*, *Phorcus turbinatus*) and shells of other taxa to be used as tools (e.g., *Glycymeris* sp.) or possibly for ornamental purposes (e.g., *Nassarius gibbosulus* and *Columbella rustica*). In the Initial Upper Palaeolithic, collection focussed on empty shells as raw material for utilitarian purposes. In the subsequent Early Upper Palaeolithic and later periods, mollusc gathering was performed in an increasing number of habitats and shifted towards collection for human consumption, which was the main reason for the introduction of shells to the site during the Epipalaeolithic. Concurrent size shifts of live collected as well as beached specimens suggests that size changes were linked to environmental change rather than to potential overexploitation of dietary taxa by humans.

1. Introduction

Hominins have consumed marine molluscs at least from the Middle Palaeolithic (Marine Isotope Stage (MIS) 5; roughly 100–115 ka) onwards in the Mediterranean region (e.g., Emiliani et al., 1964; Klein and Scott, 1986; Stiner, 1999; Colonese et al., 2011; Barker et al., 2012) and since the Middle Stone Age (MIS 6; roughly 191–123 ka) at Pinnacle Point in South Africa (Jerardino and Marean, 2010). The oldest use of shell has been documented for *Homo erectus* from Trinil (Java, Indonesia) at ≥400 ka (Joordens et al., 2014). The use of perforated shells for ornamental purposes has been documented throughout Africa and Eurasia at different stages of the Palaeolithic (e.g., Kuhn et al., 2001; Henshilwood et al., 2004; Bar-Yosef Mayer, 2005; d’Errico et al., 2005; Vanhaeren et al., 2006; Bouzouggar et al., 2007; White, 2007; Bar-Yosef Mayer et al., 2009; d’Errico et al., 2009; Stiner et al., 2013; Vanhaeren et al., 2013) and these finds have been of pivotal importance for the debate on behavioural modernity (e.g., Bouzouggar et al., 2007; Zilhão et al., 2010; d’Errico and Stringer, 2011). The earliest evidence for use of shells as ornaments comes from Qafzeh (Israel), where four perforated *Glycymeris nummaria* valves covered in ochre and dating to around 92 ka were found (Bar-Yosef Mayer et al., 2009). Other early evidence includes similarly perforated and coloured *Nassarius gibbosulus* shells from several Aterian and Middle Stone Age sites, dating to around 82 ka, in North Africa (e.g., Vanhaeren et al., 2006; Bouzouggar et al., 2007; d’Errico et al., 2009). In comparable finds of the closely-related species *Nassarius kraussianus* from South Africa (e.g., Henshilwood et al., 2004; Vanhaeren et al., 2013). In the Mediterranean, from the Middle Palaeolithic onwards, humans gathered shells of marine molluscs to be used as tools, such as cutting implements and scrapers (e.g., Stiner, 1994; Douka, 2011; Douka and Spinapolice, 2012; Romagnoli et al., 2014).

Mollusc remains are a potential source of data on past environments, human subsistence practices, and seasonality of site occupation. Reconstructions of past environments have been based on assemblage composition and diversity (e.g., Shackleton and van Andel, 1986). Metric analyses have been undertaken to explore

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human impact on coastal mollusc populations (e.g., Mannino and Thomas, 2001; Klein et al., 2004; Erlandson et al., 2011; Klein and Steele, 2013; Colonese et al., 2014). In addition, oxygen isotope analyses on shell carbonates can be used to obtain data on past sea surface temperatures (e.g., Emiliani et al., 1964; Mook and Vogel, 1968; Schöne et al., 2006; Joordens et al., 2009). These same methods allow us to infer the seasonality of shellfish exploitation, in particular of intertidal marine taxa (e.g., Deith and Shackleton, 1988; Mannino and Thomas, 2003; Mannino et al., 2007; Colonese et al., 2009; Mannino et al., 2011), which, in turn, can be useful to assess the periodicity of site occupation (e.g., Shackleton, 1973; Mannino et al., 2007, 2011; Colonese et al., 2009). Further, shell carbonates have been used as a medium for relative dating (amino acid racemization; e.g., Penkman et al., 2008; Demarchi et al., 2011), as well as numerical dating (radiocarbon; e.g., Benazzi et al., 2011; Douka et al., 2012, 2013).

The archaeological study of mollusc assemblages is informative on many aspects of past human lifeways, as well as the palaeoenvironmental and chronological context of these. Here we present a newly-recovered mollusc collection from Ksâr 'Akil in Lebanon (hereafter named '2015 collection'), a key site in the eastern Mediterranean, and re-evaluate with up-to-date zooarchaeological methods the known and previously-studied (e.g., van Regteren Altena, 1962; Kuhn et al., 2001; Douka, 2011) mollusc collection (hereafter '1962 collection'). We show the potential offered by the Ksâr 'Akil mollusc remains to throw light on past human behaviours, specifically on the interaction of humans with their environment, on mollusc consumption and on the use of shells as raw material for tools and personal ornaments.

2. Ksâr 'Akil: research history and site background

Ksâr 'Akil is a deeply stratified archaeological site in the eastern Mediterranean well-known for its long Initial (IUP) and Early (EUP)

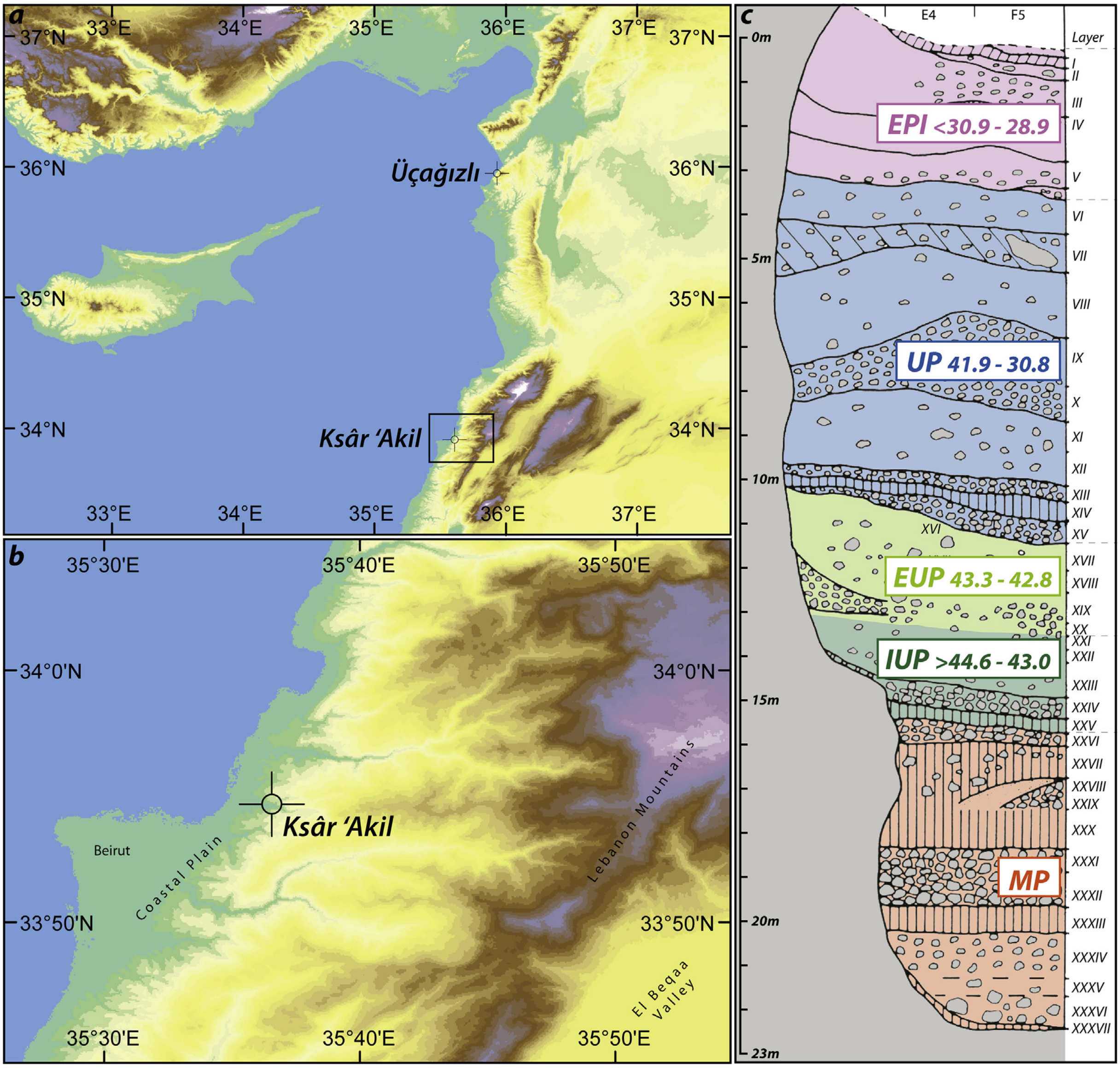

Fig. 1. Ksâr 'Akil site location and stratigraphy. (a) Map of the north-eastern Mediterranean with the location of Ksâr 'Akil (Lebanon) and Üçağızlı I (Turkey; mentioned in the text). (b) Inlet of map a, showing the location of Ksâr 'Akil in relation to the sea, coastal plain, and Lebanon mountains. (c) Stratigraphy of the 23 m thick Ksâr 'Akil sequence comprising from bottom to top Middle Palaeolithic (MP), Initial Upper Palaeolithic (IUP), Early Upper Palaeolithic (EUP), Upper Palaeolithic (UP), and Epipalaeolithic (EPI) layers. Digital elevation data in (a) and (b) originates from the Shuttle Radar Topography Mission (https://lta.cr.usgs.gov/SRTMBasic), downloaded from USGS Earth Resources Observation and Science (EROS) Center (http://eros.usgs.gov). Schematic section drawing in (c) based on Ohnuma and Bergman (1990), age-ranges after Bosch et al. (2015).

Upper Palaeolithic sequences, both of which are associated with human remains. The rockshelter was discovered in 1922 when Professor E. Day was informed of looting activity and was able to obtain some of the uncovered archaeological material (Delcourt, 1927; Ewing, 1949). It was on the recommendation of Abbé H. Breuil, who saw some of the Ksâr 'Akil lithic artefacts and bones, that Reverend J. G. Doherty from Boston College (Massachusetts, USA) and his team started the first scientific excavations in the summer of 1937 (Ewing, 1947). Excavations took place in three seasons (1937, 1938, and 1948–49), the last of which was led by J. F. Ewing who reached the bedrock at 23 m below datum (Ewing, 1949). Between 1969 and 1975, J. Tixier (CNRS, France) carried out additional excavations to a depth of 9 m below datum (Tixier and Inizan, 1981; Mellars and Tixier, 1989).

Ksâr 'Akil is located roughly 10 km northeast of Beirut (Lebanon, Fig. 1a), in the Antelias Valley (Ewing, 1947, 1948; Braidwood et al., 1951; Wright, 1962). The Antelias stream running down the valley terminates in the Bay of St. George. About 2 km inland, on the seaward-facing slopes of the Lebanon Mountains, the valley used to divide into two smaller valleys surrounding a limestone hill with a Semitic 'high place' on top (Ewing, 1947). This is probably the source of the name of the rockshelter (*Qasr* translates to inaccessible or high place and *Akil* meaning wise). The hill has been almost completely destroyed, as quarrying has reduced it almost to the valley floor (Bergman et al., 2012). The rockshelter is situated on the northern slope of the valley (Ewing, 1947; Wright, 1962; Bergman et al., 2012), and in prehistoric times the south-facing opening would have been protected by the hill in the centre of the valley. Freshwater supply would likely have come from the stream on the valley floor. The occupants of Ksâr 'Akil would have had access to a variety of habitats from the mainly rocky littoral to the small coastal plain (sahil) and from the steep and, at least, partly forested slopes of the Lebanon Mountains to the open highlands of the Beqaa Valley (Fig. 1b).

The Ksâr 'Akil sequence is 23 m thick and is subdivided in this study largely according to the archaeological division by Williams and Bergman (2010), as well as by taking into account the geological information provided in Ewing's (1949) and Wright's (in Braidwood et al., 1951; Wright, 1962) original publications. The lowermost 7 m (23–16 m below datum) contain reddish alluvial deposits with evidence of Middle Palaeolithic (MP; Layers XXXVII–XXVI) occupation, followed by very rich IUP (*sensu* Kuhn et al., 1999; Layers XXV–XXI) and EUP or Early Ahmarian (Layers XX–XIV) deposits (roughly 16–13 m and 13–10 m below datum, respectively). The subsequent Upper Palaeolithic (UP; Layers XIII–VI) deposits have been divided in various named and unnamed Upper Palaeolithic phases by different scholars (e.g., Kuhn et al., 2001; Williams and Bergman, 2010; Leder, 2014). Due to the diversity in archaeological attributions these layers, covering 7 m of deposits (approx. 10–3 m below datum), are here grouped in a broader UP. The Epipalaeolithic (EPI; Layers V to I) comprises the uppermost 3 m of the sequence (Fig. 1c) (see also Tixier, 1974; Tixier and Inizan, 1981; Azoury, 1986; Marks and Volkman, 1986; Bergman and Goring-Morris, 1987; Bergman, 1988; Bergman and Stinger, 1989; Mellars and Tixier, 1989; Ohnuma and Bergman, 1990; Williams and Bergman, 2010; Douka et al., 2013; Leder, 2014). Above 16 m, the sediments containing UP artefacts are generally brown-greyish in colour and are intersected by so-called stone complexes at a depth of 17–16 m, 11–10 m, and 2 m below datum. These stone complexes consist of angular limestone blocks, sometimes underlain by red clay bands, and are thought to have coincided with humid climatic conditions, potentially representing pluvial subphases of the last Glaciation (Braidwood et al., 1951; Ewing, 1960; Wright, 1962). The deposits containing Epipalaeolithic layers are blackish.

The material studied here originates from the excavations by Doherty in the 1930s and by Ewing in the 1940s, the only ones to cover the full depth of the sequence. Ewing and Doherty used different datum points, making it difficult to correlate material from both excavations. Lists based on notes from the original excavators that correlate the depths per square of Doherty's excavations to the layers assigned by Ewing thus linking the material from the 1930s and 1940s were kindly provided by A. Kersten (see also Hoojier, 1961; Kersten, 1991).

The envisioned large scale paleontological study of the faunal remains was originally delegated to D. Bate (Natural History Museum, London, UK), but after her death the faunal material was sent to D. Hooijer at the Museum van Natuurlijke Historie (now Naturalis Biodiversity Center) in Leiden, the Netherlands. Hooijer published a study on the vertebrates (Hooijer, 1961; see also Kersten, 1987, 1991, 1992). He also separated the majority of the invertebrate remains, mainly including complete or nearly complete specimens and gave them to C. O. van Regteren Altena for study and curation (van Regteren Altena, 1962). The Ksâr 'Akil faunal assemblages (both vertebrate and invertebrate) are currently curated in the Naturalis Biodiversity Center in Leiden. Molluscs from Tixier's excavations in the late 1960s and early 1970s were studied by Inizan and Gaillard (1978). They were not taken in consideration here, as the main aim of this paper is to compare and reunite the 1962 and 2015 collections, which both originate from Doherty and Ewing's excavations.

3. Material and methods

We conducted zooarchaeological and taphonomic investigations on the mollusc assemblage (n = 3571) consisting of two collections, both originating from the same excavation campaigns, i.e., Doherty's 1937–38 and Ewing's 1947–48 excavations (Tables 1 and 2). The first collection or '1962 collection' (n = 2804) was published by van Regteren Altena (1962) and originates from the entire excavated area. The second or '2015 collection' (n = 767) was recovered during the study of vertebrate skeletal remains of the 2 × 2 meter excavation square F4. Preparation of the square F4 vertebrate material included treatment with acid (i.e., 10% acetic acid solution over 8 h and subsequent exposure to a base, i.e., 10% sodium carbonate solution, to stop any persisting acid reaction) to loosen sediment adhering to the bones. During this process, numerous shells of terrestrial and marine molluscs were recovered. Whenever possible, shells were detached before acid treatment, others had to be loosened using the acid and shell specimens treated in this way have a light glaze on the outer surface. The newly-recovered '2015 collection' is largely fragmentary, but comprises also some intact or nearly intact specimens (n = 82). As a result of the present study, the collection from square F4 was

Table 1
Ksâr 'Akil mollusc collections. 1962: collection studied by van Regteren Altena (1962); 2015: this study. Abbreviations: n: number of specimens, NISP: number of identified specimens, MNI: minimum number of individuals, S: number of taxa, complete: percentage of complete and nearly complete specimens. F4: 2 × 2 m excavation square (see text).

	1962		2015	Total	
	All	F4	F4	F4	All
n	2804	387	767	1154	3571
NISP	2683	387	766	1103	3406
MNI	2259	322	128	436	2370
S	47	22	16	24	49
Complete (%)	76.92	72.35	10.69	31.37	63.19
Burning (%)	16.45	20.16	25.03	23.57	18.68

Table 2
Mollusc NISP per layer (I – XXVIII A) for the Ksâr 'Akil studied shell assemblage (1962 and 2015 collections combined). H: species habitat (1–5 marine, 6 freshwater, 7–9 terrestrial), 1: intertidal rocky shore, 2: estuary/lagoon, 3: subtidal rocky substrate, 4: subtidal soft bottom, 5: deep subtidal bathyal soft bottom, 6: fresh water, 7: woodland, 8: open to half shaded, 9: arid adapted, open to half shaded; MP: Middle Palaeolithic.

Species	H	Epipalaeolithic					Upper Palaeolithic								Early Upper Palaeolithic							Initial Upper Palaeolithic				MP
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XXI	XXII	XXIII	XXIV	XXVIII A
Marine gastropods																										
Patella caerulea	1		1			1	2	21	6	2	1	1					1	4								
Patella rustica	1	1	1	1		18	7	6	1	3	3						9	19								
Patella ulyssiponensis	1						2	2	2								1	1								
Patella sp.	1				1	1	2	7	1	3		1						11	2		1					
Trochidae	–											1						1								
Phorcus articulatus	1									1		8						2								
Phorcus turbinatus	1			14	5	120	25	34	13	19	21	43	7	7			37	71	6	7	2		1			
Phorcus sp.	1									3		60	3					10		1						
Bolma rugosa	4											3											2			
Cerithium vulgatum	3								1	2			1				10	5		4	5	4	13	2		
Naticarius hebraeus	4																		1				1			
Neverita josephinia	4											1						2		1			1			
Semicassis saburon	4		1																							
Euthria cornea	3																1	2								
Pisania striata	1									1		1														
Columbella rustica	3					3	2	20	16	132	37	5	4		1	1	31	115	4	10	4	2	19	2	1	
Tarantinaea lignarius	3																	2								
Nassarius gibbosulus	4				1	7	9	31	59	145	26	8	10	1			37	125	14	25	10	26	128	10	1	
Nassarius mutabilis	4									1												1				
Nassarius sp.	4																				1		1			
Bolinus brandaris	3																	2								
Hexaplex trunculus	3							2			2						2	5								
Murex sp.	3										1										1					
Mitra cornicula	1										1						1									
Conus ventricosus	3							3		4	1							5	2		3					
Marine gastropod	–										2	13						5			2		1			
Marine bivalves																										
Acanthocardia tuberculata	4		1						4	14	1	2					7	31	2				2	1		
Acanthocardia sp.	4								1			2														
Cerastoderma glaucum	2																	1								
Donax trunculus	4									1																
cf. *Callista chione*	4																	1	1							
Venus verrucosa	4																	1								
Anadara cf. *polii*	4									2																
Arca noae	3																	1								
Barbatia barbata	3																		1							
Glycymeris nummaria	4						1			2			1				10	7		1			1		1	
Glycymeris sp.	4		1		3	1		2	5	26	1	9	1			1	34	78	16	29	7	23	22	6	6	
Lima lima	3									4								2								
Ostrea edulis	3									1												1				2
Spondylus gaederopus	3											1	1											1		
Pinna nobilis	4					1						3														
Marine scaphopods																										
Antalis dentalis	5									10																
Antalis vulgaris	5									13	1															
Antalis sp.	5								2	13																
Freshwater gastropods																										
Theodoxus jordani	6									4										1						
Melanopsis buccinoidea	6							1		2										1						

(*continued on next page*)

Table 2 (*continued*)

Species	H	Epipalaeolithic					Upper Palaeolithic								Early Upper Palaeolithic							Initial Upper Palaeolithic				MP
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XXI	XXII	XXIII	XXIV	XXVIII A
Freshwater bivalves																										
Unionacea	6						1		2	1																
Potomida littoralis	6									1																
Terrestrial gastropods																										
Pomatias elegans	8																	1			1					
Pomatias olivieri	8					2	1	7	7	6	4	1	2	2			10	10	13	6	1		1			
Buliminus labrosus	7							2	1			1							2							
Pene syriacus	7								1											1						
Cristataria porrecta	7												1													
Oxychilus syriacus	8					3	1	1	4		2							2	1	1						
Helicidae	7											69						3		5	5					
Helix pachya	7	1	1	13	12	80	42	125	64	21	9	21	4	1	2		16	44	2	8		2				
Sphincterochila cariosa	9					1																				
Metafructicola berytensis	8					2	5	5	4	2	3						13	12	4	10	1		2			
Monacha nummus	8																		1			1				
Monacha syriaca	8					2	3	4	1	7	1							6		4			2			
Terrestrial gastropod	–										2	211	16					46		62	2					
Total NISP	–	2	6	28	22	242	103	273	195	446	119	465	51	11	3	2	220	633	72	177	46	60	197	22	9	2

enlarged from 387 to 1154 specimens and from 22 to 24 species (Tables 1 and 2).

The classification of the taxa in the assemblage has been updated, according to the most recent nomenclature, using the online databases WoRMS (Boxshall et al., 2014) for marine species and WMSDB (http://www.bagniliggia.it/WMSD/WMSDhome.htm) for freshwater and terrestrial species. Quantities were recorded in terms of number of shell fragments (n), number of identifiable specimens (NISP, counting refitted shell fragments as one specimen), and minimum number of individuals (MNI) (after Lyman, 2008). MNIs were calculated using landmarks, e.g., presence of apex, aperture, columella and umbo, depending on shell type (i.e., bivalve or gastropod). Scaphopod MNIs were determined by the number of specimens for which >50% of the shell was preserved. Our zooarchaeological investigations further included determination of taphonomic alterations (both pre- and post-depositional), human modifications and metric analysis. Pre-depositional alterations, comprising indicators of peri- and post-mortem exposure to a marine environment (e.g., in active beaches) include bioerosion, epizootic encrustation, seafloors with reductive conditions, surface wear and polish resulting from beach rolling, non-repaired damage of gastropod predation, crab predation, and boring sponges (Table 3). Post-depositional taphonomic alterations include decalcification, erosion, root etching, and sediment encrustations (both local, i.e., originating from the deposits present in the rockshelter, and non-local deposits, which are in essence pre-depositional alterations) (Fig. 2). Observed potential human modifications include impact fractures, retouch, apex detachment of topshells (to facilitate shellfish extraction), edge damage on limpets (congruent with damage from prying the animals off the rocks), perforations, presence of red pigments, and signs of burning. Standard measurements (in mm) comprise maximum length, width, and height for bivalves and conical gastropods, maximum height and basal diameter for scaphopods and coiled shells, and aperture height for coiled shells.

Prior to comparing the mollusc taxa from the different archaeological layers, potential biases that may have affected the assemblage need to be addressed. The Ksâr 'Akil molluscs were recovered long ago and potential loss of material, either through incomplete collection or post-excavation discard of material has to be explored. Although excavation techniques were not up to present-day standards, all sediments were dry sieved (Murphy, 1938) and shell remains were adequately recognised during the fieldwork (Ewing, 1947, 1948, 1960). Murphy (1938) writes that in the 1937 field season both lithics and bones were discarded after initial study, if they were not deemed interesting for further investigation. Regarding the vertebrate fauna, this approach seems to have changed in later seasons as high numbers of small non-identifiable (i.e., "uninteresting") fragments are present in the IUP, EUP, and UP. The majority of the molluscs in the '1962 collection' are intact or almost intact and it is possible that only a sample of the invertebrates was kept. However, species composition of the '2015 collection' includes many small fragments that were found encrusted to bones indicating that mollusc completeness in the '1962 collection' is more likely the result of incomplete separation of the mollusc remains from the vertebrate fauna in the 1960s than of post-excavation discard. Ewing made a very detailed initial account of changes in faunal distribution throughout the sequence. Regarding the invertebrate assemblage, Ewing (1947, 1948) wrote that there were many shells above 12 m depth (which relates to layer XVIII), but none below and that the most common land snail was *Helix* and the most frequent marine species were *Trochus* (now *Phorcus*) and *Patella*. He also stated that the frequency of land snails versus marine species remained the same throughout the occupation, and that three peaks in shell abundance (both terrestrial and marine) were identified at 4 m, 9.3 m, and 11.25 m below datum

Table 3
Pre-depositional taphonomic alterations in marine taxa by phase (MP – EPI) per Layer (I – XXVIII A) and divided in live-collected intertidal rocky shore taxa and beach collected empty shells. Note: as some specimens were subjected to more than one type of pre-depositional alteration the numbers of shells showing marine taphonomic alterations (column: Total MA; row: Total (n)) are lower than the sum of the occurrence of the individual pre-depositional alterations. Abbreviations: EPI: Epipalaeolithic, UP: Upper Palaeolithic, EUP: Early Upper Palaeolithic, IUP: Initial Upper Palaeolithic, MP: Middle Palaeolithic, Bio: bioerosion, Ep. encr.: Epizootic encrustations, Red. con.: exposure to sea floors with reductive conditions, B. wash: beach washed, Gast.: gastropod damage, Crab.: Crab damage, B. sponge: Boring sponge damage, total MA: total Marine Alterations.

Phase	Layer	n	Bio	Ep. encr.	Red. con.	B. wash	gast.	crab.	B. sponge.	Total MA
EPI	I	2	0	0	0	0	0	0	0	**0**
	II	6	0	0	0	0	0	0	0	**0**
	III	28	0	0	0	0	0	0	0	**0**
	IV	22	0	0	0	1	0	0	0	**1**
	V	242	0	0	0	5	0	0	2	**5**
	Total EPI	*300*	*0*	*0*	*0*	*6*	*0*	*0*	*2*	***6***
UP	VI	103	0	0	0	8	0	0	3	**8**
	VII	272	3	0	1	30	0	2	10	**34**
	VIII	195	0	0	2	50	0	8	10	**54**
	IX	448	5	0	7	222	3	30	69	**248**
	X	122	0	0	5	55	5	3	17	**56**
	XI	466	0	0	0	6	0	0	0	**6**
	XII	61	0	0	0	6	4	0	0	**10**
	XIII	11	0	0	0	1	0	0	0	**1**
	Total UP	*1678*	*8*	*0*	*15*	*378*	*12*	*43*	*109*	***417***
EUP	XIV	3	0	0	0	1	0	0	1	**1**
	XV	2	0	0	0	0	0	0	0	**0**
	XVI	220	3	1	5	42	5	0	16	**52**
	XVII	646	14	2	10	215	17	19	79	**233**
	XVIII	72	1	0	0	8	2	0	2	**10**
	XIX	191	0	0	0	27	2	1	8	**28**
	XX	48	4	0	0	10	2	2	6	**18**
	Total EUP	*1182*	*22*	*3*	*15*	*303*	*28*	*22*	*112*	***342***
IUP	XXI	60	0	0	0	18	1	0	2	**18**
	XXII	198	6	1	5	127	8	5	29	**134**
	XXIII	22	1	0	1	10	1	0	1	**12**
	XXIV	9	0	0	0	0	0	0	0	**0**
	Total IUP	*289*	*7*	*1*	*6*	*155*	*10*	*5*	*32*	***272***
MP	XXVIII A	2	0	0	0	0	0	0	0	**0**
Intertidal rocky shore taxa		**684**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**2**
Other marine taxa		**1676**	**38**	**4**	**36**	**866**	**50**	**71**	**263**	**987**
Total (n)		**2360**	**38**	**4**	**36**	**867**	**50**	**72**	**263**	**989**
Total (%)		–	**1.59**	**0.17**	**1.51**	**36.38**	**2.10**	**3.02**	**11.04**	**41.50**

(corresponding to layers V, IX, and XVI – XVII, respectively) (Ewing, 1947).

These observations match the main features of the '1962 collection' almost to the letter. Peaks in mollusc abundance have been detected in layers V, IX, and XVI – XVII, below which the number of shells greatly diminishes. A small additional peak in mollusc numbers corresponds to layer XXII, below which very few shells were recovered. *Helix*, *Phorcus*, and *Patella* are among the most frequent (and largest) taxa and throughout the sequence marine species make up approximately two-thirds and terrestrial molluscs one-third of the assemblage. Further, Ewing (1948) stated that in some parts of the deposits thousands of shells were present, which judging from the general writing style and lack of counts, may be an overestimation. Although it is possible that not all mollusc remains were kept, by comparing the '1962 collection' with the recently-acquired '2015 collection' it can be concluded that both collections combined are a representative sample of what was originally excavated, given that their taxonomic composition matches that of the preliminary observations by Ewing. The 1962, and 2015 collections taken together represent a sizeable mollusc collection ($n = 3571$) for an Upper Palaeolithic site of this antiquity. Overall, it is likely that a representative collection of the original assemblage survives and this is useful to reconstruct the salient aspects of mollusc exploitation by the occupants of Ksâr 'Akil. Moreover, the 1930s and 1940s excavations could successfully be correlated as regards to the layers and find-depths (see above) allowing us to merge the material from the two collections in a combined study.

In addition to potential recovery and curation issues, the taphonomic history may differ between layers and might have resulted in differential faunal preservation. Before comparing layers statistically, it first has to be established if these potential differences could significantly influence the results (e.g., Grayson, 1984). In addition, differences in collection techniques and small sample size could be other sources of bias. The 1962 and the 2015 collections are markedly different, given that the former consists almost completely of intact specimens, while the latter is largely fragmentary. Although the total vertebrate assemblage from the entire sequence in square F4 was subjected to acid treatment, not all layers contained new mollusc material. Therefore, fragmentation rate varies between layers and merging these two datasets might introduce significant differences in completeness between layers rendering them unsuitable for a comparative study. Further, if changes in species abundance and composition are driven by sample size, then these parameters cannot be used to inform us about human behaviour (Grayson, 1984; Lyman, 2008).

To ascertain whether shell completeness and sample size have a significant influence on the Ksâr 'Akil invertebrate assemblage, we carried out best-fit regression analysis (after Lyman, 2008). The interrelatedness between NISP and MNI is assessed by the degree of correlation of the log or lnMNI and lnNISP, as well as between lnNISP and lnS (or lnNTAXA, i.e., the number of species) per layer using Pearson's correlation coefficient (as the values are not ranked). To verify whether sample size is the main factor responsible for the faunal composition of a layer, the relative abundance of several common species (i.e., *Phorcus turbinatus*, *Columbella rustica*,

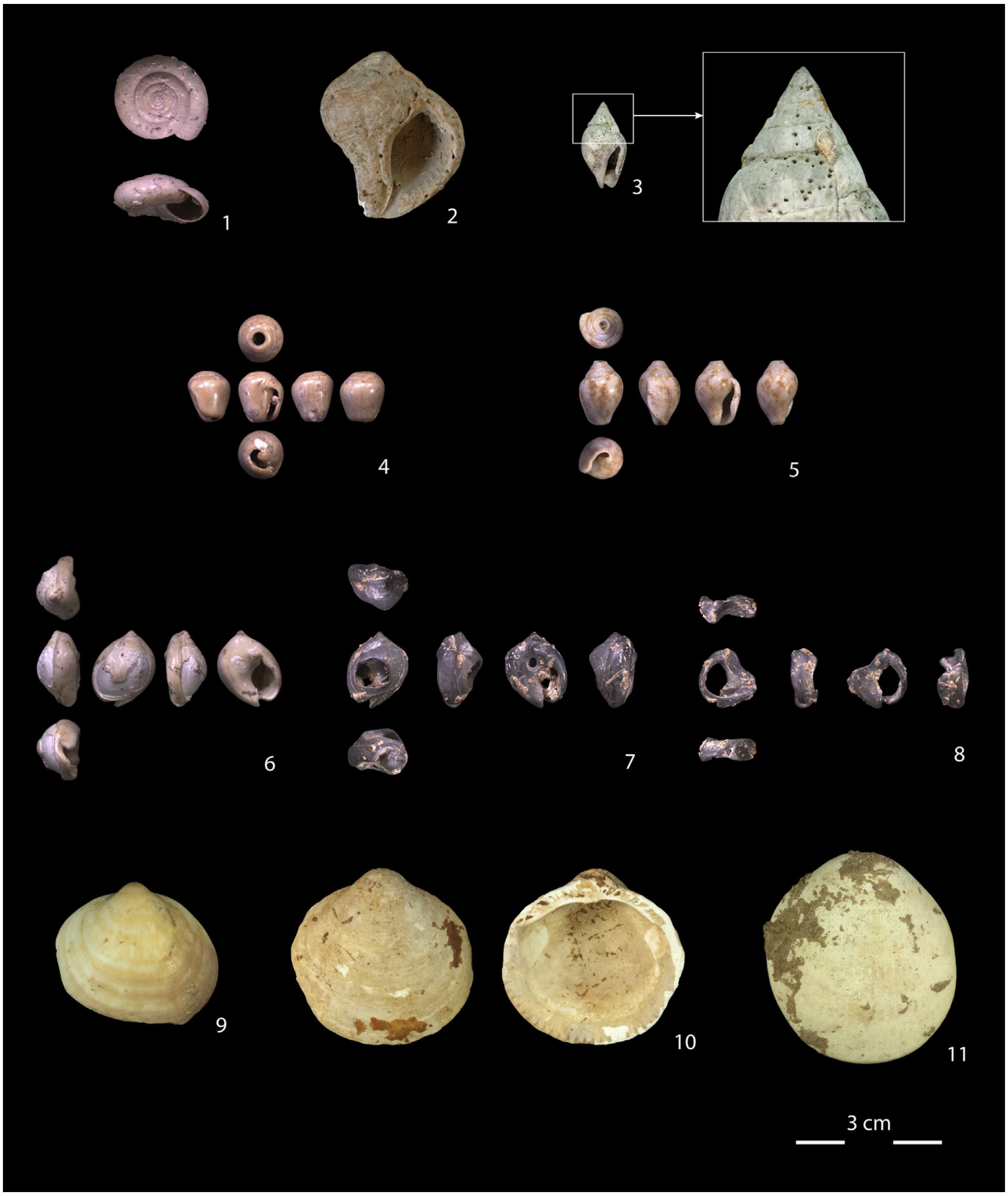

Fig. 2. Examples of taphonomic signatures. 1, 5, 9: Original pigmentation; 2, 4, 5, 8: various stages of beach washing; 2, 3: boring sponge damage (see inlet 3); 3: burning; 6, 10: localized recrystallization; 7, 8: reducing marine atmosphere; 7: gastropod perforation; 7, 10: red pigment stain; 11: fossilized; 1: no traces. Shell species shown: 1: RGM-606482, *Oxychilus syriacus*; 2: RGM-577859, *Bolinus brandaris*; 3: RGM-770824, 5: RGM-550196, *Columbella rustica*; 4: RGM-606214, *Conus ventricosus*, 6: RGM-550222h, 7: RGM-550222a, 8: RGM-550222c, *Nassarius gibbosulus*; 9: RGM-550201, 10: RGM-577852, 11: RGM-550206, *Glycymeris* sp. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

Nassarius gibbosulus and *Helix pachya*) throughout the Ksâr 'Akil assemblage were plotted against the total NISP per layer (following Lyman, 2008). If the NISP per species is not significantly related with the total NISP, this would indicate that sample size is not a driving factor in assemblage composition. We use Spearman's rho (employing a t-distribution) as a significance test because the values are ranked.

Species composition per layer is assessed through the calculation of the taxonomic richness (S), evenness (e), dominance (1/D), and heterogeneity (H) (Lyman, 2008; see also; Stiner et al., 2013). These indices all describe assemblage composition, but with subtle differences. The larger the value of H, the greater is the heterogeneity. Taxonomic evenness values range between 0 and 1, where 1 signifies that all taxa are equally abundant (Lyman, 2008). Inversely, the higher the 1/D value the more evenly species are distributed, whereas low values signify dominance by one or few species (Lyman, 2008). As taxonomic evenness and heterogeneity are calculated on the basis of NISPs, it is possible that the outcomes are driven by sample size. To assess this possibility, both values are plotted against the total NISP per layer and Pearson's correlation coefficient is used to identify significance. This type of regression analysis is also used to discern potential chronological trends in both species composition and average mollusc size (e.g., Grayson, 1984; Lyman, 2008).

4. Results and discussion

The total NISP for which a secure stratigraphic position could be ascertained on the basis of their labels is 3406. The total MNI is 2370 and is attributable to 49 taxa (Table 1). Two valves of *Ostrea edulis*, probably belonging to a single specimen, are the only invertebrate remains found in the MP deposits (Layer XXVIII A).

From the IUP onwards, mollusc remains become more frequent (n = 289) with peaks in the EUP (n = 1182) and subsequent UP layers (n = 1678). The EPI layers have yielded little material culture and faunal remains including molluscs (n = 300) (Table 2).

Overall, the molluscs include species from terrestrial, freshwater, brackish water and fully marine environments and comprise gastropods, bivalves and scaphopods (Table 2). The marine molluscs originate both from hard and soft-bottom habitats. The most common taxa are the intertidal rocky shore *Phorcus turbinatus* (NISP = 431) and *Patella* spp. (NISP = 146), the sublittoral rocky substrate taxon *C. rustica* (NISP = 409), the soft-bottom sublittoral *N. gibbosulus* (NISP = 673) and Glycymeridae (NISP = 295). Brackish and freshwater species are rare (n = 15). Terrestrial species include wooded as well as open and half shaded taxa, of which the woodland species *H. pachya* (NISP = 468) is best represented. From all habitats adult complete or semi-complete specimens dominate the assemblage.

The two collections (i.e., 1962 and 2015) differ mainly in terms of fragmentation and frequency of burning damage (Table 1). A strong significant correlation ($r = 0.97$ $p < 0.001$) exists between lnNISP and lnMNI throughout the sequence, suggesting MNI and NISP of all layers are interrelated. Similarly, lnNISP and lnS are highly negatively correlated ($r = -0.95$, $p < 0.001$). These results warrant merging of the two collections. The relative abundance of several common species, namely *Ph. turbinatus* ($r = -0.03$, $p = 0.89$), *C. rustica* ($r = 0.09$, $p = 0.68$), *N. gibbosulus* ($r = 0.16$, $p = 0.45$), and *H. pachya* ($r = -0.20$, $p = 0.36$) shows no significant correlation with total NISP throughout the sequence, suggesting that sample composition is not driven by sample size. Both, the interrelation and relative abundance analyses, suggest that the taphonomic history per layer did not differ significantly and merit inter-layer comparison.

4.1. Taphonomy

An important question, which needs to be addressed by any study of mollusc remains from archaeological sites, is establishing which agents were responsible for the introduction of the shells to a site. It is essential to distinguish between shell deposits that accumulated naturally or that were accumulated by animals other than humans, from those of anthropogenic origin (Erlandson and Moss, 2001). The Ksâr 'Akil rockshelter lies at an elevation of approximately 80 m (top of the 23 m sequence) above present-day sea level (asl). Several fossil beach deposits have been identified along the Lebanese coast up to a height of 90 m asl. (e.g. Fleisch, 1962; Wright, 1962). However, despite the potential of naturally introduced marine shells in the site, given the presence of fossil beaches at this elevation and the alluvial nature of the lowermost 7 m of the Ksâr 'Akil stratigraphy, these deposits contain virtually no invertebrate remains. The Upper Palaeolithic deposits, rich in both mollusc and archaeological remains, are the result of *in situ* accumulation of sediments (Wright, 1962). This suggests that the marine molluscs were transported to the site by either animals or humans. Many species of birds (e.g., herons and oystercatchers) are known to accumulate mollusc remains, as do many small carnivores (e.g., mustelids, but also wolves) and rodents (Claassen, 1998; Erlandson and Moss, 2001). In general, molluscs gathered by animals show specific taphonomic modifications, such as breakage patterns resulting from dropping shells from great heights on hard surfaces (i.e., birds) or canine punctures on the shell surface, in their efforts to access the mollusc flesh (Claassen, 1998). None of these taphonomic signatures have been encountered on the shells examined for this study. This and the unlikelihood that animals would accumulate hundreds of shells at a site that is relatively distant from the shore suggest that humans introduced the molluscs to the rockshelter (as will also be argued below on the basis of anthropic taphonomic alterations). Moreover, there would have been no apparent reason for birds or other animals to transport beach-rolled shells to the site. It is, therefore, reasonable to assume that at least the marine taxa were introduced to Ksâr 'Akil by humans.

4.1.1. Pre-depositional taphonomy

The taphonomic signatures observed on the shells from the assemblage vary between species. This is especially true for 'pre-depositional taphonomic alterations', which are inflicted on the shells during the time after the death of the mollusc and before final deposition and burial. These alterations are habitat-dependent and are, therefore, described below according to the environment of origin (i.e., marine, freshwater, terrestrial). Post-depositional processes that took place after the shells were incorporated in the Ksâr 'Akil deposits are more uniformly distributed and are thus described for the assemblage as a whole.

4.1.1.1. Marine species. Almost half of the marine shells (41.5%, gastropods, bivalves, and scaphopods) show taphonomic signatures resulting from exposure to marine environments and were, therefore, collected empty from active beaches. Traces of beach weathering (36.4%), staining by exposure to sea floors with reductive conditions (1.5%), boring sponge damage (11.0%), other bioerosion (1.6%), encrustation by epizootic organisms (0.2%), and predator damage from either carnivorous gastropods (2.1%) or crabs (3.0%) were found (Table 3; Fig. 3). The majority of beach-collected taxa are subtidal and live on soft-bottom and hard-bottom substrates. Intertidal and bathyal/low-subtidal soft-bottom taxa (i.e., *Antalis* spp.) are rare. Some bivalves (mainly *Glycymeris* sp., but also *G. nummaria*, *Spondylus gaederopus*, and *O. edulis*) show advanced erosion, decalcification, and fossilization that are consistent with collection from fossil deposits rather than from active beaches. Fossil marine terraces containing *Glycymeris* have been recognised along the Lebanese coast at 45, 35, 15 and 6 m asl (Fleisch, 1962; Wright, 1962).

The majority of the assemblage (58.5%) is composed by rocky shore intertidal gastropods (i.e., *Ph. turbinatus*, *Phorcus articulatus*, *Patella rustica*, *Patella caerulea* and *Patella ulyssiponensis*) that generally show no signs of peri- or post-mortem damage resulting from exposure to destructive marine organisms and/or environments, indicating that they were collected alive by humans for consumption. The frequency of marine taphonomic alterations per layer is mainly linked to the purpose and habitat of gathering. Layers containing mainly shells of molluscs primarily gathered for consumption (e.g., those attributed to the Epipalaeolithic) yielded

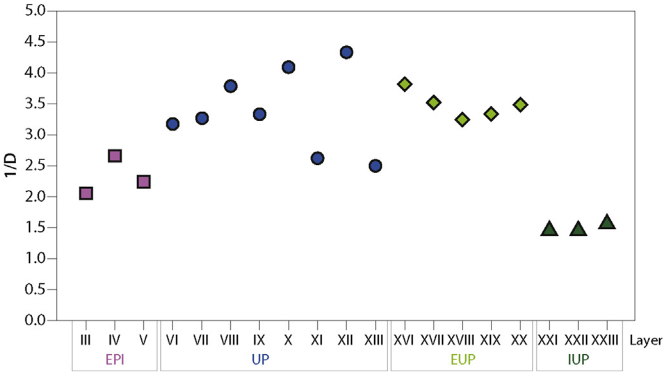

Fig. 3. Taxonomic dominance (1/D) of habitat types per layer (roman numerals). Initial Upper Palaeolithic (IUP): triangles, Early Upper Palaeolithic (EUP): diamonds, Upper Palaeolithic (UP): circles, and Epipalaeolithic (EPI): squares. Note: low sample size in layers I, II, XIV, XV, XXIV, and XXVIII A, prohibit including these layers in this analysis.

only a few specimens with taphonomic signatures compatible with a prolonged exposure to marine taphonomic agents.

4.1.1.2. Freshwater and brackish water species. Freshwater species include: the gastropods *Melanopsis buccinoidea* (n = 4) and *Theodoxus jordani* (n = 5), which are adapted to medium and high energy water regimes (Bößneck, 2011), the bivalve *Potomida littoralis* (n = 1), adapted to low energy regimes, and some unidentified *Unionacea* fragments (n = 4). The absence of taphonomic alterations suggests that all *M. buccinoidea* and the *P. littoralis* specimens were collected fresh, possibly from the Antelias stream, in line with their habitat requirements. The shell structure of the *Unioacea* specimens appears to be well-preserved, but the shells are very fragmentary possibly as a result of post-depositional damage to specimens introduced intact to the site. Preservation of *Th. jordani* varies. Two specimens of this species are fossilised and severely eroded, whilst other two show signatures typical of aquatic alterations and one bears none. Shells of *Th. jordani* could possibly have been collected from different localities (e.g., from a river, from the beach were the stream terminates, and/or from fossil deposits). The only specimen from a brackish water environment is an umbonal fragment of *Cerastoderma glaucum* showing no signs of taphonomic alterations and likely collected from a lagoonal/estuarine environment. In general, fresh and brackish water species are rare and were not an important component of the Ksâr 'Akil assemblage.

4.1.1.3. Terrestrial species. All species of terrestrial gastropods recovered at Ksâr 'Akil live in limestone environments and come from two main habitats. Woodland taxa include *Buliminus labrosus*, *Pene syriacus*, *Cristataria porrecta* and *H. pachya* (Heller, 1974; Bößneck, 2011). The latter species, is adapted to a wide range of habitats and altitudes (Bar and Mienis, 1979). Taxa of open and half-shaded environments are *Pomatias elegans*, *Pomatias olivieri*, *Oxychilus syriacus*, *Sphincterochila cariosa*, *Metafructicola berytensis*, *Monacha nummus* and *Monacha syriaca* (Broza and Nevo, 1996; Bößneck, 2011). There are slight variations in the preferred habitat of the encountered terrestrial species, all of which can be found in the Antelias Valley. The species *M. berytensis* and *O. syriacus* generally live at high elevation (>1000 m), whereas *M. nummus* and *P. elegans* are more frequent in coastal areas (Bößneck, 2011). *Sphincterochila cariosa* is a more arid-adapted species and can be found in semi-desert environments, but is also encountered in scrublands (Broza and Nevo, 1996). *P. olivieri* is a mesic prosobranch more often found in humid areas (Broza and Nevo, 1996). The presence of intact opercula in two *P. olivieri* specimens suggests that the species may have aestivated in Ksâr 'Akil (see also van Regteren Altena, 1962). Most of these species would have lived in the vicinity of Ksâr 'Akil and some specimens may have reached the site alive and died there naturally. One exception might be *H. pachya*, which is twice as numerous as all other terrestrial taxa together (see Table 2). Terrestrial molluscs do not show signs of pre-depositional alterations except perhaps some specimens of *H. pachya* A quarter of *H. pachya* (25.2%; n = 118) were covered in a layer of reddish/brownish fine dust. The red dust was in some cases (n = 14) in turn covered with hard grey encrustations characteristic of the Upper Palaeolithic deposits of the rockshelter. This indicates that the molluscs were in reddish/brownish sediments before their final incorporation into the layer in which they were recovered within the Ksâr 'Akil deposits.

4.1.2. Post-depositional processes

Post-depositional processes include all taphonomic alterations that occurred after the mollusc shells were incorporated into the Ksâr 'Akil sediments. The influence of root etching on the sample is negligible (n = 2).

Diagenetic substitutions of the original shell carbonate structure to secondary calcite generally result in white chalky surfaces (e.g., Kato et al., 2003; Busschers et al., 2014). Chalky surfaces were visible (at the macroscopic level) in 63.2% of the assemblage. This type of diagenetic alteration can have several causes including chemical reaction with acids, fossilization, and exposure to heat (e.g. Claassen, 1998; Kato et al., 2003; see). Twenty-five per cent (n = 193) of these diagenetically altered specimens bear additional damage due to heat exposure (e.g., discolouration in combination with heat cracks and/or potlids). Burning is likely anthropogenic in origin. Finally, some 100 specimens show only localized chalky patches on the shell surface (14.2%) again most likely the result of diagenetic alterations in the carbonate structure. These alterations might have occurred pre- and/or post-depositionally. Encrusting sediments adhere to 64.8% (n = 792) of the shells. They are generally grey and strongly concreted, similar to Wright's (Wright, 1962) and Ewing's (Ewing, 1947, 1948, 1949, 1960) description of the sediments of the Upper Palaeolithic deposits. These encrustations are sometimes accompanied by red stains or small clumps of red sediment either within the adhering sediment or on the shell surface directly. These red stains have not been analysed, but may consist of hematite or iron oxide. They differ in appearance from the reddish/brownish sediment found adhering to *H. pachya* specimens and seem to be incorporated in the grey encrusting sediments rather than forming a separate layer on the shell surfaces. Further investigations are needed to determine their chemical composition.

4.2. Taxonomic composition

Our study of the mollusc assemblage from Ksâr 'Akil confirms that species composition and abundance throughout the sequence are consistent with the preliminary observations made during excavation (e.g., Ewing, 1947, 1948). The nature and composition of the shell assemblages of each archaeological layer is assessed through calculation of taxonomic richness (NISP, MNI), abundance (S), evenness (e), heterogeneity (H), and dominance (1/D) at species level (Table 4). Most of these taxonomic indices are based on NISPs, hence, it is possible that the outcomes are driven by sample size. We tested this and found no significant correlation between lnNISP and 1/D (r = 0.33, p = 0.17) and between lnNISP and e (r = −0.44, p = 0.06), suggesting that sample size is not driving these indices, whereas H is significant (r = 0.56, p = 0.01). Therefore, in the following we discuss only the relation between 1/D and e.

The distribution of molluscs in the IUP (Layers XXIII to XXI) is dominated (1/D) by few species, but the NISP is not evenly distributed (evenness: e) among the taxa that are present. In the EUP (Layers XIV to XX) 1/D increases as does evenness, showing a broader range of taxa per layer and a more even distribution of NISP per taxon than in the IUP. The faunal composition fluctuates during the UP (Layers VI to XIII), but in general 1/D and e are lower than in the EUP, whereas the NISP per taxon is still relatively evenly distributed and dominant species are lacking. The taxonomic composition in the EPI (Layers V to I) is based on low NISPs and number of taxa. Specimens are relatively well distributed between taxa, and the assemblage is dominated by only a few species.

Regrouping of taxa per habitat type, as defined in Table 2, results in a similar pattern as seen in overall taxonomic composition (Fig. 3). In the IUP the majority of specimens came from subtidal soft and rocky substrates as well as terrestrial woodland habitats. In addition, there are individual specimens from intertidal rocky shores and open to half-shaded terrestrial environments. In the EUP a wider range of habitats is represented in the species (i.e., both intertidal and subtidal soft, as well as rocky bottom taxa, freshwater species and woodland and open to half-shaded terres-

Table 4
Taxonomic composition by phase (MP – EPI) and per layer (I – XXVIII A) of the Ksâr 'Akil assemblage. NISP: number of identifiable specimens that could be assigned to species level, MNI: minimum number of specimens identifiable to species level, lnNISP: log NISP, lnMNI: lnMNI, S: taxonomic richness (NTAXA), lnS: log S, H: taxonomic heterogeneity, e: taxonomic evenness, 1/D: inverse of Simpson's index of dominance, EPI: Epipalaeolithic, UP: Upper Palaeolithic, EUP: Early Upper Palaeolithic, IUP: Initial Upper Palaeolithic, MP: Middle Palaeolithic.

Phase	Layer	NISP	MNI	logNISP	logMNI	S	logS	H	e	1/D
EPI	I	2	2	0.69	0.69	2	0.69	–	–	–
	II	5	5	1.61	1.61	5	1.61	–	–	–
	III	28	27	3.33	3.30	3	1.10	0.822	0.748	2.237
	IV	18	18	2.89	2.89	3	1.10	0.787	0.716	2.013
	V	240	234	5.48	5.46	12	2.48	1.308	0.526	2.736
UP	VI	100	96	4.61	4.56	12	2.48	1.742	0.701	4.011
	VII	264	252	5.58	5.53	15	2.71	1.778	0.657	3.760
	VIII	184	169	5.21	5.13	15	2.71	1.808	0.668	4.230
	IX	400	357	5.99	5.88	25	3.22	1.912	0.594	4.042
	X	113	99	4.73	4.60	16	2.77	1.956	0.706	5.149
	XI	99	63	4.60	4.14	14	2.64	1.818	0.689	3.423
	XII	31	26	3.43	3.26	9	2.20	1.849	0.842	5.506
	XIII	11	10	2.40	2.30	4	1.39	1.034	0.746	2.045
EUP	XIV	3	3	1.10	1.10	2	0.69	–	–	–
	XV	1	1	–	–	1	–	–	–	–
	XVI	186	149	5.23	5.00	15	2.71	2.241	0.827	7.863
	XVII	479	376	6.17	5.93	26	3.26	2.200	0.675	5.762
	XVIII	54	47	3.99	3.85	13	2.56	2.127	0.829	6.890
	XIX	80	68	4.38	4.22	14	2.64	1.545	0.586	6.781
	XX	27	24	3.30	3.18	9	2.20	1.857	0.845	5.000
IUP	XXI	37	37	3.61	3.61	7	1.95	1.097	0.564	2.000
	XXII	173	160	5.15	5.08	12	2.48	1.015	0.409	1.775
	XXIII	16	16	2.77	2.77	5	1.61	1.160	0.721	2.553
	XXIV	3	3	1.10	1.10	3	1.10	–	–	–
MP	XXVIIIA	2	1	0.69	–	1	–	–	–	–

trial taxa). The habitats around the site would have been similar in the UP. In the EPI shells mainly originated from intertidal rocky and subtidal soft-bottom shores, as well as from wooded areas, whereas species from open and half-shaded terrestrial and marine subtidal rocky shore habitats were rarely taken back to the site. There is an especially marked change in the mollusc assemblage between the IUP and EUP, which cannot be explained by differences in sample size (see above). Possible reasons for this may be environmental change (e.g., in sea level and coastal morphology) and/or changes in human behaviour and exploitation patterns.

4.3. Metric analysis

Metric analyses were carried out on the four most abundant species, namely the terrestrial woodland gastropod *H. pachya*, the intertidal rocky shore gastropod *Ph. turbinatus*, the subtidal soft-bottom shore gastropod *N. gibbosulus*, and the subtidal rocky shore gastropod *C. rustica*. Shells of the genus *Patella* were measured but not used in the present biometric study, because the number of measurable specimens per species was not high enough for a meaningful analysis. Evaluation of the metric data for these four taxa allows us to compare changes in shell size of species from different habitats. It has been argued that size reduction in taxa that were consumed, might be the result of overexploitation (e.g., Mannino and Thomas, 2001; Klein et al., 2004; Erlandson et al., 2011; Klein and Steele, 2013). However, changes in shell size may also be caused by changing sea-surface temperatures, nutrient availability, and other environmental changes (e.g., Fa, 2008). Here we compare the metric data of live-collected marine taxa with those of which the empty shells were collected from beaches, in an effort to distinguish between potential overharvesting and environmental change. Gathering empty beached shells does not affect shell size in the respective living populations, whereas collecting of live specimens does. The preferential gathering of the largest molluscs by humans should, in fact, result in a decrease in mean shell size and, in more extreme cases, in the local extinction of the species in question (e.g., Klein et al., 2004). We argue that, if size change only occurred in marine molluscs collected for food and not in taxa collected as beached shells, the size change is more likely related to human predation. If, however, similar changes in size are seen for all three marine taxa (i.e., in *Ph. turbinatus*, *N. gibbosulus*, and *C. rustica* alike), these could more likely be ascribable to environmental change rather than to overexploitation by humans. Our results show that trends in shell dimensions (Fig. 4; Table 5) are similar for all three marine species: between the IUP and EUP a significant decrease in size occurs in *N. gibbosulus* (the trend is also present in *C. rustica* but is not significant). From the EUP, which saw the start of a more regular exploitation of *Ph. turbinatus*, to the UP, a significant increase in size is recorded for all three marine taxa. Both the fact that we are dealing with a size increase and that this occurred in species exploited for food and in species introduced for utilitarian purposes as empty shells, suggests that environmental change (e.g., changes in temperature and/or salinity) is the most likely cause for these changes. On the other hand, both *N. gibbosulus* and *Ph. turbinatus* decreased in size between the UP and EPI, but this was not statistically significant. No significant size-change has been observed in *H. pachya*.

4.4. Human mollusc and shell use

Our taphonomic investigations show that humans were likely responsible for introducing marine molluscs, and potentially *H. pachya*, to the Ksâr 'Akil deposits. The analysis of observed human modifications to the shells from Ksâr 'Akil may help to shed light on the purpose for which each taxon was gathered. The evidence suggests that live shellfish were transported to the site probably for subsistence purposes (van Regteren Altena, 1962; Bosch et al., 2013) and that the collection of empty shells served various utilitarian purposes, for instance use as tools (Douka, 2011) or body ornaments (Kuhn et al., 2001; Stiner et al., 2013).

4.4.1. Mollusc consumption

Species collected live include all rocky shore intertidal gastropods, as well as possibly freshwater and intertidal brackish wa-

Table 5
Comparison of size of *Helix pachya*, *Phorcus turbinatus*, *Nassarius gibbosulus* and *Columbella rustica* between technocomplexes (EPI: Epipalaeolithic, UP: Upper Palaeolithic, EUP: Early Upper Palaeolithic, IUP: Initial Upper Palaeolithic) showing trend in size (↑ = increase, ↓ = decrease, – = no difference, – = no data) and p values of pair-wise comparisons (Mann–Whitney U test; significant results in bold). H: maximum height, D: maximum diameter, A: aperture height.

Species	*Helix pachya*				*Phorcus turbinatus*				*Nassarius gibbosulus*				*Columbella rustica*			
Comparison	Trend	H	D	A	Trend	H	D	A	Trend	H	D	A	Trend	H	D	A
EPI-UP	–	0.77	0.67	0.58	↓	0.77	0.13	0.08	↓	0.42	0.27	0.06	–	–	–	–
UP-EUP	↓	0.55	0.68	0.84	↑	–	**<0.0001**	**<0.0001**	↑	**0.0001**	**<0.0001**	**<0.0001**	↑	**0.01**	0.81	**0.001**
EUP-IUP	–	–	–	–	–	–	–	–	↓	**0.001**	**0.001**	0.27	↓	0.37	0.23	0.91

ter taxa (excluding *Th. jordani* that shows signs of pre-depositional post-mortem taphonomic alterations), and the terrestrial gastropod *H. pachya*. Regarding the fresh/brackish water component, the low number of specimens and the absence of any anthropogenic modifications prevent a clear determination of the gathering purpose and, therefore, will not be considered further. Nevertheless, it is unlikely that freshwater and brackish water taxa were important in Upper Palaeolithic human subsistence at Ksâr ’Akil, given that their environments of origin were not common in the vicinity of the site.

Rocky shore intertidal gastropods include the topshells *Ph. turbinatus* and *Ph. articulatus* and the limpets *P. rustica*, *P. caerulea*, and *P. ulyssiponensis*. These molluscs can easily be gathered from rocky shores at low tides. Human collection of these taxa is evident from the overall integrity of their shells, the absence of encrusting organisms that settle on the inner shell surfaces after the death of the mollusc and of any other evidence of bioerosion, as well as from the presence of notches on the edges of *Patella* spp. specimens (n = 73; 50%), which is consistent with damage resulting from prying the animals off the rocks. Other human modifications include the intentional removal of the apex of *Phorcus* snails (n = 89; 16.5%) to facilitate flesh extraction (Fig. 5). This evidence strongly suggests that all these taxa were collected for dietary purposes.

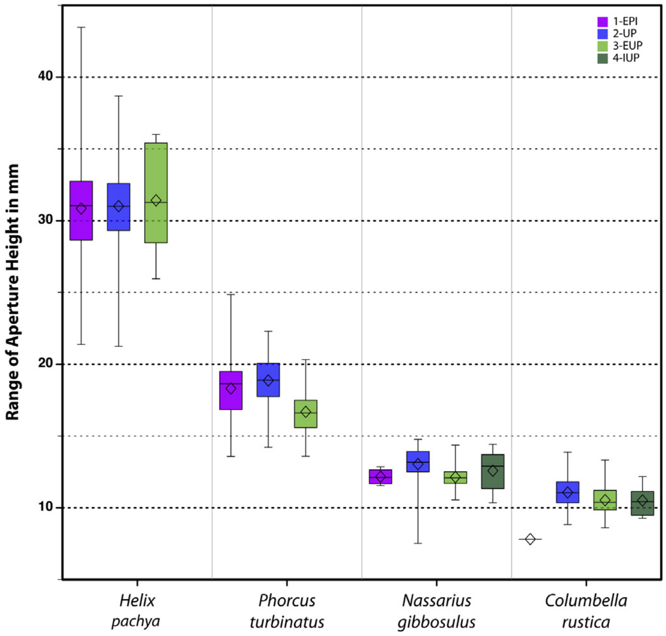

Fig. 4. Range of aperture height of *Helix pachya*, *Phorcus turbinatus*, *Nassarius gibbosulus* and *Columbella rustica* per archaeological technocomplex. The boxes of the boxplots represent 50% of the measurements. The whiskers show the full size range, and the midbar represents the median and the diamond the mean aperture height. EPI: Epipalaeolithic, UP: Upper Palaeolithic, EUP: Early Upper Palaeolithic, IUP: Initial Upper Palaeolithic.

Both van Regteren Altena (1962) and Ewing (1948) proposed the hypothesis that *H. pachya* was exploited as a food source. This assumption was in both cases based on its frequent occurrence in several archaeological layers, but *H. pachya* is adapted to a wider range of habitats and altitudes than any of the other terrestrial species, which might also in part be responsible for its common occurrence. Metric data (Fig. 6) show that *H. pachya* is solely represented by adult specimens. This suggests selective mortality rather than the composition of a natural assemblage (see also Gutiérrez Zugasti, 2011; Fernández-López de Pablo et al., 2014). Taking into account both size and quantity, it is possible that the Upper Palaeolithic occupants took the *H. pachya* specimens back to the site to be consumed. This helicid first occurs in the EUP deposits and is present up to the EPI layers (Table 2), suggesting it may have constituted a foodstuff. Recently, Fernández-López de Pablo et al. (2014) have listed Ksâr ’Akil as a Mediterranean site displaying positive evidence of land snail (undetermined species) exploitation as food source in the EPI based on data from the Tixier excavations (Tixier, 1974; Lubell, 2004).

4.4.2. Marine shells as raw material

Beached shells have been introduced to the site as raw material for tools (e.g., Douka, 2011) and potentially for ornaments (Kuhn et al., 2001; Stiner et al., 2013). Perforated shells, excluding perforations resulting from gastropod and/or crab predation, comprise bivalves (i.e., *Lima lima*, *Anadara* sp., *Acanthocardia tuberculata*, *Acanthocardia* sp., *G. nummaria*, and *Glycymeris* sp.), gastropods (i.e., *Bolinus brandaris*, *Bolma rugosa*, *Ceritium vulgatum*, *C. rustica*, *Conus ventricosus*, *Euthria cornea*, *Hexaplex trunculus*, *Mitra cornicula*, *N. gibbosulus*, *Nassarius mutabilis*, *Nassarius* sp., *Neverita josephinia*, *Pisania striata*, and the fresh water gastropod *Th. jordani*), and the naturally holed scaphopods (i.e., *Antalis dentalis*, *Antalis vulgaris*, and *Antalis* sp.). Marine taphonomic alterations, such as bioerosion caused by beach rolling, are the main factors contributing to these perforations, although some may be anthropogenic in origin. Bouzouggar et al. (2007) and d’Errico et al. (2009) compared perforation frequency and position in archaeological specimens of *Nassarius* with those in shells of the same taxon from modern thanatocoenoses, to evaluate human selectivity in shell gathering and establish whether the holes were anthropogenic or natural. A modern thanatocoenosis from Djerba in Tunisia (Bouzouggar et al., 2007) contained 44.2% of dorsally intact shells. In the Ksâr ’Akil assemblage 1.6% of *N. gibbosulus* shells (n = 11) and 3.2% of *C. rustica* (n = 13) shells were dorsally intact. The high proportion of perforated shells is not congruent with the modern thanatocoenosis data and suggests that *N. gibbosulus*, and possibly *C. rustica*, were either selectively gathered with damage and holes or were possibly perforated by Upper Palaeolithic humans. A more in-depth study of the perforations, including location, use-wear and residue analysis is planned and might provide more information on the nature and extent of human collection preferences and potential bead manufacture.

Some bivalves of *Glycymeris* sp. were collected to be used as tools. The best evidence of anthropogenic modification was found on a *Glycymeris* sp. valve reported by Douka (2011). The shell’s

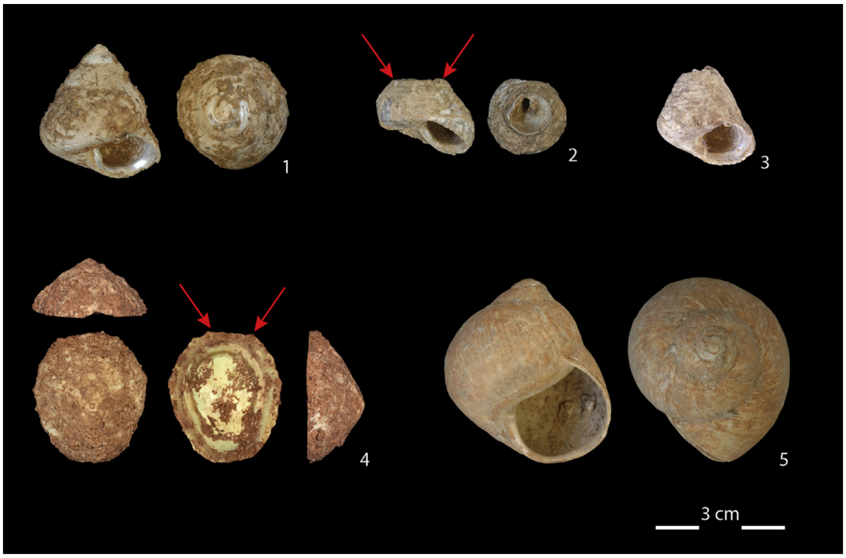

Fig. 5. Species gathered for consumption. 1: RGM-606318a, 2: RGM-606318b, *Phorcus turbinatus*; 3: RGM-606319, *Phorcus articulatus*; 4: RGM-606376, *Patella rustica*; 5: RGM-606532, *Helix pachya*. Anthropogenic modifications are indicated with arrows, 2: cut-off apex to facilitate shellfish extraction and 4: edge notches congruent with damage from prying molluscs off the rocks. Note the reddish dust on the surface of the *H. pachya* shell. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

peripheral rim shows clear retouch and was probably used as a scraper-like tool. Further, our investigations revealed that almost half of the *Glycymeris* valves had breaks resulting in long sharp edges ($n = 128$; 43%) that were possibly used as cutting implements. Some of these broken shells exhibit impact marks ($n = 15$), although it is unclear if these edges and impacts are anthropogenic or natural in origin (see Fig. 7). Other specimens show notches at one or both lateral sides of the umbo creating a small channel (e.g., Fig. 7: RGM-577868). Some of them are covered in red sediment. It is, therefore, conceivable that they were possibly used as small containers. Clearly, more detailed investigations have to be carried out before the archaeological use of individual specimens can be assigned. Here, marine shells that were collected empty and brought to the site are labelled 'non-food transported' specimens.

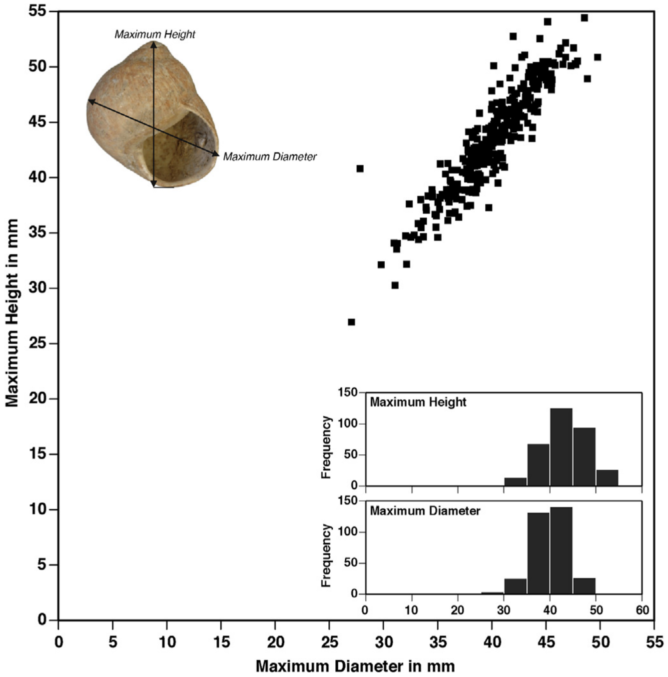

Fig. 6. *Helix pachya* measurements scatterplot: maximum basal diameter versus maximum shell height. Histograms show height (top) and maximum basal diameter (bottom) the number of shells (y-axis) in 5 mm groups (x axis). Measurement locations are shown on specimen RGM-606532 on the top left.

Changes in human exploitation patterns become evident when grouping molluscs in the following three categories: terrestrial, 'food', and 'non-food transported' taxa (Fig. 8). The purpose of mollusc and shell gathering changed from the sole collection of empty marine shells for manufacturing tools and ornaments in the IUP, to subsistence-focussed exploitation of selected marine and terrestrial species in the UP and EPI. Food species (including *H. pachya*) first occur in the IUP layers, and start to increase in numbers (both absolute and relative) from the EUP through the later UP and EPI layers, with a marked decrease in layers IX and X. The terrestrial component (excluding *H. pachya*) is small throughout the sequence.

4.5. Burning

Occasional burning (18.7%) resulting in a combination of heat cracks, discolouration (e.g., Stiner, 2005) and decalcification, is observed in the assemblage (Tables 1 and 6). In general, taxa collected by humans (i.e., food species: 14.4%; non-food transported species: 24.9%) show a higher degree of burning than terrestrial species (1.3%). There is a significant difference in burning rate amongst specimens belonging to the 1962 (16.5%) and the 2015 (25.0%) collections (χ^2 199.58, $p < 0.0001$). The higher burning rate in the more fragmentary '2015 collection' might stem from the fact that burned shells are more prone to fragmentation (e.g., Claassen, 1998). However, inclusion of the '2015 collection' does not significantly alter the rate of burning for the whole assemblage (χ^2 3.47, $p = 0.063$). The distribution of burning between food and non-food transported taxa is significantly different (χ^2 21.4, $p < 0.0001$). This burning damage might have resulted from direct or indirect (during deposition) exposure to heat. Direct heat exposure might result from roasting, waste removal practices, or accidental exposure while lying on the surface of the rockshelter after deposition. Indirect exposure to heat might have occurred by lighting a fire on top of deposits containing shell and, therefore, was not necessarily deliberate (Stiner et al., 1995). The frequency of burning in *H. pachya* ($n = 25$; 5.2%) is intermediate between that

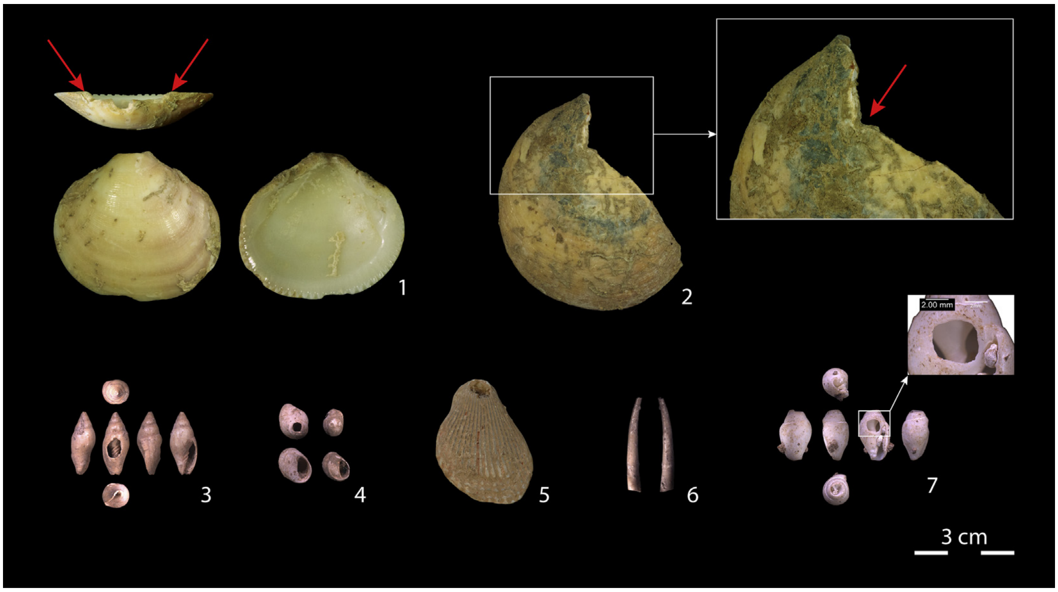

Fig. 7. Non-food transported species. 1: potential container, red arrows indicate impact points on both sides of the umbo; 2: Broken valve with long sharp edges, an impact point is indicated by the arrow in the inlet; 3, 4, 5, 7: Perforated shells. Shell species shown: 1: RGM-577868, 2: RGM-550206 *Glycymeris* sp.; 3: RGM-606218, *Mitra cornicula*; 4: RGM-606459a, b, *Theodoxus jordani*; 5: RGM-577824, *Lima Lima*; 6: *Antalis* sp.; 7: RGM-770825, *Columbella rustica* inlet detail of perforation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of all marine taxa (i.e. both ‘food’ and ‘non-food’ species) and other terrestrial gastropods. Hutterer et al., (2014) have suggested that cooking was probably necessary to extract mollusc flesh. However, cooking does not always leave recognizable taphonomic signatures, for example, when molluscs are boiled in water. Traces of burning may therefore not be informative in determining if *H. pachya* was gathered for subsistence purposes or not.

4.6. Ksâr ’Akil in its regional context

Few sites containing IUP deposits are known from the region (e.g., Goring-Morris and Belfer-Cohen, 2003), let alone sites with relatively large mollusc assemblages. The site of Üçağızlı I (Turkey) is the only recently excavated site with deeply stratified IUP and EUP deposits containing mollusc remains (e.g., Kuhn et al., 2001, 2009; Stiner et al., 2013). The IUP and EUP lithic technology at Üçağızlı I is very similar to that of Ksâr ’Akil (Kuhn et al., 2001) and a recently published account of the ornamental shells from this site (Stiner et al., 2013) enable us to evaluate our results in a regional context. The IUP and EUP at Üçağızlı I and Ksâr ’Akil largely overlap in age (e.g., Kuhn et al., 2009; Douka, 2013; Douka et al., 2013), although the IUP might start earlier at Ksâr ’Akil (Kuhn et al., 2001; Bosch et al., 2015). The Epipalaeolithic is much later at Üçağızlı I than at Ksâr ’Akil (Mellars and Tixier, 1989; Kuhn et al., 2009; Bosch et al., 2015). We, therefore, focus for our comparison on the IUP and EUP periods, which are very similar in many respects. There is a considerable overlap in species representation, diversity, and exploited habitats. At both sites, molluscs were transported for subsistence purposes and as raw material. The taphonomic signatures observed in the different groups of species (i.e., food species, non-food transported or ornamental species, and terrestrial species) are nearly identical including marine pre-depositional taphonomic alterations, the presence of localised decalcified patches (although in the case of Ksâr ’Akil these are not explained to be the results of root etching, as proposed to Üçağızlı I), as well as traces of burning (Stiner et al., 2013). At Üçağızlı I, marine food species are virtually absent from the IUP, but occur in high quantities in the EUP, the same being true for Ksâr ’Akil. Similarly, at both sites this pattern is also observed for the terrestrial molluscs. *H. pachya* is present at Üçağızlı I, albeit in low frequencies similar to other terrestrial molluscs, and it is hence not thought to have been introduced by the human occu-

Table 6
Burning damage by phase (MP – EPI), per layer (I – XXVIII A), and divided in food, non-food transported, and terrestrial taxa.

Burning					
Phase	Layer	n	Burned	Not burned	na
EPI	I	2		2	
	II	6		6	
	III	28		28	
	IV	22	1	21	
	V	242	8	234	
	Total EPI	*300*	*9*	*291*	
UP	VI	103	6	97	
	VII	272	30	242	
	VIII	195	17	177	1
	IX	448	46	398	4
	X	122	19	103	
	XI	466	139	326	1
	XII	61	12	49	
	XIII	11	2	9	
	Total UP	*1678*	*271*	*1401*	*6*
EUP	XIV	3		3	
	XV	2		2	
	XVI	220	59	161	
	XVII	646	169	476	1
	XVIII	72	15	57	
	XIX	191	21	169	1
	XX	48	8	39	1
	Total EUP	*1182*	*272*	*907*	*3*
IUP	XXI	60	23	37	
	XXII	198	72	126	
	XXIII	22	8	12	2
	XXIV	9	1	5	3
	Total IUP	*289*	*104*	*180*	*5*
MP	XXVIIIA	2		2	
na	na	117	11	106	
Total	**Food**	**1163**	**167**	**992**	**4**
	Non-food	**1690**	**421**	**1260**	**9**
	Terrestrial	**228**	**3**	**225**	
	na	**487**	**76**	**410**	**1**
	n	**3568**	**667**	**2887**	**14**

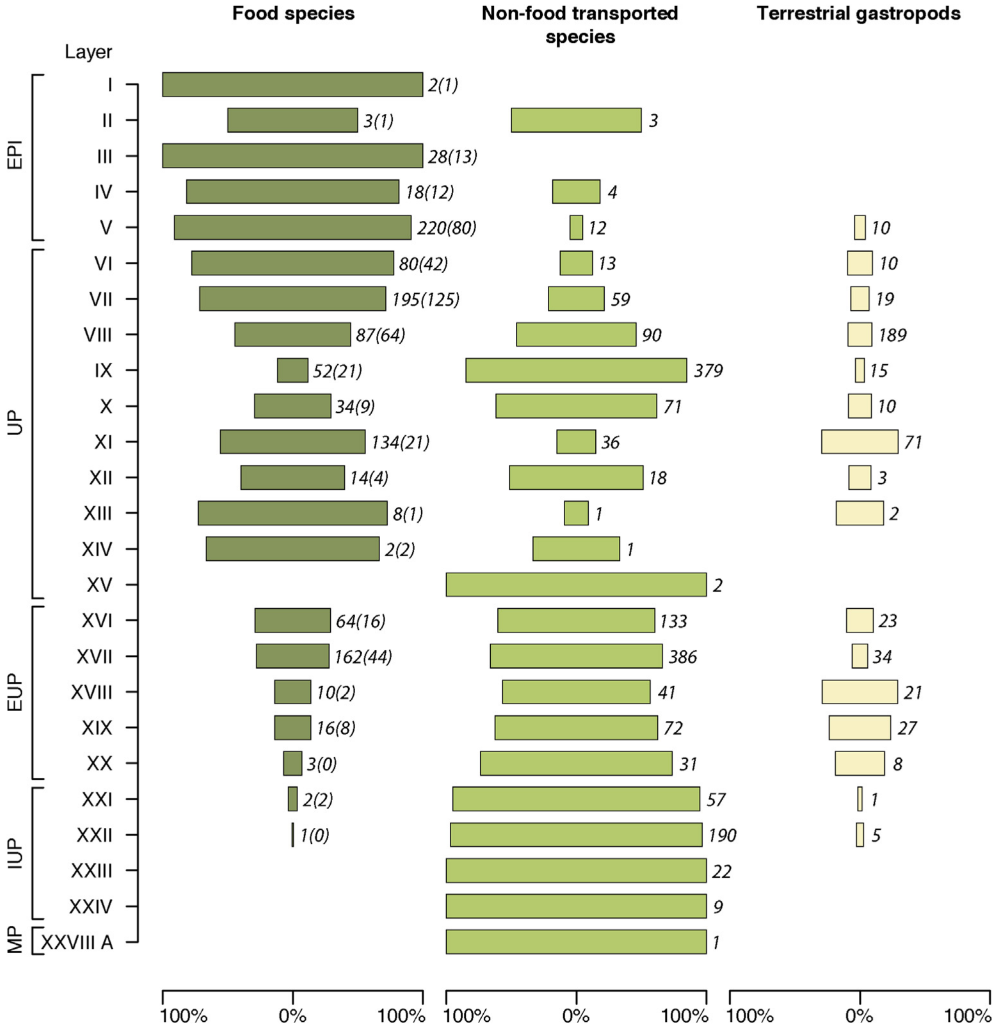

Fig. 8. Frequency and number of identified specimens per mollusc use through time by Layer (I–XXVIII A) and per Phase (MP–EPI). Dark green: food species (*Phorcus turbinatus*, *Phorcus articulatus*, *Patella rustica*, *Patella caerulea*, *Patella ulyssiponensis* and *Helix pachya*), Light green: non-food marine transported species, Yellow: non-food terrestrial species. Note: *Helix pachya* numbers are provided in brackets next to the food-species column. MP: Middle Palaeolithic; IUP: Initial Upper Palaeolithic; EUP: Early Upper Palaeolithic; UP: Upper Palaeolithic; EPI: Epipalaeolithic. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

pants of the cave for consumption. Stiner et al. (2013) see a weak positive correlation in species diversity through time at Üçağızlı I, which is not evident at Ksâr 'Akil. However, although the IUP and EUP deposits are quite similar, the later Palaeolithic sequences are markedly different in composition and age. The Ksâr 'Akil sequence contains a 10 m thick package of UP (roughly 42–31 ka cal BP) and EPI (<31–29 ka cal BP) deposits that cover the time-gap between the EUP and EPI (around 17 ka cal BP) at Üçağızlı I (Kuhn et al., 2009; Bosch et al., 2015). Therefore, trends through time could be a consequence of differences in chronology rather in differences in environmental conditions or human behaviours. Moreover, diversity indices were calculated for the total assemblage at Ksâr 'Akil, whereas they are only based on a single subgroup (i.e., ornamental species) in the study by Stiner et al. (2013). Nevertheless, species as well as habitat diversity are remarkably similar in their marked contrast between low diversity in the IUP and the much higher EUP values.

The comparison of these two Levantine Palaeolithic mollusc assemblages has also exposed some differences. In general, at Ksâr 'Akil, freshwater species, and specifically *Th. jordani*, are present in lower quantities. Scaphopods at both sites occur only sporadically, in the EPI at Üçağızlı I, and in UP Layer IX at Ksâr 'Akil. Additionally, at Üçağizli I tusk shells are fossil and probably collected from fossil marine deposits, whereas at Ksâr 'Akil at least some of them have been collected from active beaches. Bar-Yosef Mayer (2005) mentions *N. gibbosulus*, *Nassarius* sp., *C. rustica*, *Glycymeris* sp., *Mitrella scripta*, *Antalis* (*Dentalium*) sp., and *Theodoxus* sp. as common ornamental taxa, albeit found in varying frequencies in the Levantine Upper Palaeolithic. At Ksâr 'Akil the former four species are abundant, and the latter three are rare or absent. Furthermore, the rare perforation method observed in *N. josephina* and *Naticarius stercusmuscarum* at Üçağızlı I is absent at Ksâr 'Akil. More work on perforated shell (e.g., use-wear analysis, detailed investigation of perforation locations, etc.) is needed before any taxa can be reliably interpreted as being of ornamental use. For now, it suffices to say that the Ksâr 'Akil mollusc assemblage is not unique in its composition and as a source of evidence for Upper Palaeolithic human coastal adaptations. However, it offers great potential to provide a wealth of information on the human behaviour of its occupants and of hunter–gatherers in the Levant. Further studies aimed at the reconstruction of Palaeolithic human subsistence activities linked to the exploitation of marine molluscs are being conducted on the marine shells from Ksâr ’Akil to establish the role of shellfish in hunter–gatherer diets in the Levant, for instance through oxygen isotope analyses aimed at determining whether intertidal gastropods were exploited year-round or seasonally.

5. Conclusions

At Ksâr ’Akil, most mollusc shells discarded after shellfish consumption were gathered from intertidal rocky shores, while shells collected for ornamental purposes originate from subtidal soft and rocky shore habitats. The constant presence of molluscs from these intertidal and subtidal habitats suggests that coastal environments did not change significantly during the different phases of site occupation. Land snail species most frequently originate from open and half-shaded, as well as woodland, habitats suggesting these environments were available in the immediate vicinity of the site throughout the Upper Palaeolithic. Arid or semi-desert taxa as well as freshwater taxa are rare, as are brackish water species and deep marine soft bottom deep subtidal or bathyal taxa (i.e., *Antalis* spp.). Changes in marine mollusc size appear to have been driven by environmental factors (e.g. sea surface temperature, nutrient, and/or salinity fluctuations), rather than by overexploitation by humans. Mean shell size of *Ph. turbinatus* increased significantly between the EUP, when shellfish exploitation was first practised on a larger scale, and the subsequent UP. Moreover, trends in shell size are similar for all three measured species including *N. gibbosulus* and *C. rustica* that were collected dead and, therefore, unaffected by human predation.

Occasionally, shells were additionally gathered from fossil marine terraces. Shells of marine bivalves were collected and potentially used as raw material for a variety of tools (such as scrapers, knives and possible containers). Perforated specimens were probably used as ornaments. Whereas the collection of beached shells started in the IUP, shellfish exploitation was mainly practised from the EUP onward and focussed on the intertidal rocky shore limpets and topshells. The terrestrial taxon *H. pachya* was possibly used as a source of food. The number of molluscs exploited for food increased over time, both in absolute and relative terms. Further, marine taxa introduced to the site by humans show a higher degree of burning than do terrestrial species in which burning damage is nearly absent. Comparisons with the IUP and EUP mollusc assemblages from Üçağızlı I highlight the great similarities in species diversity, habitat exploitation, and human mollusc use. This suggests that the coastal adaptations documented at Ksâr ’Akil were typical of hunter–gatherers across the Levantine region.

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Chapter 6 ・Year-round shellfish exploitation in the Levant and implications for Upper Palaeolithic hunter-gatherer subsistence

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Year-round shellfish exploitation in the Levant and implications for Upper Palaeolithic hunter-gatherer subsistence

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Abstract

Recent studies have shown that the use of aquatic resources has greater antiquity in hominin diets than previously thought. At present, it is unclear when hominins started to habitually consume marine resources. This study examines shellfish exploitation from a behavioural ecology perspective, addressing how and when past hunter-gatherers from the Levant used coastal resources for subsistence purposes. We investigate the seasonality of shellfish exploitation in the Levantine Upper Palaeolithic through oxygen isotope analysis on shells of the intertidal rocky shore mollusc *Phorcus (Osilinus) turbinatus* from the key site Ksâr 'Akil (Lebanon). At this rockshelter, multi-layered archaeological deposits contained remains of both marine and terrestrial molluscs in relatively large quantities, which were consumed and used as tools and ornaments by the occupants of the site. Our results indicate that at the start of the Initial Upper Palaeolithic (IUP), there is no evidence for shellfish consumption. Humans started to take fresh shellfish to the rockshelter from the second half of the IUP onward, albeit in low quantities. During the Early Upper Palaeolithic (EUP) shellfish exploitation became increasingly frequent. Oxygen isotope data show that shellfish exploitation was practised in every season throughout most of the Upper Palaeolithic (UP), with an emphasis on the colder months. This suggests that coastal resources had a central role in early UP foraging strategies, rather than a seasonally restricted supplementary one. Year-round shellfish gathering, in turn, suggests that humans occupied the

rockshelter at different times of the year, although not necessarily continuously. Our oxygen isotope data is complemented with broader-scale exploitation patterns of faunal resources, both vertebrate and invertebrate, at the site. The inclusion of coastal marine resources signifies a diversification of the human diet from the EUP onward, which is also observed in foraging practices linked to the exploitation of terrestrial fauna.

1 Introduction

Recent archaeological discoveries indicate that the exploitation of aquatic resources has a long history among various hominin species. The earliest evidence of the exploitation of freshwater fish was documented from Koobi Fora, Kenya about 1.95 million years ago (Braun et al. 2010) for *Homo ergaster/erectus*, who made Oldowan tools. *Homo erectus* individuals may have consumed freshwater molluscs from approximately ≥ 400 thousand years ago (kya) in Trinil (Java, Indonesia) (Joordens et al. 2014). During Marine Isotope Stages (MIS) 6 and 5 (roughly 190–125 kya and 125–80 kya, respectively), Middle Stone Age (MSA) *Homo sapiens* exploited shellfish at several South African coastal sites (e.g. Klein et al. 2004; Avery et al. 2008; Jerardino and Marean 2010; Langejans et al. 2012; Clark and Kandel 2013; Kyriacou et al. 2015; Jerardino 2016). In the Mediterranean region, marine molluscs were exploited during the Middle Palaeolithic both by *H. sapiens* and *Homo neanderthalensis* from MIS 5 onward (e.g., Emiliani et al. 1964; Klein and Scott 1986; Stiner 1999; Finlayson et al. 2006, 2008; Colonese et al. 2011; Cortés-Sánchez et al. 2011; Barker et al. 2012; Fa et al. 2016).

Thus, aquatic resources played a role in early hominin diets, although their contribution has been considered as marginal for most of the Palaeolithic (e.g., Erlandson and Moss 2001; Colonese et al. 2011; Clark and Kandel 2013; Jerardino 2015). This is especially true when optimal foraging models are used, which primarily consider the caloric value and energy intake of foodstuffs (see also Grayson and Delpech 1998; Stiner, 2001, 2010). However, from a nutritional ecology perspective, shellfish are a rich source of many essential nutrients, including vitamins (i.e., A, B12, C, D, and E), iron, folate, potassium, calcium, and omega-3 fatty acids (e.g., Hockett and Haws 2003; Haws and Hockett 2004; Cunnane and Crawford 2014; Kyriacou et al. 2015). Due to their high polyunsaturated (or omega-3) fatty acid content in the form of docosahexaenoic acid and its importance for brain development, shellfish and aquatic food sources in general are thought to have been important in human brain expansion and evolution (e.g., Brenna and Carlson 2014; Cunnane and Crawford 2014; Joordens et al. 2014; Kyriacou et al. 2014). With regard to nutritional ecology, Hockett and Haws (2003; Haws and Hockett 2004) suggest that broader and nutritionally rich diets increase hominid fitness, aid to reduce child mortality, and inter-birth intervals. This in turn, would allow for population increase as for example the increase in population density thought to coincide with the start of the UP (e.g., Mellars and French 2011; French 2015).

Most of the above-mentioned essential nutrients can also be obtained in reasonable quantities through the consumption of animal organs and/or plant foods, with the possible exceptions of vitamins D and omega-3 fatty acids, which are more difficult to obtain from other, terrestrial, sources. However, due to their limited visibility in the archaeological record, it is often hard to assess the role that organ meat and plant foods played in hominin diets. Whereas shellfish are convenient 'food packages', providing an array of essential nutrients not combined in other food sources and, if available, are ideal to assess the nutritional breadth of the diet. Here we use oxygen isotope analysis as a tool to determine the nature and seasonal timing of UP shellfish exploitation. Seasonality of shellfish exploitation data, derived from oxygen isotope analysis, allow us to explore questions about whether coastal environments were used as a supplementary resource in lean times, or if they occupied a more central-place in past foraging strategies and accessed throughout the year. We further investigate whether shellfish gathering was a result of intensification of food resources with increased residency and or population pressure (e.g., Stiner et al. 2013; Marean 2014) through comparisons with exploitation patterns of other faunal resources.

Moreover, data on the periodicity of mollusc collection are helpful for gaining a fuller understanding of coastal foraging strategies (e.g., Mannino et al. 2007, 2014; Colonese et al. 2009; Prendergast et al. 2016) and allow us to address questions regarding behavioural ecology. For example, how prehistoric hunter-gatherers moved in the landscape or how they used their surroundings for raw material procurement (e.g., bivalves of *Glycymeris* sp. for the manufacture of utilitarian objects or perforated shells for personal ornamentation) or foraging. In addition, these data can be used as a proxy for the timing of site occupation (e.g., Shackleton 1973; Mannino et al. 2011). Here we investigate seasonality of shellfish exploitation by modern humans in the eastern Mediterranean UP using the Ksâr 'Akil (Lebanon) shell assemblage as a case study. To do this we conducted oxygen isotope analysis of the most common edible marine mollusc, *Phorcus turbinatus*. These data on coastal foraging are complemented with broader patterns of faunal resource and habitat exploitation.

2 Ksâr ‘Akil and its palaeoenvironmental setting

The Ksâr ‘Akil rockshelter is situated close to the eastern Mediterranean coast, approximately 10 km north of Beirut, Lebanon (Fig. 1). Its multilayered sequence is 23 m deep and spans the Middle Palaeolithic (MP) to the Epipalaeolithic (EPI) (e.g., Ewing 1947; Mellars and Tixier 1989). It yielded several human fossils (Ewing 1960; Bergman and Stinger 1989; Tillier and Tixier 1991) that are associated with rich archaeological assemblages (Fig. 2). Virtually all mollusc remains were found in UP deposits (van Regteren Altena 1962; Inizan and Gaillard 1978). The UP sequence at Ksâr ‘Akil comprises roughly the upper 16 m of sediments. In this study, the sequence is subdivided following the division in archaeological layers by Williams and Bergman (2010; see also Tixier and Inizan 1981; Azoury 1986; Marks and Volkman 1986; Bergman and Goring-Morris 1987; Kersten 1987; Bergman 1988; Bergman and Stinger 1989; Mellars and Tixier 1989; Ohnuma and Bergman 1990; Douka et al. 2013; Leder 2014; Bosch et al. 2015a). Calibrated age estimates (after Bosch et al. 2015a; see also Mellars and Tixier 1989; Douka et al. 2013; 2015; Bosch et al. 2015b) are provided at the 68.2% probability level. The lowermost UP Layers XXV–XXI comprise so-called Initial Upper Palaeolithic (IUP) assemblages *sensu* Kuhn et al. (1999), and date to at least 44,600–43,000 cal BP, however the base (i.e., Layers XXV–XXIV) of the IUP remains undated, due to lack of shells or other datable materials from those layers. The IUP is followed by the Early Upper Palaeolithic (EUP) or early Ahmarian deposits (Layers XX–XIV) dating to 43,300–42,800 cal BP. These are overlain by two “unnamed UP phases” (Layers XI–XIII and IX–X, respectively) *sensu* Williams and Bergman (2010) the lithic assemblages of which show both early Ahmarian and (Levantine) Aurignacian affinities. These two phases are grouped into a broader “UP”, because of the lack of consensus over their archaeological attribution (e.g., Bergman and Goring-Morris 1987; Williams and Bergman 2010). The subsequent Layers VIII–VII are classic (Levantine) Aurignacian and together with the two previous “unnamed UP” phases, this part of the sequence dates between 41,900 and 32,800 cal BP. Layer VI has been attributed to the Atlitian by Williams and Bergman (2010) and has an age range of 32,700–31,900 cal BP. The top Layers V–I have been described as Epipalaeolithic. The lowest of these layers (i.e., Layer V) is dated to 30,200–29,700 cal BP and a reassessment of the lithics may be prudent in relation to this date.

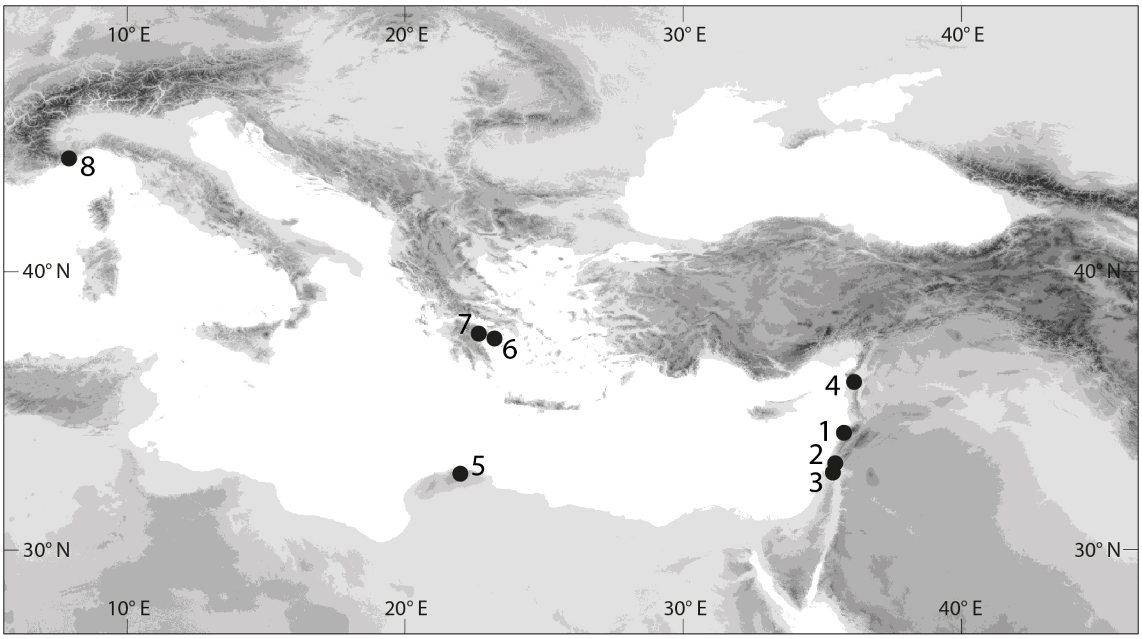

Figure 1: Map of eastern Mediterranean showing location of Ksâr 'Akil and sites discussed in text. 1: Ksâr 'Akil. – 2: Manot. – 3: Hayonim. – 4: Üçağızlı I. – 5: Haua Fteah. – 6: Franchti. – 7: Klissoura. – 8: Riparo Mochi. Digital elevation data originates from the Shuttle Radar Topography Mission (https://lta.cr.usgs.gov/SRTMBasic), downloaded from USGS Earth Resources Observation and Science (EROS) Center (http://eros.usgs.gov).

Ksâr ‘Akil is located about 3 km from the present-day coast, on the northern limestone slope of the Antelias Valley at an elevation of approximately 80 m above sea level (Ewing 1947; Wright 1962). In prehistoric times, the south-facing rockshelter would have been protected by a hill in the centre of the valley that was quarried away in historic times (Bergman et al. 2012). From the site, hunter-gatherers would have had access to a range of different landscapes, from the mostly rocky shores of the Bay of St. George and its small coastal plain to the steep slopes of the Lebanon Mountains; the top of the mountain range leads to the open highlands of the El Beqaa Valley. Freshwater was available from the stream running down the Antelias Valley and presumably from local springs (Ewing 1947).

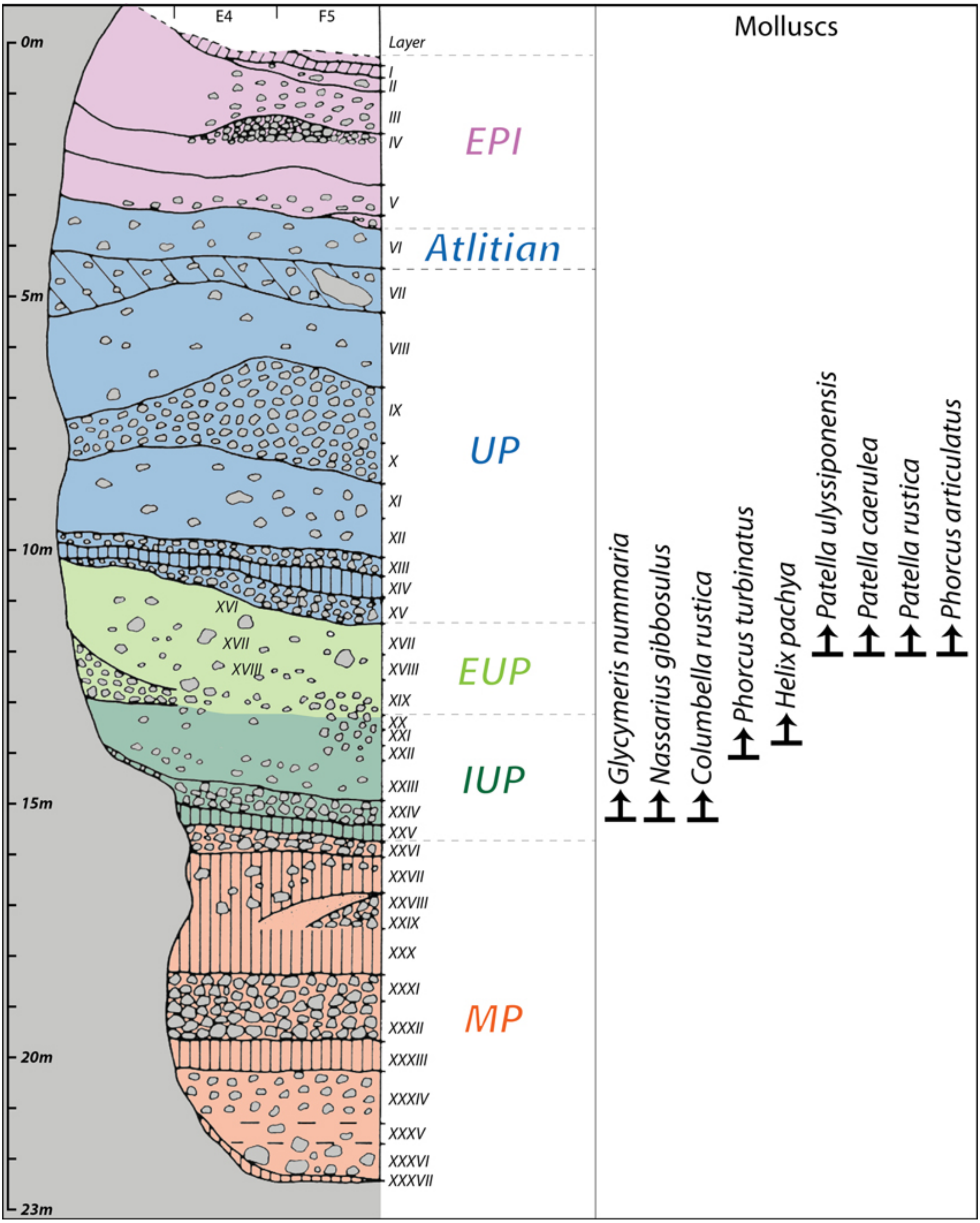

Figure 2: Ksâr 'Akil stratigraphy divided in the following phases: EPI: Epipalaeolithic, UP: Upper Palaeolithic, Atlitian, EUP: Early Upper Palaeolithic or Early Ahmarian, IUP: Initial Upper Palaeolithic, MP: Middle Palaeolithic, and the first occurrence of the main mollusc taxa discussed in the text.

The recovered faunal assemblage includes both terrestrial and aquatic molluscs, as well as avian and terrestrial vertebrates and provides us with additional information on the available habitats surrounding Ksâr ‘Akil (Table 1).

Table 1: Habitat diversity (based on various faunal indicators) per archaeological phase. Presence is indicated by a x. Habitats exploited by humans shown in bold. Birds: Kersten 1991; small (S) mammals: Kersten 1992; large (L) mammals: Hooijer 1961 and this study; molluscs: van Regteren Altena 1962 and Bosch et al. 2015c. Abbreviations: EPI: Epipalaeolithic, UP: Upper Palaeolithic, EUP: Early Upper Palaeolithic, IUP: Initial Upper Palaeolithic, MP: Middle Palaeolithic.

	habitat	forest	open woodland	steppe/ grassland	steep rocky country	freshwater	brackish	marine
EPI	*birds*	x	x		x	x		
	S mammals							
	L mammals	**X**	**X**	**X**	(x)			
	molluscs	**X**	x					**X**
	all EPI	**X**	**X**	**X**	x	x		**X**
Atlian	*birds*							
	S mammals							
	L mammals	**X**	**X**	**X**	(x)			
	molluscs	**X**	x			x		**X**
	all Atlian	**X**	**X**	**X**	(x)	x		**X**
UP	*birds*	x	x	x	x	x		
	S mammals	x						
	L mammals	**X**	**X**	**X**	(x)			
	molluscs	X	x			x		**X**
	all UP	**X**	**X**	**X**	x	x		**X**
EUP	*birds*	x	x		x	x		
	S mammals		x					
	L mammals	**X**	**X**	**X**	**X**			
	molluscs	**X**	x			x	(x)	**X**
	all EUP	**X**	**X**	**X**	**X**	x	(x)	**X**
IUP	*birds*				x			
	S mammals							
	L mammals	**X**	**X**	**X**	**X**			
	molluscs	**X**	x					**(X)**
	all IUP	**X**	**X**	**X**	**X**			**(X)**
MP	*birds*	x	x		x			
	S mammals							
	L mammals	**X**	**X**	**X**				
	molluscs							(x)
	all MP	**X**	**X**	**X**	x			(x)

The occurrence of terrestrial snails suggests that there were wooded (e.g., *Buliminus labrosus, Pene syriacus, Cristataria porrecta,* and *Helix pachya*) as well as open- to half-shaded habitats (e.g., *Pomatias elegans, P. olivieri, Oxychilus syriacus, Metafructicola berytensis, Monacha nummus,* and *M. syriaca*) in the vicinity of the site (Bosch et al. 2015c). Freshwater molluscs are rare and comprise *Theodoxus jordani, Melanopsis buccinoidea,* and *Potamida littoralis*. The latter adapted to lower-energy regimes (i.e., slow-flowing and /or stagnant water bodies). There is no brackish water component among the assemblage. A bivalve fragment (RGM-639547) thought to belong to *Cerastoderma glaucum* was misidentified and is actually a juvenile of *Acanthocardia tuberculata* (Bosch et al. 2015c). Additionally, marine intertidal rocky shore, soft and hard substrate subtidal taxa were recovered (van Regteren Altena 1962; Bosch et al. 2015c). Taphonomic signatures on the shells suggest that most marine taxa, excluding those from intertidal rocky shores, were collected as beached specimens, either from active beaches or from fossil beach deposits.

Avian taxa, studied by Kersten (1991), include open woodland (e.g., *Sturnus vulgaris*, *Columba palumbus*, and *Turdus* sp.), forest (e.g., *Garrulus gladarius* / *Pica pica*), rocky country (e.g., *Bubo bubo*, *Gyps fulvus*, *Aegypius monachus*, *Aquila* cf. *chrysaetos*, *Alectoris chukar*, and *Columba livia/oenas*), aquatic (e.g., *Phalacrocorax pygmaeus*, *Cygnus* sp., *Anas platyrhynchos*, *Anser* sp. / *Branta* sp., and *Anas* sp.), and perhaps open grassland (e.g., cf. *Otis tarda* and *Anser* sp. / *Branta* sp.) species. The occurrence of aquatic birds suggests the presence of standing or slow-flowing freshwater bodies with adjacent marshy or swampy areas, although most of the taxa are known as winter guests, which at that time of the year are also known to frequent brackish or saltwater habitats (Kersten 1991). No human modifications were found on the bird remains and it, therefore, is uncertain whether the accumulation of bird bones resulted from the activity of animal predators or humans. Small mammal remains, also studied by Kersten (1992), are extremely rare in the UP assemblages and only include the forest dweller, *Sciurus anomalus*, and the woodland taxon *Erinaceus europaeus*.

The large mammals are represented by a mix of open (e.g., *Gazella* cf. *dorcas* and *Capra aegagrus*), open woodland (e.g., *Bos* sp*, Cervus elaphus,* and *Dama mesopotamica*), and forest (e.g., *Sus scrofa* and *Capreolus capreolus*) taxa (Hoojier 1961; Bosch et al. 2015a). Thus, the combined faunal assemblages confirm the presence of forests, open woodlands, grasslands or steppes, rocky terrain, freshwater bodies, estuaries/lagoons, and marine habitats in proximity to the rockshelter.

Additionally, anthropogenically-modified mammalian and mollusc remains allow us to make inferences on the habitat types that were exploited by the prehistoric occupants of the site (Table 1 bold). These data suggest that a mix of open (e.g., *Gazella* cf. *dorcas and Capra aegagrus*), open woodland (e.g., *Bos* sp*, Cervus elaphus,* and *Dama mesopotamica*), and forest (e.g., *Sus scrofa* and *Capreolus capreolus*) habitats were exploited throughout the occupation of the site, whereas steeper rocky terrain (e.g., *Capra ibex*) and intertidal marine rocky shores (e.g., *Phorcus turbinatus, Ph. articulatus, Patella. caerulea, P. rustica,* and *P. ulyssiponensis*) started to be used from the upper layers of the IUP onward (see also Hooijer 1961; Kersten 1987; Bosch et al. 2015a, 2015c). Here we focus on UP coastal adaptations and, specifically, the exploitation of intertidal rocky shore molluscs by the hunter-gatherers who occupied Ksâr 'Akil.

3 Materials and Methods

3.1 The Ksâr 'Akil mollusc assemblage

The excavations of the 1930s and 1940s were the only ones to explore the entire archaeological sequence of Ksâr 'Akil. To get an overview of mollusc exploitation from the earliest IUP through the Epipalaeolithic, it was thus necessary to study the mollusc assemblages of these initial excavation campaigns. These included both the molluscs originally described by van Regteren Altena (1962) and recently discovered material found during the study of the vertebrate faunal assemblage in the Naturalis collections (Bosch et al. 2015c). All shell samples are currently housed at the department of Fossil Mollusca at Naturalis Biodiversity Center, Leiden.

Regression analyses indicate that both shell completeness (i.e., interdependence after Grayson 1984) and sample size do not differ significantly between layers, suggesting that a chronological evaluation of the material is warranted (Bosch et al. 2015c). The assemblage under study is consistent with preliminary data published by Ewing (1947, 1948, 1949) indicating that the collection did not suffer extensively from post-excavation loss of material or, at least, that this did not majorly alter the composition of the assemblage.

Unfortunately, different datum points were used in the various excavation seasons, making it difficult to correlate the recovered assemblages (Williams and Bergman 2010). The provenience data further differed per square. Some squares were labelled with the layer, square, and depth below datum, whereas for others only square and depth below datum were provided. Lists based on notes of the original excavators that provide depths per square were used to link the assemblages (Kersten, personal communication 2010; Hooijer 1961; Kersten 1991). Based on lithic studies, Williams and Bergman (2010) suggest that layers from the 1940s excavations correlate with deeper layers of the 1930s excavations probably due to geological sloping processes. The correlation based on the above-mentioned lists indeed shows a certain amount of sloping from the wall of the rockshelter toward the Antelias Valley, indicating that the excavators were aware of this situation and with these lists attempted to correct the offset. However, the studied material comes from old excavations, which inevitably introduces a level of uncertainty regarding find provenance. As a result of these issues, the oxygen isotope data have been grouped in broader archaeological phases, taking the excavation year into account to overcome the potential problems mentioned by Williams and Bergman (2010).

3.2 Sample selection

The intertidal gastropod *Phorcus turbinatus* was chosen as a proxy to investigate the seasonality of shellfish exploitation, because it is the most abundant marine mollusc species collected for human consumption in the Ksâr 'Akil assemblage (Bosch et al. 2015c). In addition, the physiology of *Ph. turbinatus*, a fully marine gastropod with low tolerance for temperature and salinity changes (e.g., Schifano and Censi 1983), makes it an ideal taxon to investigate sea surface temperatures (SST). It avoids locations where major fluctuations in salinity occur and lives in the lower inter-tidal zone that is regularly flushed out by tidal action (Mannino et al. 2008), even though such action would be relatively minor within the Mediterranean Basin. When salinity levels are stable, $\delta^{18}O$ values in shell carbonates can provide information about past SST (e.g., Epstein et al. 1951, 1953; Lécuyer et al. 2004). Moreover, for a species to be a good palaeoclimatic indicator, it should grow year-round and deposit measurable amounts of material in each season (Shackleton 1973). Unfortunately, we have not been able to carry out a modern validation study to ascertain whether *Ph. turbinatus* from the shores surrounding Ksâr 'Akil can be used as a reliable, seasonally resolved, SST proxy, due to the current political unrest in the area. However, several modern validation studies have been undertaken on living specimens of *Ph. turbinatus* populations in the Central and Eastern Mediterranean Sea (e.g., Schifano and Censi 1983; Mannino et al. 2008; Colonese et al. 2009; Prendergast et al. 2013, 2016). These studies show that *Ph. turbinatus* shell carbonate $\delta^{18}O$ compositions are strongly negatively correlated to SST and can, therefore, be used to study the seasonality of shellfish exploitation by prehistoric humans. Similar validation studies have recently been conducted for members of the genus *Patella* (Fenger et al. 2007; Surge et al. 2013; Prendergast and Schöne 2017; Gutiérrez-Zugasti et al. 2017), suggesting they are equally suited as paleo-SST indicators and the season of collection of a few *Patella* spp. specimens from our material was also included in the discussion.

An important prerequisite for obtaining biogenic isotope data, essential for the accurate estimation of season of collection, is that shell carbonates have not been subject to significant pre- or post-depositional diagenesis and recrystallization (e.g., Mannino et al. 2003). If this were the case, isotopic exchanges may have affected the shells, resulting in incorrect estimations of seasonality of shellfish exploitation. *Phorcus turbinatus* specimens were selected for analysis based on state of preservation and size (and thus age) following Mannino et al. (2008). Only *Ph. turbinatus* specimens in which the aragonitic layer resembled most that of living specimens, which is generally translucent and, as typical of nacreous microstructures, characterized by iridescent mother-of-pearl were selected. In fact, Milano et al. (2016) recently investigated the effects of exposure to heat on *Ph. turbinatus* shell microstructure. They found that in shells that were boiled, no significant change in structure or chemistry occurred. Shells that were roasted began to show changes in chemistry and structure only above 300°C and these changes were also visible by the naked eye. The shells in our study all preserved the mother of pearl appearance and following Milano et al. (2016) should have endured no significant chemical alteration. This implies that the specimens analysed in our study probably yielded biogenic values useful for an accurate estimation of season of death. Care was also taken to select shells with intact aperture edges and without any growth defects in the form of repair of ante-mortem damage or marked stops in growth parallel to the aperture edge.

To assess preservation, a selection of shells was cross-sectioned and stained with Feigl's solution, to test if the aragonite of the inner shell layer (i.e. the one sampled for isotopic analyses) had been subject to diagenesis. X-ray diffraction was also conducted on selected specimens to verify whether the internal layer was aragonitic and, thus, not affected by diagenesis. Shells were ground into a fine powder with a mortar and pestle and passed through a 90µm sieve. Approximately 0.1 mg was loaded onto a Si low background sample holder. All data were collected in Bragg-Brentano geometry on a D8 Bruker diffractometer equipped with a primary Ge monochromator for Cu Ka1 and a Sol-X solid state detector. Collection conditions were: 20-60° in 2θ, 0.02 step size, 4 seconds/step, divergence slits 0.2 mm, receiving slit 0.2 mm, sample spinner on. Rietveld refinements were performed with software Topas 4.1. Aragonite and calcite crystal structures were retrieved from the Crystallographic Open Database (http://www.crystallography.net/cod/) and from the Inorganic Crystal Structure Database (https://cds.dl.ac.uk) respectively. The March-Dollase model for preferred orientation was applied on the following crystal planes: (0 0 1) and (1 0 0) for aragonite; (1 0 4) for calcite. No structural parameter was refined. Peak shapes of all phases were modelled using Pseudo-Voigt functions. Further, Raman spectroscopy to determine the composition of the shell carbonates was carried out on several shells using a Horiba Jobin Yvon LabRam 800 spectrometer equipped with Olympus BX41 optical microscope (University of Mainz). It employed a 532.21 nm laser wavelength, a 400 µm confocal hole, a grating with 1800 grooves/mm, an entrance slit width of 100 µm, and 50× long-distance objective lens. The data were acquired with a time window between 3 and 5 seconds. For each sample, two measurements were taken in each shell layer. Furthermore, amino acid racemization (AAR) was conducted on three to five specimens per layer to verify the extent of intracrystalline protein diagenesis and to detect potentially compromised samples (see Penkman et al. 2008; Demarchi et al. 2015).

3.3 Methodology for deriving season of collection

In this study, we adopt the approach to establish seasonality of *Phorcus lineatus* collection originally proposed by Mannino et al. (2003) and further developed and adapted to *Ph. turbinatus* by Mannino et al. (2007, 2011, 2014) and other authors (e.g., Colonese et al. 2009; Prendergast et al. 2016). According to this method, applying oxygen isotope analyses to assess past seasonality of shellfish gathering requires, first of all, to establish the range of isotope ratios, which reflects the yearly temperature range, for each archaeological phase under study. We have therefore, sampled at least one specimen per archaeological layer (n = 11), to obtain a long sequence of samples that ideally should cover a year of growth. In all cases, except one (KSAS12XX; 15 samples), we drilled 30 calcium carbonate samples or more (up to 40), starting from the edge of the aperture and continuing along the periphery of the shell. This is the axis of maximum growth and it is, therefore, the part of the shell where sampling can attain the highest resolution to establish the full annual range of $\delta^{18}O$ values (e.g., Mannino et al. 2008). The ranges obtained were then divided into quarters, which are assumed to be roughly equivalent to seasonal $\delta^{18}O$ ranges. For the layers in which more than one long sequence was sampled, the one with the widest $\delta^{18}O$ range was used as a baseline to compare edge values of short sequences. As $\delta^{18}O$ values are negatively correlated with SST, the lowest quarter corresponds to the warmest phase of the year (defined as 'summer') and the highest quarter corresponds to the coldest phase of the year (defined as 'winter'). The two intermediate quarters comprise warming and cooling phases, respectively 'spring' and 'autumn'.

The second step in the approach proposed by Mannino et al. (2003, 2007, 2011, 2014), requires drilling three or more samples from the edge backwards, along the periphery of the shell of as many individuals possible. These samples are used to infer season of death. For specimens in which the last growth increment (i.e., from the edge of the aperture) falls into the intermediate quarters, the trend from the final three $\delta^{18}O$ values was considered to infer a 'warming' phase (defined as spring), when the values decreased, or a 'cooling' phase (defined as autumn), when the values increased. Specimens were assigned a season (e.g., summer or autumn) when their edge values are >0.2‰ (i.e., measurement error) from a boundary between two quarters. Others, of which the $\delta^{18}O$ value fell within the range of the measurement error of a boundary between two quarters, were assigned to intermediate categories (e.g., late winter to early spring). SSTs were estimated using the aragonite-temperature equation proposed by Grossman and Ku (1986) with a conversion of VSMOW (used for $\delta^{18}O_{water}$ values) to VPDB by Dettman et al. (1999) and taking into account a correction for the glacial conditions in MIS3 of 1.2‰ after Paul et al. (2001; see also Prendergast 2016).

3.4 Sample preparation and isotope analyses

First, the shells were cleaned using a combination of sonication with purified water and mechanical cleaning using a rounded 10mm drillbit. After which, the outer calcareous layer of the shell was removed creating a groove and exposing the translucent inner nacreous layer, as proposed by Mannino et al. (2003, 2007, 2008). We focus on the inner nacreous layer for oxygen isotope analysis for two main reasons: 1) to avoid potential diagenetically altered material, which is likely more extensive in the outer prismatic layer and 2) because diagenetic alterations are more easily detectable in the aragonitic part of the shell (Kato et al. 2003; Mannino et al. 2003; Milano et al. 2016). Samples of carbonate powder (approximately 100 µg) were taken from the groove exposing the inner nacreous layer using a 0.5 mm drill bit. Care was taken to sample at equal depth of roughly 0.8 mm intervals along the maximum axis of growth starting at the midpoint of the aperture and continuing along the body whorl. In addition, final growth increment $\delta^{18}O$ analysis was carried out on additional shells (n = 28) by taking three sequential samples from the shell's aperture along the periphery of the shell to represent the last growth. The quarters derived from the 'long' sequences, described above, then served as a baseline to infer season of death of other shells from the same archaeological phase for which only 'short' sequences (n = 3) were taken. This approach optimizes the number of shells that can be studied and, thereby, the amount of data on past human foraging patterns. In addition, this sampling scheme allows us to obtain accurate season of collection estimations without seriously compromising the morphology of the shells. Taken together, both long and short sequences were used to provide information on the seasonality of shellfish exploitation in the UP at Ksâr 'Akil.

Oxygen and carbon isotope measurements were undertaken at the Godwin Laboratory for Palaeoclimatic Research, University of Cambridge. Carbonate samples were transferred to exetainer vials and sealed with silicone rubber septa using a screw cap. The samples were flushed with CP grade helium, then acidified, left to react for 1 h at 70˚C and then analysed using a Thermo Gasbench preparation system attached to a Thermo MAT 253 mass spectrometer in continuous flow mode. Each run of samples was accompanied by 10 reference carbonates (Carrara Z) and two control samples (Fletton Clay). Carrara Z has been calibrated to the Vienna Pee Dee Belemite (VPDB) using the international standard NBS19. Results are reported in delta units (δ) in parts per mil (‰) with reference to the international VPDB standard and the precision is better than ± 0.08 ‰ for $\delta^{13}C$ and ± 0.10 ‰ for $\delta^{18}O$. Although discussion of $\delta^{13}C$ is beyond the scope of this paper, it is worth to note that generally, $\delta^{13}C$ sequences are cyclic and negatively correlated with $\delta^{18}O$ (Figs. 3 and 4), suggesting a seasonal influence on variability of $\delta^{13}C$ as well as in $\delta^{18}O$ in *Ph. turbinatus* (see also Mannino et al. 2008).

4 Results

4.1 Marine shellfish exploitation

The taxa exploited for dietary purposes include the intertidal rocky shore taxa *Patella caerulea, P. rustica, P. ulyssiponensis, Phorcus turbinatus, and Ph. articulatus,* as well as the terrestrial mollusc *Helix pachya* (Table 2). The marine gastropods were collected live from intertidal rocky shores. The most common species, *Ph. turbinatus*, first occurs in the IUP Layer XXII. During the EUP *Ph. turbinatus* was the most frequently-exploited taxon. In Layers XVII and XVI there was a small increase in the frequency of all three *Patella* species, whereas the proportion of the terrestrial mollusc - *H. pachya* – starts to increase in the later phases of the UP. Overall, mollusc exploitation can be characterised by an ever-increasing diversity among the edible species paralleled with terrestrial mollusc exploitation gaining in importance over time.

The anthropogenic origin of the assemblage is evident from the intentional removal of the apices of *Ph. turbinatus* to aid shellfish extraction and from the frequent edge damage on *Patella* spp. congruent with prying the animals off the rocks. Zooarchaeological investigations show a shift in *Phorcus* processing from apex removal being the norm during the EUP and start of the UP, but becoming gradually less frequent towards the (Levantine) Aurignacian and later periods (Table 3). Edge damage on *Patella* occurs in about half (i.e., 49.7%) of the specimens including fragments (Table 3). This frequency increases to 66% if only (semi) complete shells are considered. *Patella* are harder to detach from the rocky substrate than *Phorcus*, which explains the frequent edge damage on the former genus (although some edge damage can also be the result of post-depositional breakage), although this is unlikely to have been a factor limiting *Patella* exploitation.

4.2 Oxygen isotope data

Long sequences obtained for *Phorcus turbinatus* generally show sinusoidal patterns reflecting annual temperature cycles (Figs. 3 and 4). All specimens, with the possible exception of KSAS06XVII highlighted below, have clearly visible high and low $\delta^{18}O$ peaks showing annual minima and maxima and cover annual $\delta^{18}O$ variation. Three specimens (i.e., KSAS02XI, KSASXVI02, and KSASXVI03) show more than one annual cycle. In all instances, for each layer all samples of the long sequence were used to calculate the annual range of $\delta^{18}O$ variation, which implies that some ranges cover more than one year of growth. Overall, mean $\delta^{18}O$ values show a slight increase over time indicating a decrease in temperature from the EUP to the Epipalaeolithic (Table 4). Excluding KSAS06XVII, which might not represent a yearly cycle, annual ranges obtained from long sequences span between 2.01‰ and 3.35‰ representing annual SST variations of ~9°C and ~15°C.

4.2.1. Seasonality in the Early Upper Palaeolithic (Layers XX – XVI)

Seasonality data was obtained for 16 *Ph. turbinatus* specimens comprising seven long (Table 4) and nine short sequences (Table 5). For Layer XX a sequence of 15 samples (KSAS12XX) was obtained comprising both a cold and a warm temperature extreme and hence capturing an annual cycle (Fig. 3g). The $\delta^{18}O$ values increase towards the edge falling in the upper intermediate quarter, suggesting late-autumn or early winter collection. The three edge samples of KSAS04XIX (Layer XIX) show low $\delta^{18}O$ values ranging from 0.83‰ to 0.90‰. In comparison with the long sequences from both adjacent layers this suggests the specimen died in summer.

For Layer XVII two long sequences and four short sequences were obtained (Table 5). Final growth analysis suggests late autumn to early winter (KSAS06XVII) and late winter to early spring (KSASXVII02) collection for the long-sequences and winter collection for all four short-sequences (KSASXVII03 to KSASXVII06). Three of the latter specimens display edge values that extend beyond the upper range of $\delta^{18}O$ variation of the long sequence KSASXVII02 (Fig. 5), although they were found in the same layer and square as KSASXVII02. This might suggest the accumulation of the deposit lasted long enough to include shells from slightly different temperature regimes. A certain time-depth in the formation of deposits, is to be expected in archaeological assemblages covering several hundreds of years. However, this might introduce a level of uncertainty in accurately determining season of collection.

Table 2: Quantities and proportions of edible molluscs throughout the Ksâr ‘Akil sequence. Abbreviations: NISP: number of identifiable specimens, %: percentage, EPI: Epipalaeolithic, UP: Upper Palaeolithic, EUP: Early Upper Palaeolithic, IUP: Initial Upper Palaeolithic.

	layer	NISP total	Food (NISP)	Food (%)	*Helix pachya*	*Patella caerulae*	*Patella rustica*	*Patella ulyssiponensis*	*Patella* sp.	*Phorcus articulatus*	*Phorcus turbinatus*	*Phorcus* sp.
EPI	**I**	2	2	100.00	1		1					
	II	6	3	50.00	1	1	1					
	III	28	28	100.00	13		1				14	
	IV	22	18	81.82	12				1		5	
	V	242	220	90.91	80	1	18		1		120	
Atlitian	**VI**	103	80	77.67	42	2	7	2	2		25	
UP	**VII**	273	195	71.43	125	21	6	2	7		34	
	VIII	195	87	44.62	64	6	1	2	1		13	
	IX	446	52	11.66	21	2	3		3	1	19	3
	X	119	34	28.57	9	1	3				21	
	XI	465	134	28.82	21	1			1	8	43	60
	XII	51	14	27.45	4						7	3
	XIII	11	8	72.73	1						7	
EUP	**XIV**	3	2	66.67	2							
	XV	2	0	0.00								
	XVI	220	64	29.09	16	1	9	1			37	
	XVII	633	162	25.59	44	4	19	1	11	2	71	10
	XVIII	72	10	13.89	2				2		6	
	XIX	177	16	9.04	8						7	1
	XX	46	3	6.52					1		2	
IUP	**XXI**	60	2	3.33	2							
	XXII	197	1	0.51							1	
	XXIII	22	0									
	XXIV	9	0									

Table 3: Anthropogenic modifications on intertidal marine molluscs. Abbreviations: n: number, %: percentage, BD: basal diameter, SD: standard deviation, EPI: Epipalaeolithic, UP: Upper Palaeolithic, EUP: Early Upper Palaeolithic, IUP: Initial Upper Palaeolithic.

		Patella spp.			*Phorcus* sp.			
	layer	**no damage**	**edge damage (n)**	**edge damage (%)**	**mean BD (n; SD)**	**intact (n)**	**no apex (n)**	**no apex (%)**
EPI	**I**							
	II	1	1	50.00				
	III	0	1	100	24.97 (13; 2.37)	10	2	16.67
	IV	1	0	0.00	26.76 (4; 2.60)	4	1	20.00
	V	9	11	55.00	25.67 (101; 2.60)	105	1	0.94
Atlitian	**VI**	0	13	100	26.60 (22; 1.99)	21	2	8.70
UP	**VII**	13	23	63.89	26.40 (23; 2.31)	21	3	12.50
	VIII	6	4	40.00	25.32 (8; 2.87)	7	1	12.50
	IX	5	3	37.50	25.50 (4; 2.46)	4	2	33.33
	X	3	1	25.00	25.65 (9; 2.91)	4	6	60.00
	XI	2	0	0.00	26.07 (15; 3.10)	2	14	87.50
	XII					0	0	
	XIII				25.14 (4; 2.36)	1	3	75.00
EUP	**XIV**							
	XV							
	XVI	1	10	90.91	22.69 (17; 2.08)	1	18	94.74
	XVII	29	6	17.14	23.88 (21: 1.99)	1	25	96.15
	XVIII				27.18 (2; 1.32)	0	2	100.00
	XIX					0	0	
	XX					0	1	100.00

Lastly, for Layer XVI four long and four short sequences were obtained (Table 5; Figure 6.2). The range of δ^{18}O values was largest in the long sequence of KSASXVI02, namely 0.15‰–2.68‰, and encompasses the ranges of the other three long sequences (Table 4); it was therefore used to determine the quarters. The majority of the samples lack clear trends in δ^{18}O values of the three edge samples. Among the long-sequences, two (KSAS07XVI and KSASXVI02) were collected in late winter or early spring whereas the other two (KSAS10XVI and KSASXVI03) were collected in winter. The edge samples of all short-sequences fall in the intermediate quarters and were collected in autumn (KSASXVI06), probably spring (KSASXVI05), and undetermined either in autumn or spring (KSASXVI01 and KSASXVI04).

4.2.2 Seasonality in the Upper Palaeolithic (Layers XII – X)

Phorcus turbinatus not only becomes increasingly rare throughout the UP, but recovered shells also tend to be less well-preserved in terms of, e.g., translucence of the aragonitic layer and presence of mother of pearl. Almost no shells of this species were found in the (Levantine) Aurignacian Layers VIII and VII. In total eight specimens were sampled, comprising one long sequence from Layer XI (Fig. 4) and seven short sequences from Layers XII, XI, X-XI, and X. The δ^{18}O values of the edge samples of long sequence (KSAS02XI) suggest that this specimen was collected in late autumn or early winter (Table 4). Final growth analysis of the additional UP specimens suggests summer (KSAS11XII), autumn (KSASXI03), late autumn to early winter (KSASX02 and KSASX-XI01), winter (KSASXI02), spring (KSASX01), and probably spring (KSAKXI01) exploitation (Table 5).

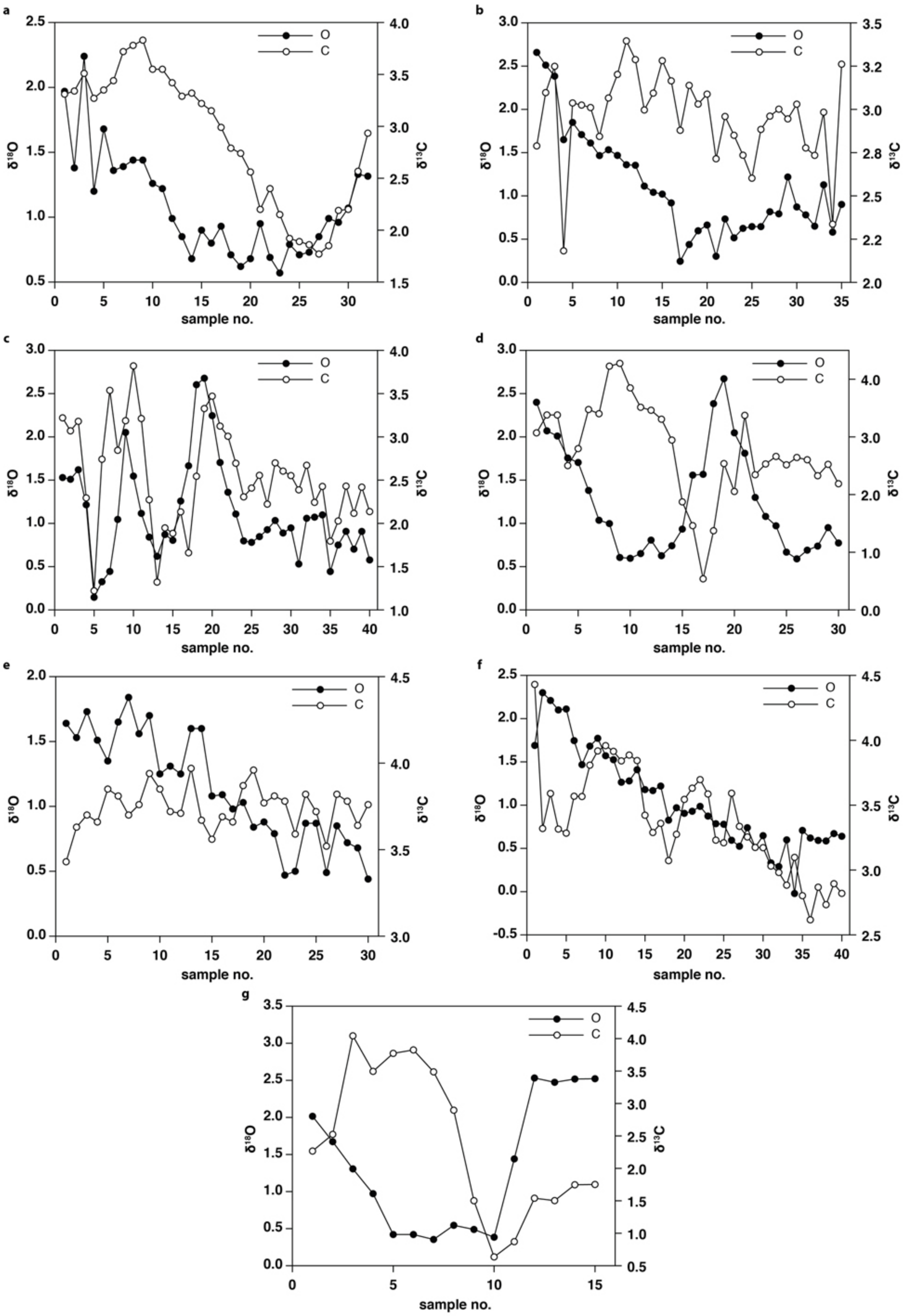

Figure 3: $\delta^{18}O$ and $\delta^{13}C$ values obtained by sampling long sequences of samples from *Ph. turbinatus* shells recovered in EUP contexts: a: KSAS07XVI (Layer XVI), b: KSAS10XVI (Layer XVI), c: KSASXVI02 (Layer XVI), d: KSASXVI03 (Layer XVI), e: KSAS06XVII (Layer XVII), f: KSASXVII02 (Layer XVII), g: KSAS12XX (Layer XX).

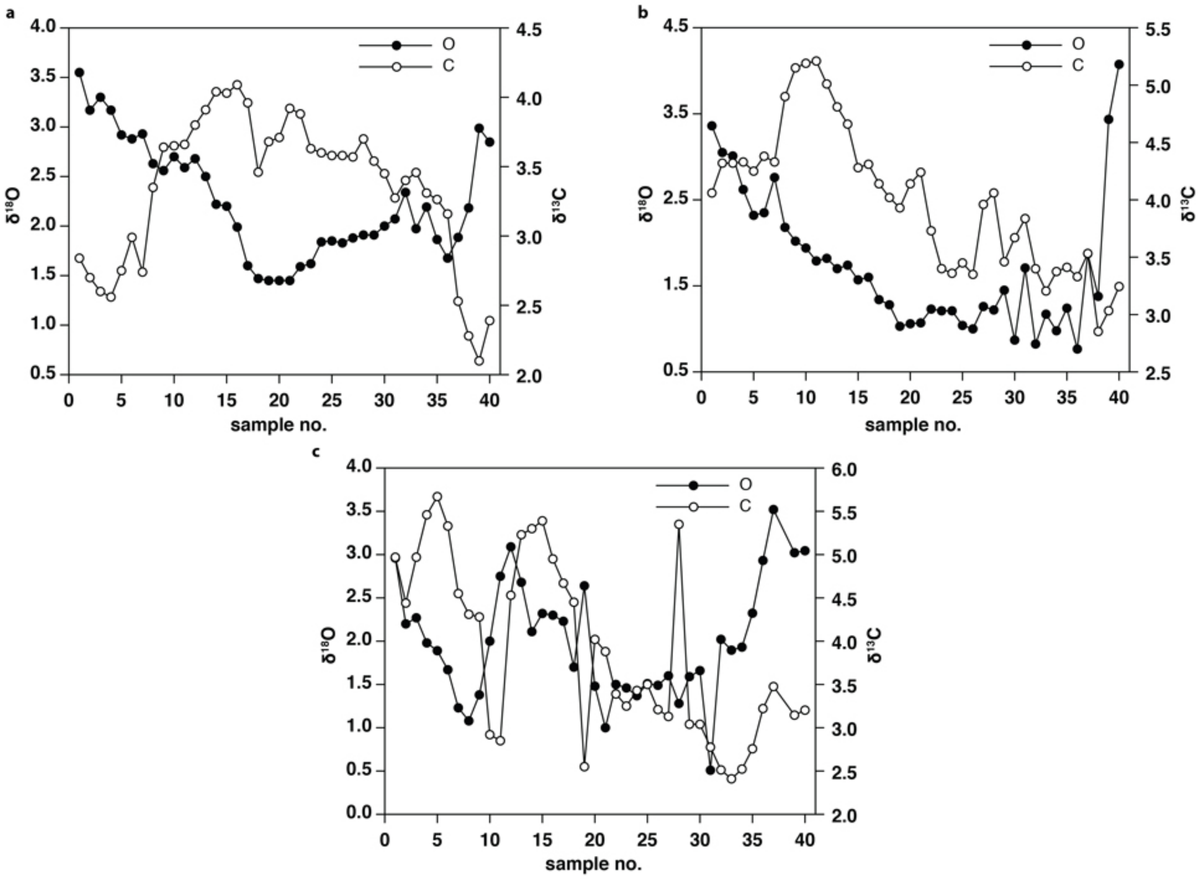

Figure 4: $\delta^{18}O$ and $\delta^{13}C$ values obtained by sampling long sequences of samples from *Ph. turbinatus* shells recovered in UP, Atlitian, and EPI contexts: a: KSAS01V (Layer V), b: KSAS08VI (Layer VI), c: KSAS02XI (Layer XI).

Table 4 (next page): Range of $\delta^{18}O$ values obtained from 'long' and 'short' sequences. Bold: long sequences used to determine quarters of the annual $\delta^{18}O$ range per layer. Abbreviations: BD: basal diameter, n samples: number of sequential samples, % range: percentage of the range of $\delta^{18}O$ values of a layer's long sequence that is covered by the range of $\delta^{18}O$ values of all edge samples (i.e., representing last growth) of that layer, the value in brackets shows % range without outlier KSASV06.

Sample ID	Layer	BD (mm)	n samples	^{14}C (ka cal BP)	long sequence			short sequences			edge samples			% range
					min	max	range	min	max	range	min	max	range	
KSAS01V	**V**	**23.91**	**40**	**30.2–29.7**	**1.45**	**3.55**	**2.1**	**0.53**	**3.55**	**3.02**	**0.53**	**3.55**	**3.02**	**>100 (79)**
KSAS08VI	**VI**	**26.84**	**40**	**32.6–31.9**	**0.77**	**4.07**	**3.30**	**1.17**	**3.36**	**2.25**	**2.19**	**3.36**	**1.17**	**35.45**
KSAS02XI	**XI**	**25.56**	**39**	**38.7–38.1**	**0.51**	**3.52**	**3.01**	**0.89**	**3.61**	**2.72**	**1.67**	**3.61**	**1.94**	**64.45**
KSAS11XII	XII	-	5	40.3–39.7	-	-	-	0.53	0.88	0.35	-	-	-	-
KSAS07XVI	XVI	21.45	32	43.5–42.9	0.57	2.24	1.67	-	-	-	-	-	-	-
KSAS10XVI	XVI	22.12	35	40.4–39.8	0.24	2.66	2.42	-	-	-	-	-	-	-
KSASXVI02	**XVI**	**20.19**	**40**	**41.7–41.2**	**0.15**	**2.68**	**2.53**	**0.62**	**2.73**	**2.11**	**1.38**	**2.66**	**1.28**	**49.61**
KSASXVI03	XVI	22.86	30	43.4–42.9	0.59	2.67	2.08	-	-	-	-	-	-	-
KSAS06XVII	XVII	22.53	30	43.4–42.8	0.44	1.84	1.4	-	-	-	-	-	-	-
KSASXVII02	**XVII**	**23.06**	**40**	**42.3–41.9**	**0.29**	**2.3**	**2.01**	**1.53**	**2.98**	**1.45**	**1.64**	**2.98**	**1.34**	**66.67**
KSAS04XIX	XIX	-	3	43.1–42.6	-	-	-	0.83	0.9	0.07	-	-	-	-
KSAS12XX	XX	-	15	43.6–43.0	0.35	2.53	2.18	1.31	2.02	0.71	-	-	-	-

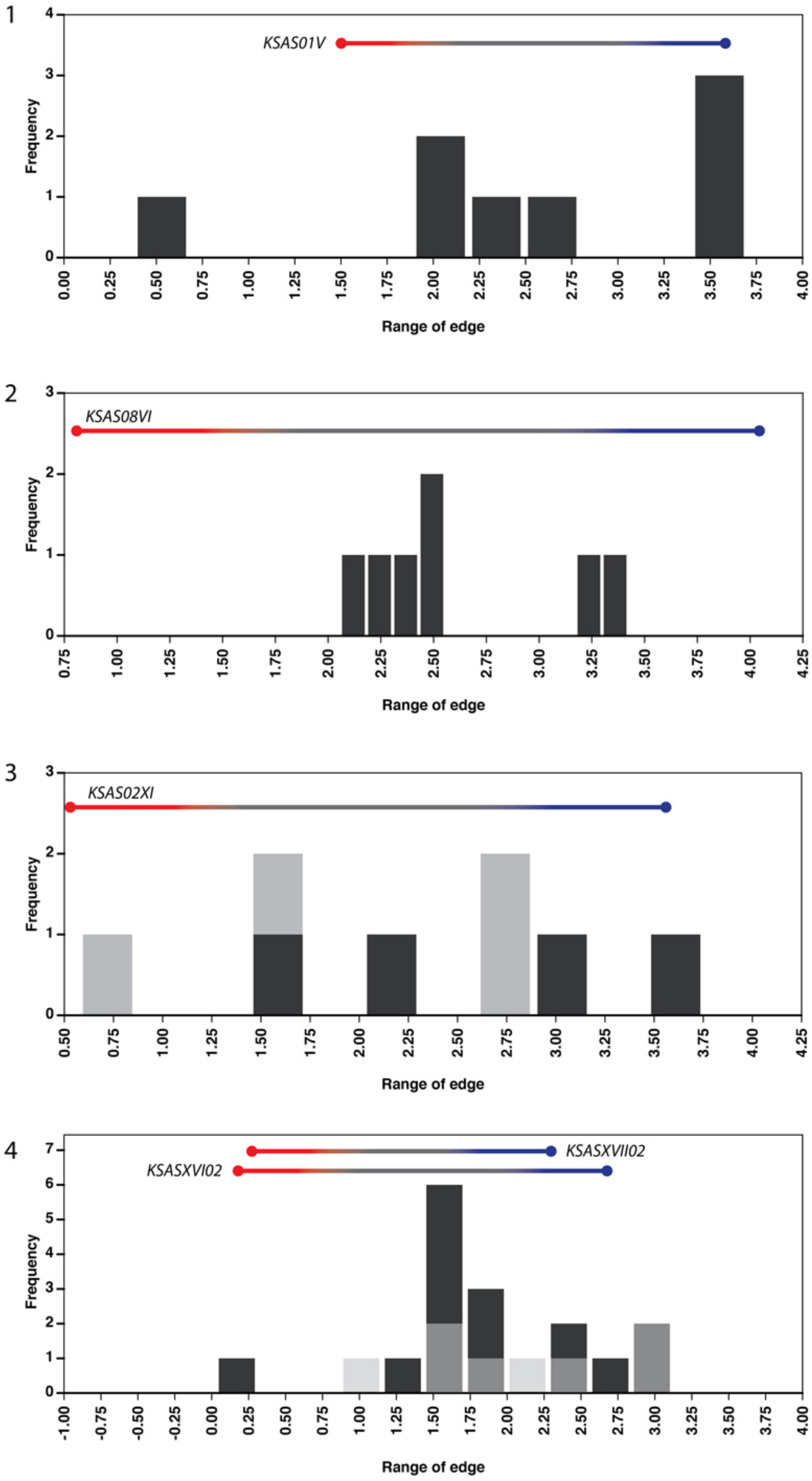

Figure 5: δ^{18}O values of edge samples of *Ph. turbinatus,* including (on top) a reference to the range of oxygen isotope values obtained from the long sequences per layer or techno-complex (red: lowest quarter defined as summer, blue: highest quarter defined as winter). 1: Epipalaeolithic, 2: Atlitian, 3: Upper Palaeolithic (Layer XI: black, other UP Layers: grey), and 4: Early Upper Palaeolithic (Layer XVI: black, Layer XVII dark grey, other EUP Layers light grey).

Table 5: Season of mollusc collection data per archaeological techno-complex. Abbreviations: ID: lab identification number, RGM-no: museum inventory number, *: samples for which a long-sequence was obtained. Trend: ↑: increase in $\delta^{18}O$ value, ↓: decrease in $\delta^{18}O$ value, -: no significant (i.e., within machine error) increase or decrease of $\delta^{18}O$ value. The first symbol in column 'trend' shows change between edge and 2nd value, second symbol in column 'trend' shows change between 2nd and 3rd value. ~ and italic: determination of season of collection based on the trend between the 3rd and edge sample (because the overall trend of the three edge samples was not sufficient to establish season of collection), EPI: Epipalaeolithic, UP: Upper Palaeolithic, EUP: Early Upper Palaeolithic.

technocomplex	ID	RGM-No.	square	edge	2nd	3rd	trend	quarter	season
EPI	KSAS01V*	606338	E4-6	3.55	3.17	3.3	↑ -	cold	winter
	KSASV01	606338	E4-6	2.56	2.69	2.17	- ↑	intermediate	autumn
	KSASV02	606338	E4-6	1.89	2.36	2.78	↓↓	warm-intermediate	late spring - early summer
	KSASV03	606336	E4-6	2.22	2.38	2.3	- -	intermediate	spring - autumn
	KSASV04	606336	E4-6	3.44	3.52	3.54	- -	cold	winter
	KSASV05	606336	E4-6	3.41	2.98	3.21	↑↓	cold	winter
	KSASV06	606336	E4-6	0.53	1.6	1.15	↓↑	warm	summer
	KSASV07	606336	E4-6	1.9	2.19	2.09	↓ -	warm-intermediate	late spring - early summer
Atlian	KSAS08VI*	606337	E4,FG3-4	3.36	3.05	3.01	↑ -	cold-intermediate	late autumn - early winter
	KSASVI01	606337	E4,FG3-4	2.19	1.63	1.25	↑↑	intermediate	autumn
	KSASVI03	606337	E4,FG3-4	2.37	1.17	1.34	↑ -	intermediate	autumn
	KSASVI04	606337	E4,FG3-4	2.44	2.52	2.5	- -	intermediate	spring - autumn
	KSASVI06	606337	E4,FG3-4	3.24	2.32	1.9	↑↑	cold-intermediate	late autumn - early winter
	KSASVI07	606337	E4,FG3-4	2.53	3	1.87	↓↑	intermediate	*~autumn*
UP	KSASX01	606323	E5	1.59	1.74	2.06	- ↓	intermediate	spring
	KSASX02	606323	E5	2.66	1.78	1.51	↑↑	cold-intermediate	late autumn - early winter
	KSASX-XI01	606321	F5	2.62	1.87	1.94	↑ -	cold-intermediate	late autumn - early winter
	KSAS02XI*	606317	E5	2.96	2.2	2.27	↑ -	cold-intermediate	late autumn - early winter
	KSASXI01	606317	E5	1.67	0.89	2.36	↑↓	intermediate	*~spring*
	KSASXI02	606317	E5	3.61	3.52	3.12	- ↑	cold	winter
	KSASXI03	606311	E4	2.27	1.64	1.38	↑↑	intermediate	autumn
	KSAS11XII	606421	E4	0.72	0.53	0.88	- ↓	warm	summer
EUP	KSAS07XVI*	606334	E5	1.97	1.38	2.24	↑↓	cold-intermediate	late winter - early spring
	KSAS10XVI*	606310	F3	2.66	2.51	2.38	- -	cold	winter
	KSASXVI01	606334	E5	1.71	1.57	1.75	- -	intermediate	spring - autumn
	KSASXVI02*	606334	E5	1.53	1.51	1.62	- -	intermediate	late winter - early spring
	KSASXVI03*	606334	E5	2.4	2.07	2.01	↑ -	cold	winter
	KSASXVI04	606334	E5	1.82	2.73	1.84	↓↑	intermediate	spring - autumn
	KSASXVI05	606334	E5	1.38	2.07	1.59	↓↑	intermediate	*~spring*
	KSASXVI06	606334	E5	1.67	1.13	0.62	↑↑	intermediate	autumn
	KSAS06XVII*	606306	F4	1.64	1.53	1.73	- -	cold-intermediate	late autumn - early winter
	KSASXVII02*	606309	E4	1.69	2.3	2.21	↓ -	cold-intermediate	late winter - early spring
	KSASXVII03	606306	F4	2.55	2.38	2	- ↑	cold	winter
	KSASXVII04	606306	F4	2.98	2.5	2.13	↑↑	cold	winter
	KSASXVII05	606306	F4	2.87	2.35	2.15	↑ -	cold	winter
	KSASXVII06	606309	E4	1.95	1.57	1.79	↑↓	cold	winter
	KSAS04XIX	639387	F4	0.9	0.83	0.87	- -	warm	summer
	KSAS12XX*	606294	F4	2.02	1.67	1.31	↑↑	cold-intermediate	late autumn - early winter

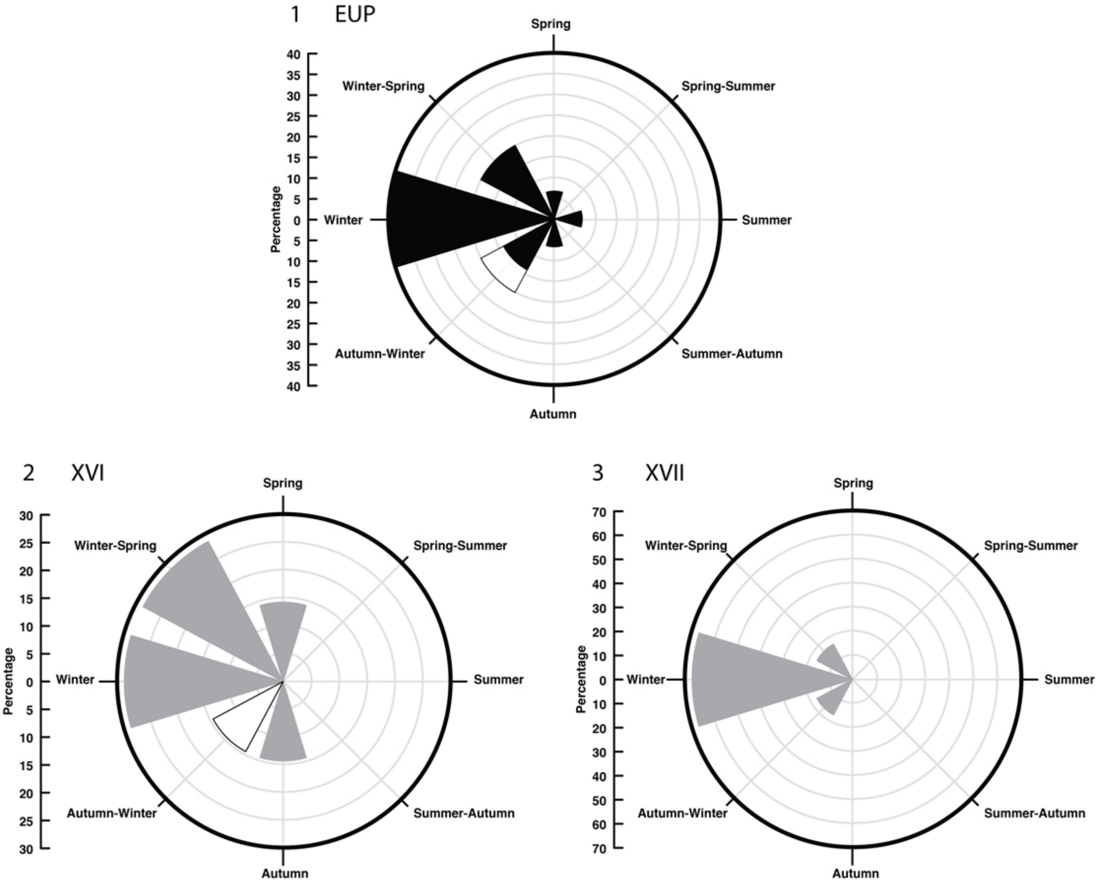

Figure 6: Rose diagrams reporting the season of *Ph. turbinatus* (per Layer: grey and per Phase: black) and *Patella* spp. (white) collection. 1: Early Upper Palaeolithic (EUP) comprising Layers XX–XVI, 2: Layer XVI, 3: Layer XVII.

4.2.3 Seasonality in the Atlitian (Layer VI)

For the Atlitian Layer VI, one long sequence and six short sequences were obtained. Increasing δ^{18}O values towards aperture suggest late autumn to early winter collection for the long sequence KSAS08VI. The additional six short sequences yielded a relatively narrow range of δ^{18}O values (i.e., 35% of the long sequence variation), falling in the cold to intermediate part of the long sequence. These data suggest that shellfish exploitation in the Atlitian was quite restricted to between autumn and early winter.

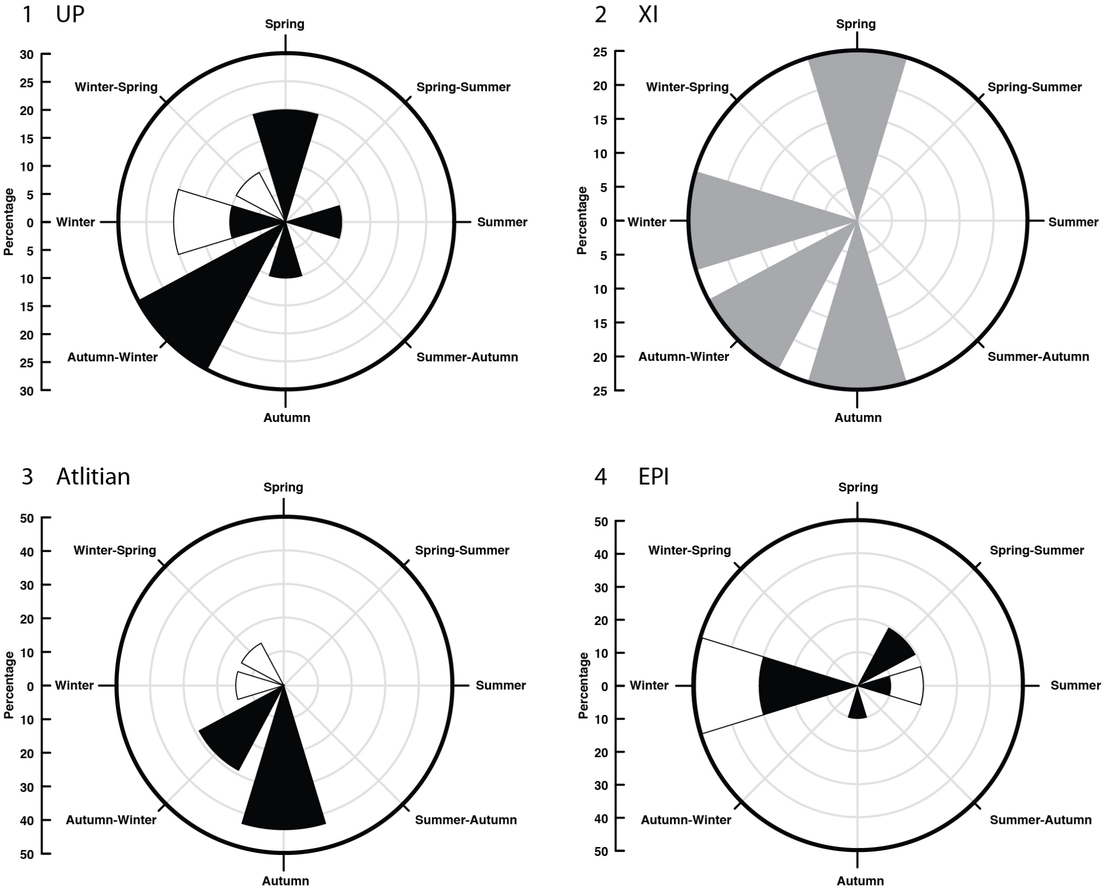

Figure 7: Rose diagrams reporting the season of *Ph. turbinatus* (per Layer: grey and per Phase: black) and *Patella* spp. (white) collection. 1: Upper Palaeolithic (UP) comprising Layers XII–VII, 2: Layer XI, 3: Atlitian, 4: Epipalaeolithic (EPI).

4.2.4 Seasonality in the Epipalaeolithic (Layer V)

One long sequence (KSAS01V) and seven short sequences (KSASV01 to KSASV07) were obtained for Layer V (Fig. 7). The δ^{18}O value of the edge sample clearly falls in the upper or cold quarter pointing to winter collection. Evaluation of trends in δ^{18}O variation of the short sequences points to winter (KSASV04 and KSASV05), late spring to early summer (KSASV02 and KSASV07), summer (KSASV06), autumn (KSASV01), and either spring or autumn collection (KSASV03).

5 Discussion

Our zooarchaeological and oxygen isotope data suggest that throughout the EUP to EPI occupations at Ksâr ʻAkil shellfish were exploited mainly during the colder part of the year, but occasionally also in the warmer and intermediate seasons. Further, there was a shift in *Phorcus* processing during the UP when removing the apex of the shells for flesh extraction was gradually abandoned. This raises a number of discussion points with regards to shellfish exploitation from a local and regional perspective, as well as from a nutritional ecology viewpoint. Below we first place our seasonality of shellfish exploitation data in the broader context of subsistence strategies throughout the occupation of Ksâr 'Akil. We then, review contextual data on shellfish exploitation from the Eastern Mediterranean Palaeolithic, before discussing the dietary and behavioural implications from a human evolutionary perspective.

5.1 The role of shellfish exploitation in subsistence at Ksâr 'Akil

5.1.1 Initial Upper Palaeolithic

During the earliest stages of the IUP, only beached marine mollusc shells were transported to Ksâr 'Akil, possibly as raw material for tools and ornaments (Layers XXIV and XXIII). Edible taxa, namely *Phorcus turbinatus*, first occur in the IUP Layer XXII. A *Ph. turbinatus* specimen from this layer was radiocarbon dated to ~40.6 ka uncal BP, which results in a calibrated age range of 44.1–43.3 ka cal BP (Bosch et al. 2015a). No human modifications were identified on this fragmented specimen and, if it had been taken back to the rockshelter for consumption, it suggests that shellfish exploitation was a marginal activity for the IUP occupants of Ksâr 'Akil. More broadly, subsistence strategies in the IUP seem to have targeted all available terrestrial habitats around the site (i.e., steep rocky country, forests, open woodlands, steppes and/or grasslands). Although coastal marine habitats seem to have been exploited occasionally, there is no evidence for the exploitation of freshwater and/or brackish water habitats (Table 1).

5.1.2 Early Upper Palaeolithic

Edible molluscs were consumed more regularly during the EUP than in the IUP. Over 90% of the *Ph. turbinatus* shells are devoid of their apex, which is probably mainly ascribable to processing by humans for the extraction of the molluscan flesh (Bosch et al. 2015c). The oxygen isotope data suggest that shellfish exploitation was most commonly practised in the colder months, as is especially evident in Layer XVII, in which all shells seem to have been collected during the winter. For the earlier part of the EUP the data are scarce, but evidence from both long and short sequences suggests that overall shellfish were collected throughout the year, including in warmer months. One of the authors, ALP, is conducting further oxygen isotope analysis on *Patella*. Preliminary season of collection data suggest late-autumn to early winter collection of a *Patella* from layer XVI (included in Fig. 6: white).

Compared to the IUP, subsistence behaviour was more diversified during the EUP. Both the inclusion of edible marine and, potentially, of terrestrial molluscs (i.e., *Helix pachya*) and the increase in taxonomic evenness suggest that the EUP occupants of Ksâr 'Akil had a more varied diet than their IUP predecessors. This is also evident from the more evenly distributed vertebrate faunal assemblages indicating that a wider range of terrestrial animals was part of the diet on a regular basis (Bosch et al. 2015a). Additionally, fresh (avian and molluscs) and perhaps brackish (avian) water species became part of the assemblages (van Regteren Altena 1962; Kersten 1991; Bosch et al. 2015c). However, none of these remains bear clear traces of human modification, and it is therefore unclear if these types of aquatic habitats were actually exploited by the EUP occupants of Ksâr 'Akil for subsistence purposes.

Thus, contrary to the IUP, during the EUP foraging strategies included the regular exploitation of coastal habitats at different times of the year, but with most common collection activities during the colder months. The fact that molluscs were collected and taken back to the site in all seasons in turn, implies that Ksâr 'Akil was inhabited throughout the year, albeit not necessarily continuously. The observed pattern of site occupation could have been either part of a residential mobility strategy, involving seasonal changes of base camp, or alternatively occupation at Ksâr 'Akil could have involved logistical mobility, characterized by extended habitation episodes spanning multiple seasons (*sensu* Binford 1980).

5.1.3 Upper Palaeolithic

The proportion of terrestrial molluscs within the edible taxa increases throughout the UP sequence, in parallel with the increasing diversity of marine species. The UP Layers XIII to VII are further characterised by a gradual change in shellfish processing, in which apex removal of *Phorcus turbinatus* shells decreased. This trend coincides with an increasing importance of *H. pachya* and with a consistent increase in *Phorcus* size. The extraction of *Phorcus* flesh is possible without removing the apex, if boiling has successfully broken or damaged the muscle attachment between the flesh and the shell and if 'pin-like' implements were used (e.g., Hill et al. 2015). Cooking the animals at temperatures below 300°C would not have left visible traces on the mollusc shells or have biased the oxygen isotope measurements (Milano et al. 2016). For *Patella* flesh extraction does not require any special processing, once the initial difficulty of prying the animals loose from the rocks is overcome (Fa 2008). These differences in edible mollusc composition and method of shellfish extraction seem to be part of a gradual change in collection and processing strategies throughout the UP rather than representing an abrupt change. However, our data suggest that the seasonality of shellfish exploitation did not change during this period (Fig. 7:1). Preliminary oxygen isotope data on *Patella caerulea* from the (Levantine) Aurignacian (Layer VII) at Ksâr ʻAkil contribute to this picture suggesting winter (RGM- 606363) and late winter to early spring (RGM- 606370) collection.

Recent and ongoing faunal investigations of the vertebrate assemblages have resulted in the identification of *Capra ibex* in the IUP and EUP deposits among the caprid remains that were previously identified solely to *C. aegagrus.* For the IUP and EUP, human modifications (e.g., cutmarks and impact fractures) on ibex remains attest to human exploitation of steep rocky uplands for subsistence purposes (Bosch et al. 2015a). It is presently unclear if there are also ibex among the caprid remains in the UP, Atlitian and, EPI layers, and it is thus unclear whether, in these periods, steep rocky terrain was exploited for subsistence purposes. Further, UP habitat exploitation is similar to EUP exploitation.

5.1.4 Atlitian

The Atlitian mollusc assemblage is diverse in terms of edible taxa and, similarly to the underlying (Levantine) Aurignacian assemblages, dominated by terrestrial molluscs. All *Patella* display edge damage, whereas only 8.7% of the *Phorcus* shells had their apices removed. Further, there are a few freshwater molluscs among the invertebrates, although the assemblage mostly consists of edible marine and terrestrial taxa.

Seasonality of *Phorcus* exploitation is restricted to autumn and late autumn to winter (Fig. 7.3). Two *Patella rustica* (both RGM-606376) from the Atlitian have been collected in winter and late winter to early spring. These data confirm that mollusc collection took place in the colder part of the year, albeit less restricted in terms of seasonally than evidenced by the *Phorcus* data alone. The reduction in seasonality could either be an indication of a more restricted period of site occupation and of residential mobility or it could imply a shift in subsistence strategy, with shellfish exploited seasonally despite year-round site occupation. Evaluation of the seasonality of terrestrial animal exploitation could potentially help to solve this question. In addition to the intertidal coastal zone, exploited habitats included forests, open woodlands, and steppes or grasslands. Contrary to the EUP and UP, there are no indicators of freshwater or brackish water among the Atlitian fauna.

5.1.5 Epipalaeolithic

The Epipalaeolithic mollusc assemblage is almost entirely composed of edible species, with fluctuating marine and terrestrial proportions. Shellfish exploitation was less restricted seasonally compared to the Atlitian, including collection episodes both in colder (i.e., autumn and winter) and warmer (i.e., late spring to early summer and summer) conditions (Fig. 7:4). These data are complemented by season of collection data of three *Patella rustica* (all: RGM-606377) from Layer V two of which were collected in winter and one in summer, indicating that for the first time, a larger proportion of shellfish collection occurred in the warm part of the year.

The vertebrate assemblage shows a shift in ungulate exploitation from Layer V to IV. Overall, the vertebrate fauna is dominated by *D. mesopotamica,* followed by *C. aegagrus* and *C. capreolus* (Hooijer 1961). However, the relative abundance of the former taxon increases at the expense of the latter two taxa in Layer IV with respect to Layer V (Kersten 1987). Despite this increase in taxonomic dominance in the vertebrate fauna, the same locally-available environments, continued to be exploited by the Epipalaeolithic inhabitants of the rock shelter.

5.2 Coastal exploitation in a Mediterranean context

Not much is known about the seasonality of mollusc collection for the eastern Mediterranean Palaeolithic. In the following section evidence for the exploitation of coastal habitats in the eastern part of the Mediterranean (roughly east from Italy-Libya, see Fig. 1) is presented in chronological order. There is no evidence for shellfish exploitation during the Middle Palaeolithic at Ksâr 'Akil, although this is attested from other Eastern Mediterranean sites (for a summary see Colonese et al. 2011). For example, at Üçağızlı II in Turkey (Stiner 2010), shellfish may have been exploited during the Middle Palaeolithic. Shellfish were also gathered for subsistence purposes by the so-called 'pre-Aurignacian' Middle Palaeolithic occupants of Haua Fteah in Libya; although the Mousterian groups who occupied the same site did not take marine molluscs back to the cave (Klein and Scott 1986; Barker et al. 2012; Hill et al. 2015).

For both the IUP and EUP occupations at Ksâr 'Akil, the site of Üçağızlı I provides us with a good comparative framework for the interpretation of coastal subsistence patterns. Üçağızlı I with its rich IUP and EUP deposits is very similar to Ksâr 'Akil in terms of its lithic technology (Kuhn et al. 2001, 2009) and shellfish exploitation seems to have been practiced in a similar way (Kuhn et al., 2009; Stiner, 2010; Stiner et al. 2013; Bosch et al. 2015c). The IUP invertebrate assemblages of Üçağızlı I comprise beach-collected marine shells, probably used as raw material for tools and ornaments, similarly as at Ksâr 'Akil. At both sites, shellfish gathering for dietary purposes started in the second half of the IUP, but only became a regular practice from the EUP onwards (Stiner 2010; Bosch et al. 2015c). For Üçağızlı I there is no data available on the seasonality of shellfish collection, but seasonality data derived from terrestrial fauna seem to suggest that the site was inhabited in autumn and late winter based on the intensity of marrow extraction, and not in late spring and early summer, based on the absence of foetuses and fawns (Stiner 2010). Whereas analysis of seasonality data on the terrestrial fauna of Ksâr ʻAkil is in progress, our oxygen isotope data suggest that, similarly to Üçağızlı I, Ksâr ʻAkil was occupied by Palaeolithic hunter-gatherers mainly in late autumn and winter, albeit also visited at other times of the year. Lieberman (1993) has argued that this pattern, which he calls a 'radiating' or logistic (*sensu* Binford 1980) mobility pattern is rare in the southern Levantine UP. He argues that this mobility pattern is inherently unstable in most environments due to the risk of resource depletion and that it has only been recorded in (non-trading) modern-day hunter-gatherers living in rich environments such as what he calls 'marine' habitats or sites located in proximity to multiple exploitable habitats. Although it is hard, if not impossible, to make any statements on regional mobility patterns based on seasonality of exploitation of a single taxon let alone from a single site, both these conditions are met at Ksâr ʻAkil and could well explain why it seems to have been sustainable in this instance.

From the UP shellfish exploitation has been reported at Riparo Mochi (Italy). High proportions of edible taxa are reported in (Proto-) Aurignacian deposits reaching up to roughly 60 - 70% of the total mollusc assemblage (Stiner 1999). In the eastern Mediterranean, shellfish have further been found in the early UP layers of Klissoura Cave (Greece), for which the intensity of exploitation has been suggested to relate to increased occupation intensity (Stiner et al. 2012). The mollusc assemblages from the slightly more recent UP and EPI deposits of Franchthi Cave (Greece) were thought to attest fluctuating proportions of molluscan taxa, as a result of changing sea levels and subsequent changes in the proximity of the site to the coast (Stiner and Munro 2011; Stiner et al. 2012). However, a recent study by Perlès (2016) has shown that the exploitation of fish, edible molluscs, and ornamental species are in fact independent from each other which suggests that marine resource exploitation was not correlated to sea level variations. Moreover, shells of edible taxa are occasionally found at sites farther from the coast, for example in the Aurignacian deposits of Manot Cave (Israel), attesting that shellfish were part of the diet, but no quantitative data is available on the scale of this subsistence activity (Hershkovitz et al. 2015). At other sites, such as in the Aurignacian layers of Hayonim Cave (Israel), the marine mollusc assemblage comprises only beached shells used as ornaments (Belfer-Cohen and Bar-Yosef 1981) suggesting that coastal habitats were used (either directly or via social exchange networks) by hunter-gatherers living further from the coast, albeit not necessarily for subsistence purposes.

During the Epipalaeolithic and later periods at Haua Fteah (Libya), shellfish exploitation intensified with increasing evidence for overexploitation (Hunt et al. 2011). Oxygen isotope analysis on *Phorcus turbinatus* indicates that shellfish exploitation was practised in all seasons in the Oranian (around 15–13 ka cal BP), but shifted to mainly winter gathering in the subsequent

Capsian and Neolithic (Prendergast et al. 2016). These data correspond well with winter shellfish exploitation patterns of other (early) Holocene sites in the northern Mediterranean (e.g., Colonese et al. 2009; Mannino et al. 2007, 2011, 2014).

5.3 Implications of shellfish exploitation for UP Levantine hunter-gatherer groups

Intertidal marine molluscs are easily acquired predictable resource available year-round (e.g., Shackleton and van Andel 1986; Kyriacou et al. 2014; Marean 2014; Jerardino 2016). Due to this predictability, shellfish are thought to have been fall-back resources to tap into during times of resource stress (e.g., Meehan 1977; Waselkov 1987). In the eastern Mediterranean for example, at Haua Fteah during the Capsian and Neolithic intertidal marine molluscs were predominantly gathered in winter, whereas seasonality data for terrestrial fauna indicates that hunting was practiced mainly during the summer, leading Prendergast et al. (2016) to suggest that shellfish were dietary supplements at times of resource depression. For Ksâr 'Akil, investigations on the seasonality of terrestrial fauna exploitation are in progress, therefore patterns in shellfish exploitation and hunting strategies can at present not be compared. However, our oxygen isotope data suggest that, although shellfish exploitation seems to have been restricted to the colder months during the accumulation of some layers (e.g., Layers XVII and VI), in general shellfish were collected during different seasons. Previously published biometric data (Bosch et al. 2015c) do not show any evidence for long-term depletion and over-exploitation (e.g., Mannino and Thomas 2002; Fa 2008) of intertidal rocky shore edible taxa. This in turn suggests that shellfish, perhaps accompanied by terrestrial molluscs, could have been a regular food supplement for the occupants of Ksâr 'Akil from the EUP onwards.

Intensified use of coastal resources is often taken to be an indicator of reduced residential mobility and / or population pressure (e.g., Stiner et al. 1999; Stiner 2001; Finlayson et al. 2006; Fa 2008; Steele and Klein 2013; Marean 2014; Prendergast et al. 2016). Moreover, it has been argued, on the basis of the broad spectrum revolution hypothesis (MacArthur and Pianka 1966), that increased population density can be seen in the archaeological record by a diversification in exploited faunal taxa. However, due to the low carrying capacity of eastern Mediterranean coasts, it is unlikely that the exploitation of intertidal rocky shore molluscs alone could have supported a substantial population increase. For the eastern Mediterranean, increased dietary breadth, and especially the inclusion of small-bodied fast-moving taxa (such as birds and hare), has been documented for the Upper Palaeolithic (e.g., Stiner 2001, 2010). At Ksâr 'Akil no dietary diversification is evident in the IUP and - similarly to what is attested by the MP deposits - faunal exploitation focused on few species, namely *Dama mesopotamica, Capra aegagrus,* and *Sus scrofa.* Moreover, shellfish exploitation seems to have occurred on a low level at the end of the IUP, but there is no evidence that these resources were exploited by the earliest anatomically modern humans who occupied the site (i.e., at the time of the modern human fossil named "Ethelruda", recovered in Layer XXV). In the EUP, however, broadening of the diet is reflected in the increased taxonomic evenness of hunted vertebrates, the increase in the number of habitats exploited for subsistence purposes, as well as in the regular consumption of both shellfish and terrestrial molluscs into the diet. A similar pattern in shellfish exploitation has been documented at the roughly contemporary site of Üçağızlı I (Stiner 2010). Taken together, this evidence suggests there was an increasing strain on resources in the northeastern Mediterranean coastal zone during the EUP. In turn, this evidence for resource depression may be indicative of an increased population density.

To determine if shellfish exploitation at Ksâr 'Akil can be interpreted as a coastal adaptation first the definition of a 'coastal adaptation' should be explored. Marean (2014; see also Jerardino 2016) argues that the exploitation of coastal habitats should be a central part of subsistence and mobility strategies and marine foods should form a substantial part of the diet. In the eastern Mediterranean coastal resources were exploited since at least MIS 5 (Stiner 2010; Colonese et al. 2011), but this does not equate to a fully developed coastal adaptation. Archaeological proxies such as the ratio between terrestrial fauna and marine molluscs, comparing taxonomic diversity, shell sizes, and shell density have been used to identify intensity of shellfish exploitation in UP contexts (e.g., Steele and Klein 2009; Jerardino and Marean 2010; Stiner 2010; Stiner and Munro 2011; Langejans et al. 2012; Clark and Kandel 2013; Perlès 2016). It is hard to identify a full coastal adaptation in terms of Marean's (2014) criteria at Ksâr 'Akil given the low productivity (in terms of caloric value) of the eastern Mediterranean coastal zone. There is however ample evidence of regular exploitation of coastal habitats. Our data suggest that the importance of shellfish gathering steadily increased from the IUP to the EPI. However, there is no evidence for long-term overharvesting of these coastal resources at any time, nor could we detect any trends in taxonomic diversity of molluscs. Our seasonality data contribute to this picture by showing that shellfish exploitation occurred throughout the year, and, although there seems to be an emphasis on the colder months, it was not a seasonally restricted activity. In other words, coastal habitats were frequented increasingly often and intertidal molluscs would have been regularly included in hunter-gatherer subsistence strategies. Albeit, with the possible exception of the Atlitian, during which coastal exploitation could only be demonstrated from autumn to early spring. Thus, our data do not support the classification of a full coastal adaptation *sensu* Marean (2014), they do however, attests of the regular use of coastal habitats from the EUP onward.

Shellfish consumption was probably advantageous both in terms of macro (protein) and micro (essential nutrients) acquisition. From a nutritional ecology perspective, the regular intake of essential nutrients including vitamins A, B12, C, D, E, iron, folate, potassium, calcium, and omega-3 fatty acids would have been especially beneficial. Several body functions and systems require these essential nutrients for example the immune system (Vitamin A), blood formation and oxygen transport (B12 and iron), bone mineralisation (D and calcium), collagen synthesis and wound healing (C), the nervous system (B12 and E), heart function (Potassium), muscle and body growth (A and E), vision (A), and brain function (B12, E, folate, and omega-3 fatty acids). Folate and omega-3 fatty acids are thought to be especially important in fetal and infant brain development (e.g, Brenna and Carlson 2014; Cunnane and Crawford 2014). Hockett and Haws (2003; Haws and Hockett 2004) suggest that broader and nutritionally rich diets increase hominin fitness, contribute to reduce child mortality and inter-birth intervals. Thus, hunter-gatherers that regularly ingest a wide range of essential nutrients would have a better position to compete with groups that have less balanced diets. It has been argued that women are likely to have had less access than men to nutritiously rich terrestrial resources, such as organ meat and brains, as these tissues decay swiftly and the bulk would have been eaten immediately by the hunters (Parkington 2003). However, especially pregnant women and children require more omega-3 fatty acids and quality nutrition in general. In modern hunter-gatherers, shellfish are mainly gathered by women and children providing them access to the much-needed essential nutrients (e.g., Meehan 1982). Our data suggest that at Ksâr 'Akil shellfish exploitation indeed occupied a central place in hunter-gatherer foraging strategies from the EUP onward rather than being restricted to certain times of the year.

6 Conclusions

At Ksâr 'Akil shellfish exploitation is first attested in the upper layers of the IUP, albeit in low quantities. From the EUP onwards shellfish exploitation played a more important role in hunter-gatherer foraging strategies, given that it was practised in each season, with an emphasis on winter collection. During the UP, shellfish were also collected in every season, but the focus was more on late autumn to winter and spring. The Atlitian witnessed a short-lived reduction in seasonality of shellfish exploitation, in which marine molluscs seem only to have been gathered in the colder months (i.e., from autumn to early spring). With the start of the EPI, in Layer V, shellfish were again gathered throughout the year and were for the first time more frequently gathered in the warmer part of the year (i.e., late spring to early summer and summer). Although some layers show more restricted gathering episodes, overall shellfish exploitation seems not to have been seasonally restricted.

When the seasonality data is taken as a proxy for site occupation, it appears that hunter-gatherers occupied Ksâr ‘Akil during different times of the year, although perhaps not continuously. This pattern could either be explained through the existence of a residential mobility strategy, which would have seen hunter-gatherer groups returning to the site in different seasons, or of a logistical mobility strategy, which would have entailed occupation periods lasting multiple seasons. Moreover, Layers XVII and VI show temporally more restricted exploitation that could either be indicative of shorter periods of site occupation, or if people were present they did not always gather shellfish and/or bring them to the rockshelter. Seasonality of terrestrial fauna exploitation, as an alternative proxy for site-occupation, could help answer this question.

The more regular inclusion of coastal marine resources from the EUP onwards signifies a broadening of the human diet, which is also reflected in the number of exploited habitats, by the more evenly distributed exploitation of mammals and by the inclusion of edible terrestrial molluscs. Overall, this suggests hunter-gatherer groups tried to optimize their strategies to exploit fuller the carrying capacity of their immediate surroundings. This in turn may indicate an increase in population density along the eastern Mediterranean coast in the EUP and later periods compared to the IUP. In addition to merely broadening animal resource exploitation, the regular consumption of shellfish was likely beneficial for past hunter-gatherer diets, considering it provided them with essential nutrients otherwise not available in the terrestrial foods that constituted the main component of the diet. According to nutritional ecology theory (e.g., Hocket and Haws 2003), the regular ingestion of these nutritionally rich molluscs would have resulted in improved fitness. This, in turn, could have contributed, along with a range of other resources, to an increase in population density that characterizes the Early Upper Palaeolithic record.

In the wider regional setting, marine resources (particularly intertidal gastropods) seem to have been consistently exploited in the Levantine coastal zone. In the future, the data presented here should be contextualised with seasonality data on terrestrial fauna exploitation from Ksâr ‘Akil. This would serve to broaden our knowledge on seasonal activities at the site and provide a better view on the full extent of site-occupation and timing of resource exploitation. These data, in turn, should be compared with seasonality data from other Levantine sites (e.g., Lieberman

1993), allowing evaluation of subsistence and mobility strategies of past hunter-gatherers on a broader regional scale.

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Chapter 7 ・ Discussion and Conclusion

This thesis investigates the subsistence behaviour of early Upper Palaeolithic (including IUP and EUP) *Homo sapiens* based on the remains of molluscs and terrestrial animals recovered from the Ksâr 'Akil rockshelter in Lebanon. Specifically, I aimed to gain insight into the timing and intensity of shellfish exploitation in the Levantine early Upper Palaeolithic. To answer these questions, it was important to know (1) when early UP hunter-gatherers were using Ksâr 'Akil, (2) what marine and terrestrial resources were available in the surrounding landscape for EUP foragers to access, and (3) what the archaeological fauna assemblages (both molluscs and vertebrates) could tell us about how early Upper Palaeolithic foragers exploited those resources. In this chapter, I further discuss what influences that dietary choices may have had on human health and development and on population density. This is important, as increased population density is thought to influence human dispersal events and ties in with the debate surrounding early Upper Palaeolithic dispersals from the Levant into Europe. More specifically, this thesis addresses the following research questions:

(1) When were early Upper Palaeolithic foragers using the Ksâr 'Akil rockshelter?

(2) What do both the mollusc and vertebrate faunas from Ksâr 'Akil tell us about how early UP foragers exploited those resources, in terms of selection and frequency?

(3) What role does shellfish exploitation play in early Upper Palaeolithic subsistence practices?

(4) Are there differences between IUP and EUP subsistence strategies, and if so, how may they be explained?

(5) Are there general inferences from the Ksâr 'Akil case study for wider debates about landscape use, human health, demography, and their potential relationships to human dispersals?

To pursue these research questions, I conducted zooarchaeological investigations combining optimal foraging theory using a diet breadth approach with nutritional ecology theory to evaluate subsistence practices and dietary adaptations of IUP and EUP groups. Specifically, I analysed mollusc assemblages to investigate shellfish use and consumption using a combination of zooarchaeological (including taphonomic), radiometric, and stable isotopic methods. These data were interpreted in the context of patterns and trends gleaned from the vertebrate faunal assemblage, using a diet breadth approach to evaluate the exploitation of both sets of animal food resources.

Below, I briefly summarise the results outlined in detail in the previous chapters, after which I discuss how these results contribute to addressing my research questions.

7.1 The Site of Ksar Akil and Its Vertebrate Assemblages

Chapter 2 serves two purposes. First, it addresses the rationale behind choosing the site and the respective faunal assemblages studied in this thesis. Second, it provides zooarchaeological information (including the taphonomy and composition of the vertebrate fauna) to help contextualise the mollusc data discussed in Chapters 5 and 6. The Ksâr ʻAkil faunal collections were selected for several reasons: (1) The site has played a central role in the Upper Palaeolithic dispersal debate because of its location in the Levantine Corridor (e.g., Bar-Yosef 1987) on the edge of Europe; (2) It is one of the few sites in the Levant with deeply stratified IUP and EUP deposits yielding rich mollusc and vertebrate assemblages; and (3) The IUP and EUP faunas had not been investigated from a zooarchaeological perspective and contained abundant small unidentifiable long bone shaft fragments. This indicates that there had not been a substantial excavation bias towards identifiable remains and/or that the collections had not suffered from post-excavation loss of ʻuninterestingʼ (i.e., hard to identify) material. Analysing unidentifiable shaft fragments is important to determine skeletal element abundances and imperative to carry out in-depth taphonomic investigations needed to establish the extent to which the accumulation of bones has been biased by, for example, cortical surface weathering and carnivore ravaging. Such analyses are also critical for establishing the extent of human involvement evidenced by bone modifications such as cutmarks, impact fractures, and in some cases, burning.

Taphonomic investigations show that cortical bone surface preservation was sufficiently good to convey human and animal modifications and that the acid treatment prior to analysis did not substantially compromise the visibility of these modifications. The investigations further show that carnivores contributed little to the formation of the IUP and EUP assemblages and that humans were the main contributor to the accumulation of these archaeological deposits.

In terms of NISP (Number of Identified Specimens) and relative abundance, the faunal composition shows that the onset of the Early Ahmarian (see Chapter 5) coincided with a shift towards a more even distribution of less-frequently obtained prey. This, in turn, suggests a general broadening of the human diet across various habitats and exploited faunal resources. From an optimal foraging perspective, using the broad-spectrum revolution hypothesis (Flannery 1969), such a broadening of the diet suggests an increase in dietary stress. This could be caused by an increase in population density or deterioration of environmental conditions resulting in a decrease in prey availability.

7.2 The Ksâr 'Akil chronology

Chapter 3 presents a new chronology of the Ksâr 'Akil deposits and the implications of the age of specific technocomplexes and human fossils for understanding the timing and patterning of the early Upper Palaeolithic human colonisation of Europe. The new chronology was built on 16 AMS radiocarbon dates, which involved novel methodological approaches, partly developed in the framework of this thesis, to detect potentially compromised samples. The study employed rigorous evaluation of sample integrity and tested the validity of the chronology using four different independent data sets, namely amino acid racemization, geochemical characterization of all dated shells, oxygen isotope analyses, and Bayesian modelling.

Our proposed chronology is in line with previous age estimations by some scholars (e.g., Mellars and Tixier 1989) but deviates substantially from another recent chronology of the site (Douka et al. 2013). Douka et al. (2015) raised issues with how we constructed our Bayesian model and how we chose samples, although they stated that the ^{14}C determinations themselves were not in question. Chapter 4 discusses the discrepancies between the two chronologies and proposes steps towards resolving the remaining questions. Douka et al.'s (2013) and our chronology provide age estimates that are approximately 3000–4000 radiocarbon years apart for both the IUP and EUP deposits, suggesting that either approach (or both) is subject to diagenetically or otherwise compromised samples. Douka et al.'s (2015) proposed alternative ways of modelling the data do not significantly alter our results, nor do their suggestions contribute to resolving why our radiocarbon data sets were so different. However, in the Supplementary Information from our original paper (Bosch et al. 2015a), we had already narrowed down the potential sources of the differences between Douka et al.'s (2013) and our data sets to sampling strategy and/or pre-treatment method. It appears that the CarDS method used by Douka et al. (2013) does not in all instances eliminate all contamination, resulting in too young age estimations (see also Douka et al. 2011, 2013). Additionally, selecting beach-collected ornamental shells that show signs of diagenetic alterations—all samples used by Douka et al. (2013) are such beach-collected ornamental shells—for dating only serves to increase the risk of producing unreliable dates (see, for example, notes on the Columbellidae and *Ostrea edulis* in Douka et al. 2013; see also Busschers et al. 2014; Stutz et al. 2015). AMS radiocarbon dating of shells is non without problems and is perhaps best avoided when other types of material (e.g., charcoal and bone) are available. Unfortunately, for Ksâr 'Akil there were no other organic materials available that could produce radiocarbon data. Moreover, one of the aims of this study was to date shellfish exploitation. Dating the shells of the exploited molluscs, therefore brought the 'dated event' (i.e., deposition of carbonates during the molluscs' life) as close as possible to the 'target event' (i.e., the time of shellfish exploitation). In sum, the best way forward is to select the best-preserved shells and find independent methods to determine whether a sample could be compromised.

7.3 Mollusc collection and taphonomy

Moving to zooarchaeological investigations, Chapter 5 evaluates the integrity of the mollusc assemblage as well as potential biases (e.g., post-depositional processes, excavation, and collection bias). Although there is in some instances evidence of time averaging (i.e., the assemblages formed over an extended yet indeterminate amount of time), there is no tangible evidence for the actual mixing of deposits and/or archaeological materials either post-depositionally or post-excavation. Molluscs were used for several purposes. For example, they were utilised as tools, as seen in the examples of the retouched valve of a *Glycymeris* (Douka 2011) and another showing notches on both sides of the umbo, which was likely used as a container or for pouring (Bosch et al. 2015b). Molluscs were also used as a food resource, and perforated, beach-collected specimens were likely used as ornaments. The chapter especially focusses on the chronological patterns of change in the proportions of molluscs used as a food resource and as raw material for tools and ornaments. In general, topshells of the genus *Phorcus* and limpets comprising three taxa of patellids lack taphonomic damage indicative of post-mortem exposure to marine environments, suggesting that they were life collected. In addition, edge damage found on patellids is congruent with anthropogenic damage resulting from prying the animals off the rocks. Furthermore, nearly all EUP Phorcus are devoid of their apex, which is evidence of a common practice to facilitate shellfish extraction by severing the ligament that attaches the animal to its shell.

In summary, the paper concludes that both *Phorcus* and *Patella* were consumed, and their shells were deposited at the site as food refuse. As for terrestrial taxa, *Helix pachya* demography reveals the sole presence of large adults. This selective rather than natural age profile, together with this taxon's frequent occurrence compared to other terrestrial taxa, suggest that *Helix pachya* was also consumed by the EUP and later Upper Palaeolithic occupants of Ksâr 'Akil. Finally, similar trends in morphometric analysis of both live- and beach-collected taxa suggested that average shell size variation was likely driven by environmental change affecting all measured taxa rather than by overharvesting of only the edible taxa by humans.

7.4 Seasonality of shellfish exploitation

Chapter 6 discusses the nature and timing of Upper Palaeolithic shellfish gathering at Ksâr 'Akil on the basis of results from oxygen isotope analysis of shells. Specifically, this chapter addresses when shellfish started to habitually consumed at the site, what role shellfish played in past human subsistence strategies of people occupying Ksâr 'Akil, and whether any seasonal patterns of collection could be detected. The results indicate that shellfish exploitation was practiced from the second half of the IUP onwards. From the start of the EUP, this practice became more frequent and occurred throughout the year, albeit with a focus on the colder months. This indicates that coastal resources had a central, rather than a seasonally restricted supplementary, role in EUP foraging strategies These data also provide better insight into the timing of site occupation, past hunter-gatherer mobility, and overall landscape use. The fact that the refuse of shellfish exploitation from all different seasons was recovered at the site implies that humans occupied the rockshelter at different times of the year, although not necessarily continuously. When these data were substantiated with evidence from other faunal categories, such as avian and micro- and macro-vertebrate assemblages, a general increase in the exploitation of different faunal resources and habitats from the EUP onwards becomes evident. In other words, our research indicates that EUP occupants of Ksâr 'Akil had a broader diet than their IUP forbearers.

7.5 Archaeological implications

Having summarised the different research projects carried out for this thesis, in the following section I discuss each of the research questions posed in the introduction and the archaeologocal implications of my research results.

7.5.1 When were early UP foragers using the Ksâr 'Akil rockshelter?

The chronology of the IUP and EUP assemblages at Ksâr 'Akil has broader implications for the debate surrounding early Upper Palaeolithic dispersals into Europe. The early Upper Palaeolithic of the Levant, including the IUP and EUP, is key in the debate over the timing of *Homo sapiens* dispersals into Europe. In light of the scarcity of early Upper Palaeolithic human remains in many parts of Europe, lithic assemblages are often used as proxies to track human dispersals through time and space (e.g., Mellars 1989, 2006; Bar-Yosef 1998, 2007; Davies 2001; Tostevin 2003; Hublin 2015). Such extrapolations should be treated with caution, especially when they are extended to other closely related assemblages, which are not associated with *Homo sapiens* remains, over a large geographical area. Nevertheless, several links were drawn between Levantine and European early Upper Palaeolithic technocomplexes based on similar lithic technologies (and sometimes also organic ones, such as split-based bone points and ornaments) (e.g., Mellars 1989; Davies 2001; Tostevin 2003; Zilhao 2006; Bar-Yosef 2007). The correlation of *Homo sapiens*-associated technocomplexes (e.g., the IUP/Emirian in the Levant) with similar technocomplexes (e.g., the Bohunician in Central Europe) allows tracking of potential dispersal routes in the archaeological record. Such archaeological data as well as genetic data suggest that the modern human colonisation of Europe happened in multiple dispersal episodes rather than in one large exodus (e.g., Davies 2001; Tostevin 2003; Reyes-Centeno et al. 2014, 2015; Hublin 2015).

Regarding the timing of early Upper Palaeolithic dispersals, on an interregional scale, similar Upper Palaeolithic lithic technocomplexes (e.g., IUP/Bohunician and Early Ahmarian/Proto-Aurignacian) first appear in the Levant, as Chapter 3 shows. However, on the basis of their proposed chronology, Douka et al. (2013) hypothesize that shell beads, and by proxy Upper Palaeolithic *Homo sapiens*, appeared first in Europe. These groups later moved into the Levant, which Douka (2013) describes as a 'cul-de-sac'.

Our new chronology for Ksâr 'Akil contributes to the debate on *Homo sapiens* dispersal patterns by providing age estimations for Upper Palaeolithic assemblages containing *Homo sapiens* fossils. Namely, IUP groups associated with the Ethelruda fossil in Layer XXV arrived at the site prior to 45.9 ka cal BP. Early Ahmarian groups, including those associated with the fossils of Egbert and a second individual in Layer XVII, were present between 43.3 ka cal BP and 40.0 ka cal BP.

Comparison of our age estimations with those of European *Homo sapiens* fossils places Ethelruda before the first occurrence of *Homo sapiens* in Europe. Similarly, Egbert's layer predates any known Aurignacian and other early Upper Palaeolithic *Homo sapiens* in Europe. Our data fit well with other early IUP and EUP Levantine sites, such as Boker Tachtit, Manot, Kebara (all Israel) and potentially Üçağızlı I (Turkey) (Marks 1983; Kuhn et al. 2009; Rebollo et al. 2011; Hershkovitz et al. 2015). The presence of both Upper Palaeolithic technocomplexes and *Homo sapiens* remains in the Levant prior to their occurrence in Europe indicates that *Homo sapiens* carrying an Upper Palaeolithic toolkit were present in the Levant before arriving in Europe. This contradicts Douka et al.'s (2013) hypothesis that Upper Palaeolithic *Homo sapiens* appeared first in Europe. In turn, this implies that the Levant served as a corridor for *Homo sapiens* dispersing out of Africa and into Europe rather than being a 'cul-de-sac' where *Homo sapiens* arrived after they dispersed into Europe.

From an archaeological perspective, the success of some of these early dispersals seems short-lived. For example, the central European Bohunician lithic technocomplex shows similarities with the Levantine Emirian but is argued to have no continuation into the subsequent European Upper Palaeolithic record, i.e. Aurignacian and Gravettian (e.g., Svoboda and Bar-Yosef 2003). In contrast, the Levantine Ahmarian that shares many traits with the European Proto-Aurignacian appears to be long lived (i.e., including Early and Late Ahmarian, which lasts >20.000 years) in the Levant (for a summary, see Goring-Morris and Belfer-Cohen 2003). Moreover, the Proto-Aurignacian seems to have (at least partly) developed into a widespread Early Aurignacian tradition in Europe. Thus, the archaeological record is congruent with genetic and fossil data suggesting that some of these Upper Palaeolithic dispersal events had more long-term success than others. This raises the important question of which factors facilitate long-term human expansion, to which I return below.

7.5.2 What do faunal assemblages tell us about early Upper Palaeolithic foraging strategies at Ksâr ‘Akil?

In this section, I discuss how the Ksâr ‘Akil faunas, both molluscs and vertebrates, inform us about how early Upper Palaeolithic foragers exploited those resources. However, I first highlight some aspects of past human diets that the Ksâr ‘Akil case study cannot shed light on. For example, the lack of preserved and/or recovered plant remains hinders our understanding of the role of plant foods in Ksâr ‘Akil diets. Henry and her team (Plant Foods in Hominin Dietary Ecology Research Group, MPI EVA) have endeavoured to extract information about plant foods from excavated sediments at the site as well as from dental calculus preserved on Mesopotamic fallow deer dentitions; unfortunately, they have had little success. The initial loss of the site’s human remains, Ethelruda (which has recently been rediscovered; Metni 1999; Yazbeck 2004), and up to now still lost Egbert and his contemporary, make it impossible to assess their diet through stable isotope analysis, dental macro/microwear or dental calculus analysis. Moreover, the Ksâr ‘Akil vertebrate bones do not generally preserve collagen (based on tests run by Nehlich and Talamo, Department of Human Evolution, MPI-EVA), which suggests that stable isotopic investigations would have been unsuccessful even if the human fossils were available.

Nonetheless, both the vertebrate and mollusc collections are informative about early Upper Palaeolithic diets in terms of habitat and resource exploitation. On the basis of faunal remains found at the site, we presume that from the IUP onwards, forests, open woodland, steppe/grassland, and—contrary to the preceding MP—steep rocky terrain were terrestrial habitats regularly exploited by humans (Bosch 2015). Marine habitats, specifically the eulittoral ones, started to be exploited from the second half of the IUP, whereas evidence for exploitation of freshwater and potentially brackish water habitats first appears in the EUP. The EUP deposits witness a higher variety of bird remains from different habitats, including winter guests that often reside in sheltered shallow sea coasts, brackish estuaries, and lagoons (Kersten 1991). Oxygen isotope analysis on intertidal gastropods suggests that humans were present in winter, and therefore, Ksâr ‘Akil’s inhabitants might well have encountered these birds in brackish water environments. However, whether these bird species were consumed remains unclear, as no anthropogenic modifications on their bones have to date been identified. Thus, it seems that early Upper Palaeolithic foragers exploited a wealth of habitats in the vicinity of the site. The dominance of woodland species including the three species of deer (i.e., *Cervus elaphus*, *Dama mesopotamica*, and *Capreolus capreolus*) and wild boar (*Sus scrofa*) suggests that foragers were geared towards exploiting the Mediterranean woodland zone in which Ksâr ‘Akil is located.

Judging from the vertebrates from square F4, the start of the IUP is signified by the discontinuation of Rhinoceros (cf. *Stephanorhinus kirchbergensis*) remains and the introduction of smaller-bodied mammals such as *Capra ibex*, *Gazella* cf. *gazella*, *Lepus* sp., *Vulpes vulpes*, and *Felis silvestris.* Throughout the early Upper Palaeolithic, vertebrate faunal composition stays largely the same and includes, aside from the above-mentioned taxa, *Cervus elaphus*, *Dama mesopotamica*, *Capreolus capreolus*, *Bos* sp., *Capra aegagrus, Gazella* cf. *dorcas*, *Sus scrofa*, *Testudo* sp., and various bird and carnivore taxa. *Dama mesopotamica* is the dominant species, and indices of taxonomic heterogeneity (H), evenness (e), and dominance (1/D) are similar (see Chapter 4). Thus, the number of exploited taxa does not change significantly across the studied assemblages, and moreover, the assemblages are neither heterogeneous nor dominated by a single species. However, faunal composition does change, especially between the IUP and EUP layers where a shift to a more evenly distributed occurrence of various less-common small-bodied taxa occurs. From an optimal foraging perspective, this suggests that hunter-gatherer subsistence strategies were not simply opportunistic. Although people were not specialising on a single species, overall, they seem to have focussed on targeting size three class animals (i.e., ~50–200 kg), and, to a lesser extent, size two class (i.e., ~20–50 kg) ungulates.

7.5.3 What role does shellfish exploitation play in early Upper Palaeolithic subsistence practices?

The anecdotal occurrence of edible mollusc taxa in the IUP deposits at Ksâr 'Akil, including *Phorcus turbinatus, Patella* sp*.,* and *Helix pachya,* suggests that mollusc exploitation was not regularly part of IUP foraging strategies. This changes during the EUP deposits, from which the remains of hundreds (n = 254) of edible molluscs were recovered. Due to the steep coastal morphology, potential sea level changes between these periods are not likely to have caused changes in availability of edible rocky shore molluscs. Therefore, the perceived increase in shellfish exploitation, is likely caused by a change in foraging behaviour. Moreover, mollusc remains recovered at Ksâr 'Akil probably only represent a fraction of the actual shellfish consumed by humans. Ethnographic examples suggest that shellfish are mostly eaten at the shore rather than transported to a site at least three kilometres from the shore (e.g., Meehan 1982; Claassen 1998). Bird and Bliege Bird (1997), however argue, based both on ethnographic observations and central place modelling predictions, that intertidal rocky shore molluscs are those most likely to be taken back to home bases. Oxygen isotope analyses on final growth increments of the most common edible taxon *Phorcus turbinatus* indicate that, during the EUP, intertidal molluscs were gathered throughout the year, but with a focus on the colder months. In fact, this pattern is also evident in most of the overlying Upper Palaeolithic and Epipalaeolithic, albeit with perhaps a more restricted autumn-winter exploitation during the Atlitian (32.7–31.9 ka cal BP).

As mentioned in the introduction, the exploitation of shellfish and other aquatic resources is thought to have been important at several key points in hominin evolution, for example, during early hominin encephalization (e.g., Cunnane and Crawford 2014; Joordens et al. 2014; Kyriacou et al. 2016) and as a fall-back food resource in lean times (e.g., Meehan 1977; Waselkov 1987; Prendergast et al. 2016). The exploitation of coastal habitats has played a somewhat prominent role in debates concerning the development of inter-group behaviour (e.g., Marean 2014, 2015; see also Lahr et al. 2016 for a similar discussion involving lake shores), and the predictable availability of intertidal molluscs has been argued to facilitate dispersals along coastal routes (e.g., Stringer et al. 2000; Mannino and Thomas 2002; Finlayson 2005; Mellars 2006; Fa 2008). Furthermore, incorporation of shellfish into the diet is sometimes seen as evidence of intensified use of resources, and in turn, is considered an indicator of reduced residential mobility and/or population pressure (e.g., Stiner 2001, 2009; Steele and Klein 2013; Marean 2014). In the following sections, I discuss how the Ksâr 'Akil data may or may not contribute to these debates. Naturally, the Ksâr 'Akil data set cannot contribute to the discussion of early hominin brain development. However, at the end of this section, I discuss the implications and potential health benefits of introducing shellfish to the diet from a nutritional ecology perspective, including those for foetal and child brain development

7.5.3.1 A fall-back resource in lean times

Ethnographic studies have shown that intertidal marine molluscs may be used as fall-back food resources in lean times (e.g., Meehan 1977; Waselkov 1987) due to the ease of access and their year-round availability (e.g., Shackleton and van Andel 1986; Kyriacou et al., 2014; Marean, 2014; Jerardino, 2016). Several studies have investigated the seasonality of shellfish exploitation to test this archaeologically (e.g., Shackleton 1973; Mannino et al. 2007, 2014; Colonese et al. 2009; Prendergast et al. 2016). The rationale behind these studies is that shellfish, as a low-ranking foodstuff, were only gathered if hunting of more profitable prey failed. For example, for the eastern Mediterranean, Prendergast et al. (2016) have compared the timing of terrestrial faunal exploitation with that of shellfish. They found that during the Epipalaeolithic Capsian and Neolithic periods at Haua Fteah (Libya), most of the recovered shellfish were gathered in winter, whereas terrestrial fauna exploitation predominantly occurred in summer. This led Prendergast et al. (2016) to suggest that, during the Capsian and Neolithic, shellfish were indeed relied upon during times of the year when terrestrial fauna might have been sparse.

For Ksâr ʻAkil, investigations on the seasonality of terrestrial fauna exploitation are in progress. Therefore, patterns in shellfish exploitation and hunting strategies of terrestrial animals can at present not be compared. However, our oxygen isotope data suggest that, although EUP shellfish exploitation seems to have been more prominent during the colder half of the year, shellfish collection occurred throughout the year. This suggests that shellfish played a more central role in human foraging strategies rather than a restricted seasonal one.

7.5.3.2 Overharvesting

Shellfish exploited at Ksâr ʻAkil are predictably found on the intertidal rocky shores they inhabit. Like any slow-moving animal (e.g., tortoise), they are at risk of being overexploited, resulting in diminishing populations and an easily depleted food source (e.g., Stiner et al. 2000; Mannino and Thomas 2002; Fa 2008; Steele and Klein 2013). The importance of shellfish gathering at Ksâr ʻAkil steadily increased from the IUP to the Epipalaeolithic; therefore, the potential of overharvesting needs to be explored. Humans tend to select the larger specimens of a species to maximize net return rates, as is, for example, evident from the mortality profile of the terrestrial snail *Helix pachya*, which at Ksâr ʻAkil consists entirely of mature individuals in the top 10% of their size range across all deposits. If molluscs were overharvested, this would result in a decrease of average shell size. Several studies have employed morphometrics on intertidal molluscs to ascertain whether taxa were overharvested (e.g., Mannino and Thomas 2002 and references therein; Steele and Klein 2013), although size change can also be triggered by other factors such as changes in environmental conditions or coastal morphology. Among the marine taxa at Ksâr ʻAkil, *Phorcus turbinatus* was most frequently exploited. Although there is a small increase in the frequency of all three *Patella* species in Layers XVII and XVI, there were not sufficient numbers of well-preserved specimens available to include them in the study of overharvesting.

The results of our oxygen isotope study suggest that sea surface temperatures became colder towards the Epipalaeolithic. Additionally, no significant changes in taxonomic diversity of molluscs could be detected across assemblages. This suggests that the temperature change remained within the temperature tolerance of the various taxa, and their populations as a whole were not majorly affected by the temperature change. Alternatively, various taxa adapted to these changing temperatures with similar success. It further indicates that no edible mollusc was exploited in larger quantities than others which would result in a decrease in relative abundance for that taxon (e.g., Yesner 1987).

To investigate potential overharvesting, I compared changes in the dimensions of life collected *Phorcus turbinatus* with those of the two most abundant beach-collected taxa, namely *Tritia (Nassarius) gibbosula* and *Columbella rustica*— the hypothesis being that if *Phorcus turbinatus* was overharvested they would show an observable decrease in average shell size, which would not necessarily be evident in the beach-collected taxa (as collecting already dead, beached specimens would not affect the average shell size of the living populations). If, however, a potential decline in shell size was caused by deteriorating environmental conditions, the expectation would be that both life- as well as beach-collected taxa would be affected in similar ways, as taxonomic composition did not significantly change. Results showed that not only did *Phorcus turbinatus* shell size increase significantly from the EUP to Upper Palaeolithic, similar significant increases were also recorded for both *Columbella rustica* and *Tritia gibbosula.* Thus, despite the steady increase in importance of shellfish gathering from the IUP to the Epipalaeolithic, there is no evidence for long-term overharvesting of these coastal resources. In terms of foraging behaviour this suggests that shellfish were an occasional supplement to the diet, but contrary to other sites, they were exploited throughout the year.

7.5.3.3 Intergroup behaviour: hyperprosociality

The exploitation of coastal habitats has been key in debates surrounding the development of modern human inter-group behaviour during the Southern African late MSA (e.g., Marean 2014, 2015). Marean (2014) hypothesises that consistent use of coastal habitats gave rise to the need to defend these territories, which likely led to inter-group conflict. This, in turn, would have stimulated intra-group cooperative behaviours and so-called hyperprosociality (*sensu* Richerson and Boyd 2008). Marean (2015) argues that this hyperprosociality is one of the trademarks unique to modern humans. Marean's hypothesis assumes reliance on intertidal marine resources and, therefore, a central role of the coastal zone in hunter-gatherer mobility. From this, questions have arisen as to what the definition of coastal adaptation is, what the systematic utilisation of coastal resources entails, and whether dependence of coastal habitats appeared gradually or abrupt (e.g., Jerardino 2016).

Marean (2014) argues that in order to speak of full coastal adaptation the exploitation of coastal habitats should be a central part of subsistence and mobility strategies and marine foods should form a substantial part of the diet. For example, in terms of shellfish gathering, it has been suggested for the oceanic South African coast that collecting species from the lower intertidal may require planning and adept knowledge of the tidal cycle (e.g., Marean 2014; Jerardino 2016). Selection of these lower intertidal taxa, therefore, would represent a full-fledged premeditated adaptation to coastal subsistence (Jerardino 2016). Below I explore whether we observe similar patterns in the eastern Mediterranean and if we can speak of coastal adaptation with regard to the year-round shellfish gathering evidenced from Ksâr 'Akil.

All intertidal rocky shore species consumed at Ksâr 'Akil have slightly different preferences regarding their microhabitat. For example, *Phorcus turbinatus* is less tolerant to salinity and temperature changes than *Phorcus articulatus* (Schifano and Censi 1983; Menzies et al. 1992). As a result, *Phorcus turbinatus* favours the lower and mid-intertidal zone that is regularly flushed out by marine tidal water, whereas *Phorcus articulatus* tends to forage in rock pools higher on the shoreline (e.g., Menzies et al. 1992; Mannino et al. 2008; Prendergast et al. 2013). Regarding the Patellidae, *Patella rustica* prefers vertical walls and steep surfaces in the upper eulittoral zone (e.g., Lima et al. 2006), whereas *Patella caerulea* frequents relatively horizontal surfaces in the lower parts of the eulittoral zone (e.g., Bannister 1975). Lastly, *Patella ulyssiponensis* prefers pools and crevasses in the low- (to mid-) intertidal zone (Firth and Crowe 2008).

Therefore, does the abundance of *Phorcus turbinatus*, favouring the lower tidal zone, among the exploited taxa signify a similar premeditated coastal foraging strategy, as has been argued for prehistoric humans collecting the South African lower intertidal taxa?

The eastern Mediterranean intertidal zone is much narrower (10–20 cm) than the South African oceanic coast (>1metre). As a result, niche partitioning in the case of Mediterranean rocky shore molluscs does not reach the same extent as oceanic molluscs (e.g., Fa 2008), and all five taxa are often found in close proximity. Moreover, in rock pools that are frequently affected by wave action, one can often find both species of *Phorcus* in the same rock pool. On days with calm seas, most of the taxa in question can easily be collected even when the tide is not fully low due to the generally low tidal action. Thus, the abundance of *Phorcus turbinatus*, favouring the lower tidal zone, across the Ksâr 'Akil sequence does not necessarily suggest that Upper Palaeolithic hunter-gatherers inhabiting the site were fully adapted coastal foragers. This is confirmed by the lack of evidence for overharvesting.

According to Marean's (2014) criteria, no full coastal adaptation can be identified at Ksâr 'Akil. In terms of systematic utilisation of coastal resources, however, the seasonality data derived from oxygen isotope analysis suggest that during most of the Upper Palaeolithic, including the EUP, shellfish were exploited throughout the year. This suggests that coastal habitats were regularly included in subsistence strategies.

Another question is whether dependence of coastal foraging happened gradually or abruptly. With regard to Ksâr 'Akil and the eastern Mediterranean, note that regular visits of coastal habitats are not the same as a dependence on coastal habitats. However, it seems that during the IUP, the hunter-gatherers using Ksâr 'Akil made trips to the coast, but mainly to collect beached shells as raw material for tools and ornaments. Although it can of course not be excluded that during these trips shellfish were consumed at the coast, they were only rarely taken back to the rockshelter. From the EUP onwards, shellfish exploitation increased gradually. Year-round exploitation of shellfish further suggests that, although there seems to be an emphasis on collecting during the colder part of the year, exploitation of coastal habitats was not a seasonally restricted activity. Thus, these habitats were frequented increasingly often, and intertidal molluscs likely played a central role in hunter-gatherer subsistence.

7.5.3.4 Facilitating coastal route dispersals

The richness and predictability of coastal resources are also seen by some as an argument in favour of *Homo sapiens* dispersals along coastal routes (e.g., Stringer et al. 2000; Finlayson 2005; Mellars 2006). In unknown terrain, hunting terrestrial fauna might prove difficult, whereas marine molluscs are generally abundantly available on intertidal rocky shores. However, Fa (2008) argues that the low tidal amplitude of the eastern Mediterranean shores, due to the reduced zonations, would have supported fewer edible littoral molluscs than, for example, the shores of the western Mediterranean or South Africa. He further argues that, therefore, shellfish communities in the eastern Mediterranean would be rapidly depleted. This, in turn, would necessitate moving to a new coastal patch and thereby increase hunter-gatherer mobility. Similarly, Mannino and Thomas (2002) suggest that localised over-exploitation and patch depletion of intertidal rocky-shore molluscs would have resulted in increased residential mobility (*sensu* Binford 1980) if large-scale human dispersals along coastal routes were the result of many small-scale dispersal events and if subsistence practices relied substantially on exploiting coastal resources. In these scenarios, the availability of edible shellfish would influence human mobility and dispersals, although short-term local over-exploitation would not necessarily be evident in the archaeological record, as humans would be passing through rapidly and might not have had a long-term impact on mollusc communities (Fa 2008).

Dispersal patterns are better explained from a multi-site perspective; however, Ksâr 'Akil is often mentioned in the early Upper Palaeolithic dispersal debate. The site's location on the eastern Mediterranean coast with its low carrying capacity does fit the scenarios proposed by Fa (2008) and Mannino and Thomas (2002). Additionally, the lack of evidence of overexploitation in the (early) Upper Palaeolithic may be explained by Fa’s (2008) hypothesis of people quickly passing through. However, the intensity of site occupation and the diversity in the archaeological material culture suggest that Ksâr ‘Akil was used as residential base rather than an ephemeral short-term camp.

7.5.3.5 Population pressure: reduced residential mobility

Contrary to the coastal dispersal hypothesis, evidence for the intensified use of coastal resources is often considered an indicator of reduced residential mobility and of population pressure (e.g., Stiner 2001, 2009; Steele and Klein 2013; Marean 2014). Based on optimal foraging theory, the broad-spectrum revolution hypothesis (Flannery 1969) suggests that increased population density can be seen in the archaeological record by a diversification in exploited faunal taxa. For the eastern Mediterranean, for example, increased dietary breadth, and especially the inclusion of small-bodied fast-moving taxa, has been documented for the Upper Palaeolithic (e.g., Stiner et al. 1999; Stiner 2001; 2010). Incorporation of shellfish into the diet arguably would have allowed for higher population densities (e.g., Stiner 2001) or would have sustained smaller groups for a longer time (e.g., Finlayson et al. 2006; Fa 2008; Prendergast et al. 2016).

Hunter-gatherer foraging strategies are highly variable (e.g., Kelly 1995), but they are generally grouped into two overarching strategies: (1) residential mobility in which a group’s camp is moved to a new location when resources run low (i.e., resulting in frequent residential moves); and (2) logistical mobility with a central multipurpose camp to which resources are moved from a multitude of short-term camps that are close to key resources (i.e., resulting in less frequent residential moves) (Binford 1980). Residential mobility patterns are sometimes suggested to involve seasonal moves and follow an annual circular pattern (e.g., Binford 1980). They are found in a variety of environments from the arctic steppe to tropical forests (Gamble 1986; Kelly 1995) and are thought to be relatively stable because the seasonal moves would avoid overexploitation and resource depletion (see, e.g., Lieberman 1993). Logistical mobility patterns, however, are less common in modern hunter-gatherers (Kelly 1995) and more unstable in most environments due to the risk of resource depletion (Lieberman 1993). To evaluate this in the southern Levant, Lieberman (1993) conducted seasonality studies using seasonal bands in gazelle dental cementum. Results indicated the use of seasonally restricted sites, which he considers indicative of residential mobility, for most of the Upper Palaeolithic (with the exception of the Natufian). He argues that hunter-gatherer logistical mobility is only possible through trade with non-hunter-gatherers or in extremely rich environments such as what he calls ‘marine’ habitats or sites located in proximity to multiple exploitable habitats.

As mentioned above, Ksâr ʻAkil was likely used as a residential camp, and during the EUP, people frequented the site in all seasons. Lieberman (1993) suggests this pattern could be indicative of a logistical mobility strategy (Binford 1980), characterized by extended habitation episodes spanning multiple seasons, but in theory could also signify a residential mobility strategy, involving multiple short-term visits throughout the year rather than a few seasonally restricted ones. This pattern could also be caused by multiple groups visiting the site in different seasons. The absence of evidence for overexploitation of marine molluscs may be indicative of multiple short-term stays. However, EUP foragers using Ksâr ʻAkil were not dependent on coastal resources alone. The eastern Mediterranean woodland zone is rich in a variety of floral and faunal resources (e.g., Danin 1992). In summary, although it is hard, if not impossible, to make any statements on regional mobility patterns based on seasonality of exploitation of a single site, the Ksâr ʻAkil microhabitat appears extremely rich, especially when compared with other sites in the region (e.g., Mt. Carmel and Negev sites). This may explain why seasonality patterns are different here than in other parts of the Levant and why a radiating mobility strategy may have been sustainable in this instance.

7.5.3.6 Shellfish exploitation and human health

From the EUP onwards, shellfish were used regularly as a dietary supplement throughout the year. The contribution of shellfish to past hominin diets has been considered marginal for most of the Palaeolithic (e.g., Erlandson 1988; Erlandson and Moss 2001; Colonese et al. 2011; Clark and Kandel 2013; Jerardino 2015). This is certainly true for Ksâr ʻAkil when considering an optimal foraging model, which primarily considers the caloric value and energy intake of foodstuffs (see also Stiner 2001, 2010). However, nutritional ecology theory suggests that the dietary implications of including shellfish in the diet are perhaps more influential in terms of micro (essential) nutrients (e.g., vitamins and minerals) than in terms of macro (protein) nutrients.

Hockett and Haws (2003; Haws and Hockett 2004) argue that diversification of foods would result in a more varied and nutritious diet. One way of doing this is to incorporate shellfish rich in essential nutrients into the diet, whereas another way would be to increase consumption of terrestrial-based animal organs and/or to eat more and diverse plant foods.

Nutritional ecology theory is about quality of the diet, not the quantity of food; therefore, the presence of low quantities of shellfish, as is evident at Ksâr ʻAkil, is informative about their dietary nutritional value. Shellfish are rich in several nutrients (e.g., vitamins A, B12, C, D, E, iron, folate, omega-3 fatty acids, potassium, calcium), which are needed for several biological systems to operate properly, if for example, the immune system (vitamin A), blood formation and oxygen transport (B12 and iron), bone mineralisation (D and calcium), collagen synthesis and wound healing (C), the nervous system (B12 and E), heart function (potassium), muscle and body growth (A and E), vision (A), and brain function (B12, E, folate, and omega-3 fatty acids). Folate and omega-3 fatty acids are thought to be especially important in foetal and infant brain development (e.g., Brenna and Carlson, 2014; Cunnane and Crawford 2014).

Changing the currency of the foraging model from energy to essential nutrients opens up a new area of exploration in human dietary studies. For example, it is known that especially pregnant women and children require more omega-3 fatty acids and higher-quality nutrition in general. However, Parkington (2003) has argued that prehistoric women are more likely to have had access to nutritionally rich aquatic resources rather than terrestrial ones such as organ meat and brains (see also Claassen 1998). This is because the latter tissues decay quickly, and most would probably have been eaten immediately by the hunters. Among modern hunter-gatherers, shellfish are mainly gathered by women and children, providing them access to the much-needed essential nutrients (e.g., Meehan 1982). From a nutritional ecology perspective, this access to nutritionally rich resources and their inferred benefits to personal and population health, could have contributed to the EUP population increase (Hockett and Haws 2003), which in turn, could have facilitated human dispersals into Europe (see section 7.5.5). Furthermore, access to these foods could have given shellfish-eating groups a key advantage in competition with others exploiting similar geographic regions and environments who solely subsisted on terrestrial resources.

7.5.4 Are there differences between IUP and EUP subsistence strategies, and if so, how may they be explained?

At Ksâr 'Akil, no dietary diversification is evident in the IUP. Similar to the MP, faunal exploitation in the IUP is dominated by few species, namely *Dama mesopotamica, Capra aegagrus,* and *Sus scrofa.* Moreover, shellfish exploitation seems to have occurred in low quantities only in the later stages of the IUP, i.e., from Layer XXII onwards. However, there is no evidence that these taxa were exploited from the start of the IUP, i.e., contemporary to the *Homo sapiens* fossil named Ethelruda from Layer XXV prior to 45.9 ka cal BP.

Landscape use changed slightly with the onset of the EUP. This is evident from an increase in the exploitation of coastal habitats and steep rocky terrain between 43.3 and 40.0 ka cal BP, dates which are associated with the skeleton of Egbert and his contemporary in Layer XVII. In turn, subsistence strategies broadened with the inclusion of new taxa, e.g., intertidal marine molluscs (*Patella rustica*, *Patella caerulea*, *Patella ulyssiponensis*, *Phorcus articulatus*) and higher frequencies of terrestrial molluscs (*Helix pachya*), small to medium ungulates such as Nubian Ibex (*Capra ibex*), and a larger gazelle (*Gazella* cf. *gazella*), as well as more evenly represented small mammals among the less common taxa (see Chapter 2).

Shellfish were exploited year-round, suggesting that these resources were eaten regularly, albeit likely in small quantities, and not only during the winter when other resources might be sparse. Even when consumed solely as a dietary supplement, rather than representing the bulk of the diet, shellfish provide an array of essential nutrients to the diet. Thus, from a nutritional ecology perspective, EUP diets at Ksâr 'Akil are likely more balanced and nutrient rich than diets during the IUP. This perceived improvement in dietary health may have triggered lower interbirth intervals, a decrease in child mortality, and in turn, may have contributed to the observed increase in population density in the EUP.

7.5.5 Are there general inferences from the Ksâr 'Akil case study for wider debates about landscape use, human health, demography, and their potential relationships to Upper Palaeolithic dispersals?

Not much is known about the seasonality of shellfish exploitation for the eastern Mediterranean Palaeolithic. However, there are an increasing number of regional sites that attest to shellfish consumption during the Palaeolithic. It is important to note that, although there is no evidence for shellfish exploitation prior to the IUP at Ksâr 'Akil, such evidence does exist at other Eastern Mediterranean sites (e.g., Colonese et al. 2011) and in the 'pre-Aurignacian' deposits at Haua Fteah in Libya (Klein and Scott 1986; Barker et al. 2012; Hill et al. 2015).

The site of Üçağızlı I in southeastern Turkey is very similar in terms of material culture and richness of deposits (e.g., Kuhn et al. 2001, 2009) to both the IUP and EUP occupations at Ksâr 'Akil. Similarly, exploitation of coastal resources is also quite similar. For example, at the onset of the IUP, the Üçağızlı I mollusc assemblage comprises almost exclusively beach-collected marine shells, which were probably used as raw material for tools and ornaments. Shellfish gathering for subsistence purposes is first recorded in the second half of the IUP deposits, and at both sites, shellfish exploitation becomes more frequent from the EUP onwards (Stiner 2010).

The dietary diversification during the EUP at both sites could be explained by an increase in population density in the eastern Mediterranean forest zone in which both sites are situated. Bar-

Yosef (1978) sees a similar increase in sites with EUP or Early Ahmarian lithic artefacts and sites more frequently located in semi-arid environments when compared to the IUP. He argues that this pattern testifies to the improved adaptive strategies of the Early Ahmarians compared with people in preceding periods.

As mentioned in the introduction, many scholars have argued that, at the onset of the Upper Palaeolithic, parts of Eurasia saw an increase in population density. The EUP shows increasing population density both in the Levant (e.g., Bar-Yosef 1987; Goring-Morris and Belfer-Cohen 2003) and Europe (e.g., Bocquet-Appel et al. 2000; Lahr and Foley 2003; Davies 2007; Mellars and French 2011). From the EUP onwards, *Homo sapiens* dispersed into Europe in steadily rising numbers. What were the underlying factors that facilitated this process?

Factors that are thought to play key roles in human dispersals are (high) mobility, (high) population density, and changing (either improving or deteriorating) or instable environmental conditions (e.g., Shennan 2001; Henrich 2004; Powell et al. 2009; Grove et al. 2015). Both improving and deteriorating environmental conditions may trigger population movements into new territories (i.e., dispersal). Conceivably, groups move away from their original territory and inhabit new (more favourable) ones in deteriorating conditions. This would result in lower population densities in the original territory. Inversely, favourable environmental conditions may allow for population increase and the need for additional territory (i.e., range expansion), resulting in increasing population density in both the original as well as the new territory. For range expansion to be successful, sufficient population density needs to be maintained to ensure long-term occupation of and connectivity within increased territory (e.g., Powell et al. 2009).

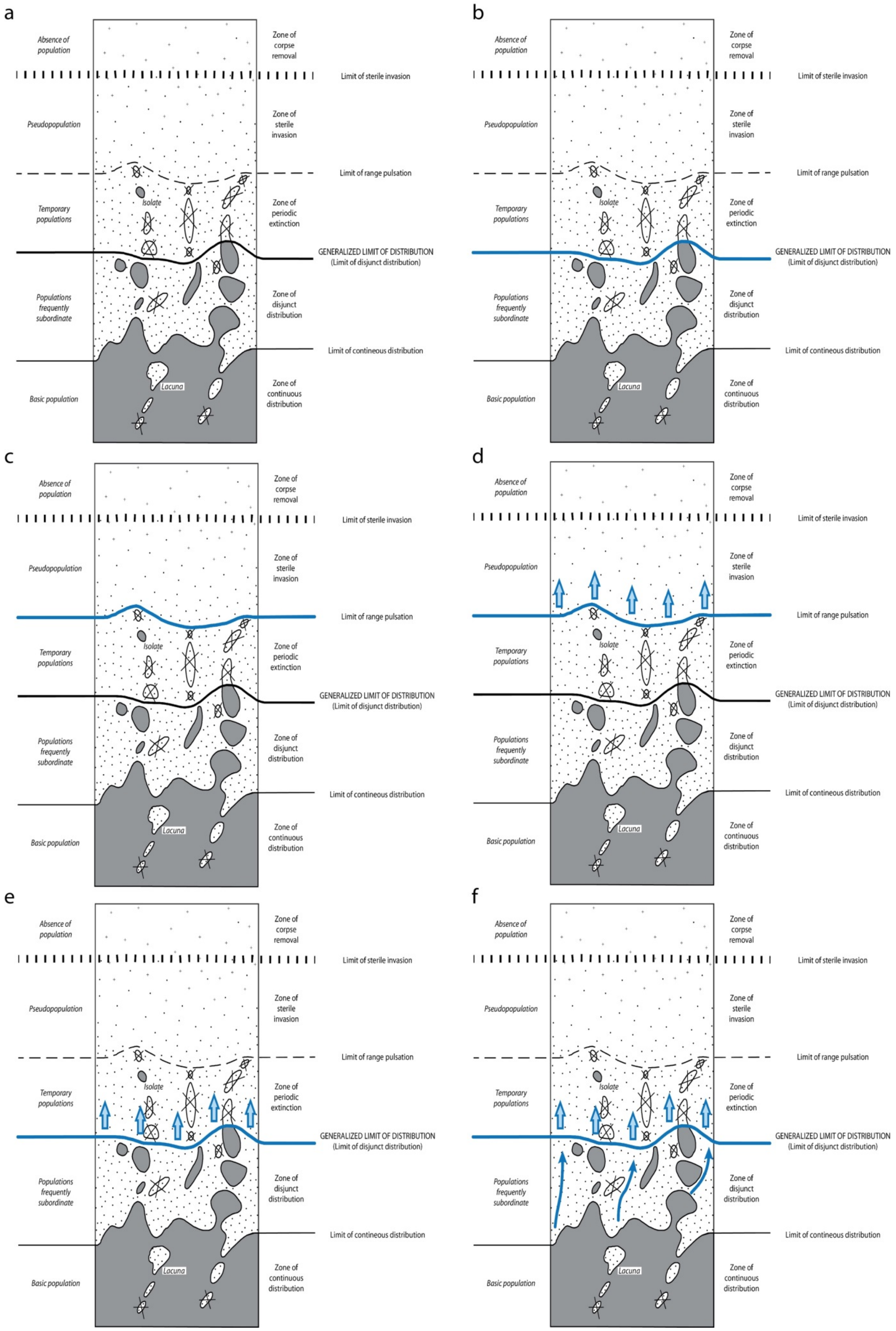
Gorodkov's (1986) ecological model of a species range is a useful framework to consider dispersal mechanisms (see Fig. 7.1a). He describes the distribution of a species as a gradual transition from optimal zones with high populations (zone of continuous distribution; Fig. 7.1b) to less densely populated minimal zones (zone of insular distribution; Fig. 7.1c), to a zone where populations suffer from isolation and periodic die-offs under extreme conditions (zone of periodic extinction), and finally a zone of sterile invasion. Gorodkov (1986) argues that range expansion can be achieved through several mechanisms: (1) expansion of the optimal zone or the zone of continuous distribution (Fig. 7.1e), for example, by climate improvement to more ambient conditions or by behavioural adaptations that help cope with habitats previously regarded as suboptimal (Fig. 7.1 d); (2) highly mobile taxa can have an apparent continuous presence in the zone of periodic extinction by compensating for partial die-offs by immigration from more favourable regions (i.e., the zone of continuous distribution; Fig. 7.1f).

The long-term success of dispersal into the zone of sterile invasion, which was previously outside of the taxon's range, depends on the capability of a species to disperse and make immediate use of any favourable change in climatic or biotic situations for extending its range. In this light, Gorodkov (1986) suggests that the limit of range pulsation may be pushed forward by adaptation (physical or social) of a species to cope with harsher environmental conditions than before. Grove (2016; Grove et al. 2015) argues that in the past many major dispersal events were preceded by episodes of instable climatic conditions. These created the need for a higher level of climatic tolerance, or in other words, the ability to adapt to a variety of habitats and environmental conditions. This increased adaptability would consequently be expressed in dispersal events in subsequent stable climatic conditions.

The observed intensification of habitat exploitation at Ksâr 'Akil but also the broader regional expansion into semi-arid environments as highlighted by Bar-Yosef (1987) could be indicative of the increasing adaptability of EUP hunter-gatherers. However, it is unclear how useful some of these traits were to groups dispersing into central and eastern Europe where foods such as edible terrestrial molluscs were available and steep rocky terrain as well as riverine and lake environments may have been encountered; coastal zones are clearly absent. Even if all adaptations were not useful in new environments, increased population density in the optimal zone may push forward the boundaries of this zone and would instigate dispersals into less amiable territories such as the zone of periodic extinction (Fig. 7.1f).

In addition, although in ecological terms the general limit of a species' range is placed at the limit of the zone of discontinuous distribution, from an archaeological perspective, one might consider exploiting the edge of the zone of periodic extinction because temporary occupation might leave archaeological remains. Thus, population pressure resulting in more dispersals into the zone of periodic extinction would increase archaeological visibility in this zone. Although periodic extinctions would still occur, they would appear to be (falsely) continuous to archaeologists because of the timescales they are forced to work with.

Figure 7.1 (next page): (a) Ecological model of a species range redrawn after Gorodkov (1986) and Roebroeks (2006). (b) The maximum extent of the zone of continuous distribution (blue). (c) The maximum extent of the zone of insular distribution. (d) Range expansion where environmental change and/or human adaptation enables survival in habitats previously beyond the species range. (e) Range expansion where environmental change and/or human adaptation enables dispersals into the discontinuous zone without changing the limits of this zone. (f) Range expansion fuelled by increased population density in the zone of continuous distribution.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Absence of population
Zone of corpse removal
Limit of sterile invasion
Pseudopopulation
Zone of sterile invasion
Limit of range pulsation
Temporary populations
Isolate
Zone of periodic extinction
GENERALIZED LIMIT OF DISTRIBUTION (Limit of disjunct distribution)
Populations frequently subordinate
Zone of disjunct distribution
Limit of contineous distribution
Basic population
Lacuna
Zone of continuous distribution
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Absence of population
Zone of corpse removal
Limit of sterile invasion
Pseudopopulation
Zone of sterile invasion
Limit of range pulsation
Temporary populations
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Pseudopopulation
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GENERALIZED LIMIT OF DISTRIBUTION (Limit of disjunct distribution)
Populations frequently subordinate
Zone of disjunct distribution
Limit of contineous distribution
Basic population
Lacuna
Zone of continuous distribution

Therefore, taking the Ksâr 'Akil data as an example, the observed regular shellfish consumption and increased diet breadth would add a range of essential nutrients to the diet. The intake of these resources would result in healthier populations with greater reproductive success and ultimately contribute to population increase. Higher population density, in turn, could fuel dispersals that are either successful due to the increased adaptability of EUP groups to a higher variety of environments or a series of less successful dispersals which leave a multitude of ephemeral sites resembling a zone of continuous distribution in the archaeological record. These possible outcomes raise several important questions for future research. For example: Is there evidence for populating the central and eastern European landscape with dispersing groups coming from the Levant? What is the longevity of early Upper Palaeolithic groups settling in Europe? How can we gain better insight on the scale of increasing population density during the EUP in the eastern Mediterranean woodland zone? Were the foraging strategies employed in the Levantine EUP also used in European inland sites?

7.6 Future research: mobility, dispersals, and shell beads

The discussions above stimulate a number of potential avenues for future studies. Such research would contribute to a better understanding of early Upper Palaeolithic *Homo sapiens* population dynamics in the Levant as well as of early Upper Palaeolithic dispersals into Europe and the mechanisms driving and/or aiding them.

To broaden our knowledge on seasonal activities during the IUP and EUP at Ksâr 'Akil and to provide a better view on the full extent of site occupation and the timing of resource exploitation, the seasonality of the terrestrial fauna should be investigated to complement the seasonality signal provided by the molluscs. Similarly, on a larger scale, to better grasp mobility strategies and population dynamics in eastern Mediterranean EUP, more data are needed on the seasonal patterns of shellfish exploitation from other sites. Ksâr 'Akil is the first site for which such a seasonality study of EUP molluscs has been undertaken. Similar investigations, for example, on the mollusc assemblages of Üçağızlı I, would serve to reinforce or complement the Ksâr 'Akil data set. Such data should be compared with seasonality data from other Levantine sites, which would allow for an evaluation of a wide array of subsistence and mobility strategies of past hunter-gatherers on a broader regional scale (e.g., Lieberman 1993). This, in turn, may help us gain better insight into the scale of increasing population density in the Levant during the EUP.

Another way to look at EUP dispersals is through the use of shells as personal ornaments. This type of symbolic behaviour is argued to be important in maintaining contact over long distances and may inform us about contacts between Levantine and European groups. Gamble (1998) argues that objects with symbolic meaning and the ability to transfer the properties of people to objects are key in negotiating extended and/or global networks. In this framework, socially imbued objects are needed to overcome the problems of stretching social systems to the point where people are no longer in direct contact (i.e., extended and global networks) to identify distant relatives and/or 'comparative strangers'.

Richerson and Boyd (2008) suggest that one of the most striking features of human sociality is the symbolic marking of group boundaries. This can be done through seemingly arbitrary things such as clothing, hairstyle, speech, and ornamentation (see also Hodder 1977). These symbolic markers convey common beliefs and norms within a group (e.g., ethnic or ethnolinguistic groups), but they can also convey the position of an individual within a group, such as gender, status, profession, or provenance (e.g., Vanhaeren and d'Errico 2006; d'Errico and Stringer 2011). While a large part of the material culture might be symbolically imbued, beads are one of the few archaeological objects whose function is exclusively symbolic. Using the Aurignacian as a case study, Vanhaeren and d'Errico (2006) have shown that shell beads can be used to identify and track cultural diversity in the archaeological record.

The shell bead assemblages of such sites as Ksâr 'Akil, Üçağızlı I, and Manot (Stiner et al. 2013; Hershkovitz et al. 2015) could be used to study diversity in bead working in the Levantine region. They could also be used to compare the Levantine materials with those from Europe in terms of uniformity and diversity of raw materials, technological processes, morphology, and use wear, as well as ecological context of beads. In this context, the reported Mediterranean shell found in the early Upper Palaeolithic of Kostenki 14 (Sinitsyn 2015), deep in the Eastern European mainland is highly interesting.

Coming back to the Gorodkov model, studying shell ornaments may shed light on distinguishing between an overall range expansion versus an increased frequency of occupation in the discontinuous zone (see Fig 7.1). If the Levantine and European early Upper Palaeolithic are related, one would expect to see similarities in manufacture processes and modes of use. In distant groups without continuous contact (into the zone of periodic extinction), one could expect aesthetic appearance to show standardisation so that new arrivals may be identified as like-minded or belonging to the same meta-group. In populations that are in regular contact (range expansion), one may expect beads to reflect more similarities in manufacture processes and more individual variation and invention among the end-products to convey personality and style within a larger group.

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Appendix A • Data recording protocol

For data recording I used a MS Access database and the data entry software E4 made by Shannon McPherron and Harold Dibble and freely available at: http://www.oldstoneage.com/software/e4.shtml. With E4 you tailor a configuration file (in .cfg format) to your needs. You can create menu's with the applicable variables for a field and the system allows you to directly input measurements with electronic callipers that both serve to avoid typo's. An Access database is created automatically from the configuration file, and in my experience is very stable. An excellent feature that makes data recording much faster is the option to use conditional statements that allow an entry field only to show up if previous variables are met. For example, in my configuration for recording molluscs I am only asked to describe and measure perforations if I have chosen the variable "perforation" in the "Breakage" field.

Overall, my configuration records find provenience, species identification, basic measurements, a series of taphonomic alterations, and a few fields that focus on perforated shells (i.e. inclusions, perforation locations, perforation-edge morphology and perforation measurements). The latter, are taken over and in part expanded from the criteria used in d'Errico et al. (2009) and Bouzouggar et al. (2007). Similarly, for bone recording I have used published criteria for several taphonomic processes, such as Behrensmeyer's (1978) criteria for bone-surface weathering with a few personal additions, and Stiner et al's. (1995) criteria for burning. Identification largely follows guidelines offered in Todd's (1998) "bison bone guide", including the three-part hierarchy determination of the element, portion and, segment of bones (e.g., Gifford and Crader 1977). Shaft portions or "zones", the preserved part of shaft length, and circumference are recorded to determine the extent of carnivore ravaging (*sensu* Marean and Spencer [1991]). Shaft portions are internally related to so-called "landmarks". In other words, I am only asked about the presence/absence of an elements landmark if it is situated in the recorded zone. The landmarks are compatible with Lam et al's. (1999) scan sites to assess density mediated attrition. And the manner of recording dental elements and their state of attrition is designed to be compatible with MNISQL software developed by Richard Klein to facilitate calculating MNIs from both toothrows as well as isolated teeth (see, e.g., Klein and Cruz-Uribe [1984]).

Changing an E4 configuration file (for example adding a variable) is quite easy making data recording very flexible, and as a result it evolves in accordance with novel insights and new questions. That said if I would write a configuration from scratch I would probably do some things different, such as giving every “natural alteration” in the shell cfg-file its own field rather than collating it in one. In sum, E4 has substantially streamlined and speeded up my data recording and I can highly recommend using it. Below I have provided my configuration files (i.e., one for vertebrates and one for molluscs) to serve two purposes, first to show which criteria I used while recording data, and second in the hope that it will be useful for others who would like to record shell and/or bone assemblages to answer similar questions addressed in this thesis. In the latter case I would recommend to use this configuration as a starting point to improve upon and change it to fit your needs.

Shell – configuration file (cfg)

```
[E4]
Filename=KsarAkil_shell.mdb
Instrument=xyz
Table=ModernShell
BackColor=16776960

[RGMNumber]
Type=Text
Prompt=Enter RGM number please
Length=15
Carry=True

[CatalogNumber]
Type=Text
Prompt=Enter RGM subnumber please
Length=15
Carry=True

[Layer]
Type=Text
Prompt=Enter the layer please
Length=10
Carry=True

[Depth]
Type=Text
Prompt=Enter the depth below datum please
Length=15
Carry=True

[Square]
Type=Text
Prompt=Enter the square please
```

```
Length=10
Carry=True

[ShellType]
Type=Menu
Prompt=Please enter type of shell
Menu=bivalve,coiled-shell,conical-gastropod,Scaphopod,NID
Length=17
Carry=True

[Species]
Type=Menu
Prompt=Enter the species please
Menu=Acanthocardia-tuberculata,Acanthocardia-sp,Anadara-polii,Anadara-sp,Antalis-dentalis,Antalis-vulgaris,Antalis-sp,Arca-noae,Arca-sp ,Barbatia-barbata,bivalve,Bolinus-brandaris,Bolma-rugosa,Buliminus-labrosus,Buliminus-sp,Callista-chione,Callista-sp,Cerastoderma-glaucum,Cerithium-vulgatum,Columbella-rustica,Conus-ventricosus,Cristataria-porrecta,Donax-trunculus,Euthria-cornea,gastropod,Glycymeris-nummaria,Glycymeris-sp,Helicidae,Helix-pachya,Hexaplex-truncullus,indet,Lima-lima,marine-gastopod,Melanopsis-buccinoidea,Metafruticicola-berytensis,Mitra-cornicula,Monacha-nummus,Monacha-syriaca,Monacha-sp,Murex-sp,Nassarius-gibbosulus,Nassarius-mutabilis,Nassarius-sp,Natica-hebraea,Naticarius-hebraeus,Neverita-josephinia,Ostrea-edulis,Oxychilus-syriacus,Patella-caerulea,Patella-rustica,Patella-ulyssiponensis,Patella-sp, Pene-syriacus,Phorcus-articulatus,Phorcus-turbinatus,Phorcus-sp,Pinna-nobilis,Pisania-striata,Pisania-sp,Pomatias-elegans,Pomatias-olivieri,Pomatias-sp,Potomida-littoralis,Prosobranchia-sp,scaphopod,Sernicassis-saburon,Sphincterochila-cariosa,Sponylus-gaederopus,Tarantinaea-lignarius,terrestrial-gastropod,Theodoxus-jordani,Trochidae,Venus-verrucosa,Vexillum-ebenus
Length=30
Carry=True

[Side]
Type=Menu
Prompt=Enter side of bivalve please
Menu=sin,dex,indet,both
Length=10
Condition1=ShellType bivalve

[NaturalAlterations]
Type=Menu
Prompt=please enter natural alteration, if multiple define in notes field please
Menu=none,gastropod-perforation,crab-attempt,predator-attempt,boring-sponge-damage,bioerosion,beach-washed,epizootic-encrustrations,encrustation,encrustation-non-local-deposit,erosion,reducing-beach-environment,multiple,beach-washed+boring-sponge-damage,beach-washed+gastropod-perforation,na
Length=50
Carry=True

[Inclusions]
Type=Menu
Prompt=Enter any inclusions please
Menu=none,beach worn pebble,beach worn shell,beach worn shell and pebble,na
Length=30
Condition1=ShellType coiled-shell

[EpizooticEncrustrations]
Type=Menu
Prompt=Enter location of Epizootic encrustriation please
Menu=dorsal,ventral,both sides,not specified
```

```
Length=13
Condition1=NaturalAlterations epizootic-encrustrations

[Bioerosion]
Type=Menu
Prompt=Enter location of boierosion please
Menu=dorsal,ventral,both sides,not specified
Length=13
Condition1=NaturalAlterations bioerosion

[Heating]
Type=Menu
Prompt=Please insert traces of burning
Menu=none,light,medium,severe,na
Length=10

[Decalcification]
Type=Menu
Prompt=Is the specimen decalcified
Menu=no,yes,na
Length=10

[Breakage]
Type=Menu
Prompt=Insert type of breakage please
Menu=none,perforation,recent,old,anthropic,na,natural
Length=15

[HumanModification]
Type=Menu
Prompt=Enter any human modifications please
Menu=none,scratching,punching,impact,na
Length=15

[FragmentationCoiledShell]
Type=Menu
Prompt=Insert part of the coiled shell that is available (choose one)
Menu=intact with apex,intact without apex,almost intact,apex,apex fr,aperture,aperture fr,body whorl fr,columella,columella fr,na,fragment
Length=20
Condition1=ShellType coiled-shell

[FragmentationConicalGastropod]
Type=Menu
Prompt=Insert part of the conical gastropod that is available (choose one)
Menu=intact with apex,intact without apex,almost intact,na,fragment with apex,fragment without apex,fragment
Length=21
Condition1=ShellType conical-gastropod

[FragmentationBivalve]
Type=Menu
Prompt=Insert part of the bivalve that is available (choose one)
Menu=intact,almost intact,umbo,umbo fr,na,fragment
Length=13
Condition1=ShellType bivalve
```

```
[DorsalPerforation]
Type=Menu
Prompt=Insert code for dorsal perforation type please
Menu=a,b - small hole on apex,c - apex gone,d - small hole mid dorsalplain,e - dorsal side apeture,f - medium hole mid dorsal plain,g - f+c,h - lateral opposite apeture,i - 2 holes both lateral sides of dorsal plain,j - large hole dorsal plain,k - j+c,l - apeture broken,m - apeture left,n - c+d,o - hole all dorsal plain incl apex,p - i+b,q - e+c,r - l+c,s - hole on umbo,t - i+c,u - f+l,na,v - hole on valve,w - o+l,x - h+l,y - l+j+c,z - l+j,aa - m+e,ab - h+l+c,ac - f+l+c,ad - f+b,ae - j+b,af - i+l+c,ag - e+b,ah - h+c,ai - l+e+c
Length=50
Condition1=Breakage perforation

[DorsalPerforationEdge]
Type=Menu
Prompt=Insert state of dorsal perforation edges please
Menu=smoothed,irregular,irregular with chipping inside,na
Length=30
Condition1=Breakage perforation AND
Condition2=DorsalPerforation NOT a

[VentralPerforation]
Type=Menu
Prompt=Insert code for ventral perforation type please
Menu=a,b - predator hole midventral plain,c - medium hole midventral plain,d - small hole on apex,na
Length=50
Condition1=Breakage perforation

[VentralPerforationEdge]
Type=Menu
Prompt=Insert state of ventral perforation edges please
Menu=smoothed,irregular,irregular with chipping inside
Length=30
Condition1=Breakage perforation AND
Condition2=VentralPerforation NOT a

[MaximumDimention]
Type=Instrument
Prompt=Insert max  dimention please
Length=10

[LengthMax]
Type=Instrument
Prompt=Insert max length in mm please
Length=10
Condition1=ShellType bivalve,conical-gastropod

[WidthMax]
Type=Instrument
Prompt=Insert max width (perpendicular to max length) in mm please
Length=10
Condition1=ShellType bivalve,conical-gastropod

[HeightMax]
Type=Instrument
Prompt=Insert max height in mm please
Length=10

[DiameterMax]
```

```
Type=Instrument
Prompt=Insert max diameter (perpendicular to max height) in mm please
Length=10
Condition1=ShellType coiled-shell,Scaphopod

[HeightApeture]
Type=Instrument
Prompt=Insert Aperture height in mm please
Length=10
Condition1=ShellType coiled-shell

[PerforationDiameterDorsalMax]
Type=Instrument
Prompt=Insert max diameter of dorsal perforation in mm please
Length=10
Condition1=Breakage perforation AND
Condition2=DorsalPerforation NOT a

[PerforationDiameterDorsalMin]
Type=Instrument
Prompt=Insert min diameter of dorsal perforation in mm please
Length=10
Condition1=Breakage perforation AND
Condition2=DorsalPerforation NOT a

[PerforationDiameterVentralMax]
Type=Instrument
Prompt=Insert max diameter of ventral perforation in mm please
Length=10
Condition1=Breakage perforation AND
Condition2=VentralPerforation NOT a

[PerforationDiameterVentralMin]
Type=Instrument
Prompt=Insert min diameter of ventral perforation in mm please
Length=10
Condition1=Breakage perforation AND
Condition2=VentralPerforation NOT a

[Picture]
Type=Menu
Prompt=Is there a picture taken
Menu=No,Yes
Length=10

[Sampled]
Type=Menu
Prompt=Is the specimen sampled
Menu=none,C14,isotopes,AAR
Length=10

[Remarks]
Type=Text
Prompt= Enter any useful remarks please
Length=255
```

Bone – configuration file (cfg)

```
[E4]
Filename=KsarAkil_fauna.mdb
Instrument=xyz
Table=KsarAkilFauna
BackColor=16776960

[CatalogNumber]
Type=Text
Prompt=Enter the cat. no. please
Length=15
Unique=True

[DMBNumber]
Type=Text
Prompt=Enter the DMB no. please
Length=10
Carry=True

[Layer]
Type=Text
Prompt=Enter the layer please
Length=10
Carry=True

[Square]
Type=Text
Prompt=Enter the square please
Length=10
Carry=True

[Species]
Type=Menu
Prompt=Enter the species please
Menu=AL,AM,AV,BO,BOV,BOV1,BOV1-2,BOV2,BOV2-3,BOV3,BOV3-4,BOV4,BOV4-5,BOV5,CA,CAE,CAU,CE,CER,CER1,CER1-2,CER2,CER2-3,CER3,CER3-4,CER4,CER4-5,CER5,CH,CL,CN,CP,CPI,CR,CRD,DA,DAM,DM,EC,EQ,FC,FE,FP,FS,GF,GZ,GZD,GZ1,GZ1-2,GZ2,GZ2-3,GZ3,GZ3-4,GZ4,HS,HY,IS,LC,LE,MA,MAM1,MAM1-2,MAM2,MAM2-3,MAM3,MAM3-4,MAM4,MAM4-5,MAM5,ME,MO,MU,PA,PI,RE,RH,RO,SC,SE,SU,TE,UA,UNG1,UNG1-2,UNG2,UNG2-3,UNG3,UNG3-4,UNG4,UNG4-5,UNG5,UR,VU,NID
Length=10
Carry=True

[Element]
Type=Menu
Prompt=Enter the Element please
Menu=ACC,ANT,AS,AT,AX,CALC,CAP,CAR,CB,CC,CLA,CMC,COS,CP,CP3,CR,CS,CU,CU1,CU2,CU3,CUB,CX,DINF,DSUP,DUN,FB,FE,FI,HAM,HC,HU,HY,LB,LTM,LUN,MAN,MAX,MC,MC1,MC2,MC3,MC4,MC5,MC1/4,MC2/3,MP,MP3/4,MPA,MT,MT1,MT2,MT3,MT4,MT5,MT1/4,MT2/3,NAV,NID,PE,PH,PH1,PH2,PH3,PIS,PLA,PO,PT,PYS,RA,RCA,RUL,SAC,SC,SCP,SED,SEP,SES,SN,TI,TMT,TR,TRA,TRI,TT,TZD,UCA,UL,VCA,VCE,VLM,VSA,VT,VTH
Length=35
Carry=True
Condition1=Species NOT NID
```

```
[Portion]
Type=Menu
Prompt=Enter the Portion please
Menu=ACE,ACL,ACM,ACO,ACP,ACS,ANC,ANG,APA,APP,AXE,BA,BDR,BE,BL,BRC,BSP,C,CN,CNE,CNW,CO,COC,CON,COR,COS,CUS,DC,DE,DF,DI1,DI2,DI3,DIST,DIUN,DP1,DP2,DP3,DP4,DPUN,DSE,DSH,DUN,EPS,FK,FN,FR,GL,GNB,GO,GS,HOR,I1,I2,I3,IFK,ILD,ILI,ISC,ISD,IUN,JUG,LAC,M1,M2,M1/2,M3,MANF,MAX,MF,MUN,NA,NAS,NSL,NU,OCC,OLC,OLCT,P1,P2,P3,P4,PAR,PB,PCO,PER,PET,PLE,PLH,PLHA,PLHP,PLN,PLM,PLX,PMAX,PMUN,PNU,PRE,PROX,PSH,PUN,PY,RAM,ROOT,SH,SP,SPY,SYM,TIN,TMP,TRP,TW,TWA,US,VER,ZGO
Length=30
Carry=True
Condition1=Species NOT NID

[Segment]
Type=Menu
Prompt=Enter the Segment please
Menu=ABA - abaxial (PH),ACO - almost complete,ACR - anterior crest,AL - anterolateral,ALV - alveolus,AM - anteromedial,AN - anterior,ANF - anterior nutritional foramen,AXI - axial (PH),CAU - caudal,CDL - lateral condyle (FE TI),CDM - medial condyle (FE TI),CO - complete,CRA - cranial,DR - dorsal,DIST - distal,DT - deltoid tuberosity (HU),DU - distal ulna (UL),EX- exterior,FF - frontal foramen (FN),FOR - foramen,FR - fragment,FT - facial tuber (MAX),GT - groove lat dig extensor tendon (TI),HE - head (HM FE),IN - interior,IOS - interosseous space (RUL),LEP - lateral epicondyle (HU),LSP - linea aspera (FE),LT - lateral,ME - medial,MEP - medial epicondyle (HU),MJO - major trochanter (FE),MLT - major lat tuberosity (HU),MM - medial maleolus (TI),MO - minor trochanter (FE),MST - med supracondyloid tuberosity (FE),NE - neck (SC),OCD - occipital condyles (OCC),PAL - palatine (MAX),PD - pedicle,PDA - pedicle with antler,PL - posterolateral,PLF - posterolateral nutrient (HU-RA-TI),PLSP - prox linea aspera (FE),PM - posteromedial,POF - prox olecranon fossa (HU),PROX - proximal,PS - posterior,PSF - posterior foramen (MP),RFO - radial fossa (HU),RT - radial tuber (RA),SF - supracondyloid fossa (FE),SGT - supra glenoid fossa (SC),SH - shaft,STY - styloid (RA),TBC - tubercle (COS),TIT - tibial tuberosity (TI),TM - teres major tubercle (HU),TMJ - temporo-mand. joint (CR),TRL - trochlea (FE HU),TRO - 3rd trochanter (equid FE),US - unspecified,VN - ventral
Length=40
Carry=True
Condition1=Species NOT NID

[Jaw]
Type=Menu
Prompt=Enter which jaw please
Menu=L,U,I,NA
Length=10
Condition1=Species NOT NID AND
Condition2=Element CR,DINF,DSUP,DUN,MAN,MAX

[Side]
Type=Menu
Prompt=Enter a value for Side
Menu=D,CfD,S,CfS,I,B,A
Length=20
Condition1=Species NOT NID

[sex]
Type=Menu
Prompt=Give indication on sex please
Menu=indet,male,female
Length=10
Condition1=Species NOT NID
```

```
[PFUS]
Type=Menu
Prompt=Enter a value for Proximal fusion (0-5) please
Menu=5 - unapplicable,0 - unfused,1 - partially fused,2 - fusing (line visible),3 - fully fused,4 - broken
indeterminate
Length=30
Condition1=Species NOT NID AND
Condition2=Element
AT,AX,CALC,CC,CLA,CMC,COS,FE,FI,HU,LB,MC,MC1,MC2,MC3,MC4,MC5,MC1/4,MC2/3,MP,MP3/4,MPA,
MT,MT1,MT2,MT3,MT4,MT5,MT1/4,MT2/3,PH,PH1,PH2,PO,PYS,RA,RUL,TI,TMT,TT,UL,VCA,VCE,VLM,VSA,
VT,VTH

[DFUS]
Type=Menu
Prompt=Enter a value for Distal fusion (0-5) please
Menu=5 - unapplicable,0 - unfused,1 - partially fused,2 - fusing (line visible),3 - fully fused,4 - broken
indeterminate
Length=25
Condition1=Species NOT NID AND
Condition2=Element
AT,AX,CC,CLA,CMC,FE,FI,HU,LB,MC,MC1,MC2,MC3,MC4,MC5,MC1/4,MC2/3,MP,MP3/4,MPA,MT,MT1,M
T2,MT3,MT4,MT5,MT1/4,MT2/3,PH,PH1,PH2,RA,RUL,SC,TI,TMT,TT,UL,VCA,VCE,VLM,VSA,VT,VTH

[ShaftLength]
Type=Menu
Prompt=Enter a value for Shaft length (0-4) please
Menu=0 - not applicable,1 - < 1/4 diaph. length,2 - 1/4 to 1/2,3 - 1/2 to 3/4,4 - > 3/4 diaph. length
Length=23
Condition1=Element
CC,CLA,CMC,FE,HU,LB,MC,MC1,MC2,MC3,MC4,MC5,MC1/4,MC2/3,MP,MP3/4,MPA,MT,MT1,MT2,MT3,
MT4,MT5,MT1/4,MT2/3,RA,RUL,TI,TMT,TT

[ShaftCircumference]
Type=Menu
Prompt=Enter a value for Shaft Circumference (0-3) please
Menu=0 - not applicable,1 - < half diameter,2 - > half diameter,3 - complete
Length=19
Condition1=Element
CC,CLA,CMC,FE,HU,LB,MC,MC1,MC2,MC3,MC4,MC5,MC1/4,MC2/3,MP,MP3/4,MPA,MT,MT1,MT2,MT3,
MT4,MT5,MT1/4-MT2/3,RA,RUL,TI,TMT,TT

[ShaftPortion1]
Type=Menu
Prompt=Is shaft portion 1 available?
Menu=No,Yes
Length=10
Condition1=Element
FE,HU,LB,MC,MC1,MC2,MC3,MC4,MC5,MC1/4,MC2/3,MP,MP3/4,MPA,MT,MT1,MT2,MT3,MT4,MT5,MT
1/4,MT2/3,RA,RUL,TI

[ShaftPortion2]
Type=Menu
Prompt=Is shaft portion 2 available?
Menu=No,Yes
Length=10
```

```
Condition1=Element
FE,HU,LB,MC,MC1,MC2,MC3,MC4,MC5,MC1/4,MC2/3,MP,MP3/4,MPA,MT,MT1,MT2,MT3,MT4,MT5,MT
1/4,MT2/3,RA,RUL,TI

[ShaftPortion3]
Type=Menu
Prompt=Is shaft portion 3 available?
Menu=No,Yes
Length=10
Condition1=Element
FE,HU,LB,MC,MC1,MC2,MC3,MC4,MC5,MC1/4,MC2/3,MP,MP3/4,MPA,MT,MT1,MT2,MT3,MT4,MT5,MT
1/4,MT2/3,RA,RUL,TI

[ShaftPortion4]
Type=Menu
Prompt=Is shaft portion 4 available?
Menu=No,Yes
Length=10
Condition1=Element
FE,HU,LB,MC,MC1,MC2,MC3,MC4,MC5,MC1/4,MC2/3,MP,MP3/4,MPA,MT,MT1,MT2,MT3,MT4,MT5,MT
1/4,MT2/3,RA,RUL,TI

[ShaftPortion5]
Type=Menu
Prompt=Is shaft portion 5 available?
Menu=No,Yes
Length=10
Condition1=Element
FE,HU,LB,MC,MC1,MC2,MC3,MC4,MC5,MC1/4,MC2/3,MP,MP3/4,MPA,MT,MT1,MT2,MT3,MT4,MT5,MT
1/4,MT2/3,RA,RUL,TI

[LandmarkFemurHe]
Type=Menu
Prompt=Femur head (HE) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element FE AND
Condition3=ShaftPortion1 Yes

[LandmarkFemurPLSP]
Type=Menu
Prompt=Proximal linea aspera (triangular junction with MO (PLSP) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element FE AND
Condition3=ShaftPortion1 Yes

[LandmarkFemurMJO]
Type=Menu
Prompt=Major Trochanter (MJO) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element FE AND
Condition3=ShaftPortion1 Yes
```

```
[LandmarkFemurANF]
Type=Menu
Prompt=Anterior Nutritional Foramen (ANF) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element FE AND
Condition3=ShaftPortion2 Yes

[LandmarkFemurMO]
Type=Menu
Prompt=Minor Trochanter (MO) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element FE AND
Condition3=ShaftPortion2 Yes

[LandmarkFemurSF]
Type=Menu
Prompt=Supra condyloid fossa (SF) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element FE AND
Condition3=ShaftPortion4 Yes

[LandmarkFemurCDL]
Type=Menu
Prompt=Lateral condyle (CDL) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element FE AND
Condition3=ShaftPortion5 Yes

[LandmarkFemurCDM]
Type=Menu
Prompt=Medial condyle (CDM) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element FE AND
Condition3=ShaftPortion5 Yes

[LandmarkFemurTRL]
Type=Menu
Prompt=Trochlea (TRL) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element FE AND
Condition3=ShaftPortion5 Yes

[LandmarkHumerusHE]
Type=Menu
```

```
Prompt=Humerus head (HE) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element HU AND
Condition3=ShaftPortion1 Yes

[LandmarkHumerusMLT]
Type=Menu
Prompt=major (lateral) tuberosity (MLT) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element HU AND
Condition3=ShaftPortion1 Yes

[LandmarkHumerusTM]
Type=Menu
Prompt=Teres Major (TM) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element HU AND
Condition3=ShaftPortion2 Yes

[LandmarkHumerusDT]
Type=Menu
Prompt=Deltoid tuberosity (DT) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element HU AND
Condition3=ShaftPortion2 Yes

[LandmarkHumerusPLF]
Type=Menu
Prompt=Humerus posterior lateral foramen (PLF) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element HU AND
Condition3=ShaftPortion3 Yes

[LandmarkHumerusPOF]
Type=Menu
Prompt=olecranon fossa (POF) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element HU AND
Condition3=ShaftPortion5 Yes

[LandmarkHumerusRFO]
Type=Menu
Prompt=Radial fossa (RFO) available?
Menu=No,Yes
Length=10
```

```
Condition1=Species NOT NID AND
Condition2=Element HU AND
Condition3=ShaftPortion5 Yes

[LandmarkHumerusMEP]
Type=Menu
Prompt=Medial epidondyle (MEP) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element HU AND
Condition3=ShaftPortion5 Yes

[LandmarkHumerusLEP]
Type=Menu
Prompt=Lateral epicondyle (LEP) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element HU AND
Condition3=ShaftPortion5 Yes

[LandmarkHumerusTRL]
Type=Menu
Prompt=Humerus trochlea (TRL) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element HU AND
Condition3=ShaftPortion5 Yes

[LandmarkRULOLCT]
Type=Menu
Prompt=Ulna Olecranon tuber (OLCT) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element RUL AND
Condition3=ShaftPortion1 Yes

[LandmarkRULOLC]
Type=Menu
Prompt=Ulna Olecranon (OLC) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element RUL AND
Condition3=ShaftPortion1 Yes

[LandmarkRULANC]
Type=Menu
Prompt=Ulna Anconeal process (ANC) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element RUL AND
Condition3=ShaftPortion1 Yes
```

```
[LandmarkRULRT]
Type=Menu
Prompt=Radius Radial tuberosity (RT) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element RUL,RA AND
Condition3=ShaftPortion2 Yes

[LandmarkRULPLF]
Type=Menu
Prompt=Radius Posterior lateral foramen (PLF) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element RUL,RA AND
Condition3=ShaftPortion2 Yes

[LandmarkRULIOS]
Type=Menu
Prompt=Interosseous space ra-ul (IOS) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element RUL,RA AND
Condition3=ShaftPortion2 Yes

[LandmarkRULSTY]
Type=Menu
Prompt=Styloid process (STY) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element RUL,RA AND
Condition3=ShaftPortion5 Yes

[LandmarkUlnaOLCT]
Type=Menu
Prompt=Ulna Olecranon tuber (OLCT) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element UL

[LandmarkUlnaOLC]
Type=Menu
Prompt=Ulna Olecranon (OLC) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element UL

[LandmarkUlnaANC]
Type=Menu
Prompt=Ulna Anconeal process (ANC) available?
Menu=No,Yes
```

```
Length=10
Condition1=Species NOT NID AND
Condition2=Element UL

[LandmarkUlnaIOS]
Type=Menu
Prompt=Interosseous space ra-ul (IOS) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element UL

[LandmarkUlnaDU]
Type=Menu
Prompt=Distal Ulna (DU) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element UL

[LandmarkTibiaCDL]
Type=Menu
Prompt=Lateral condyle (CDL) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element TI AND
Condition3=ShaftPortion1 Yes

[LandmarkTibiaCDM]
Type=Menu
Prompt=Medial condyle (CDM) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element TI AND
Condition3=ShaftPortion1 Yes

[LandmarkTibiaTIT]
Type=Menu
Prompt=Tibial tuberosity (TIT) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element TI AND
Condition3=ShaftPortion1 Yes

[LandmarkTibiaACR]
Type=Menu
Prompt=Anterior crest (ACR) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element TI AND
Condition3=ShaftPortion2 Yes

[LandmarkTibiaPLF]
```

```
Type=Menu
Prompt=Posterior lateral foramen (PLF) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element TI AND
Condition3=ShaftPortion2 Yes

[LandmarkTibiaMM]
Type=Menu
Prompt=medial maleolus (MM) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element TI AND
Condition3=ShaftPortion5 Yes

[LandmarkTibiaGT]
Type=Menu
Prompt=groove for lat digital extensor tendon (GT) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element TI AND
Condition3=ShaftPortion5 Yes

[LandmarkScapulaACM]
Type=Menu
Prompt=Acromion (ACM) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element SC

[LandmarkScapulaNE]
Type=Menu
Prompt=Scapula Neck (NE) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element SC

[LandmarkScapulaSGT]
Type=Menu
Prompt=Supra glenoid tuber (SGT) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element SC

[LandmarkMandibleSYM]
Type=Menu
Prompt=Symfyses (SYM) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element MAN
```

```
[LandmarkMandibleMF]
Type=Menu
Prompt=Mental foramen (MF) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element MAN

[LandmarkMandibleBDR]
Type=Menu
Prompt=distal border (base) of horizontal ramus (BDR) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element MAN

[LandmarkMandibleANG]
Type=Menu
Prompt=Angle (ANG) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element MAN

[LandmarkMandibleMANF]
Type=Menu
Prompt=Mandibular foramen (MANF) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element MAN

[LandmarkMandibleCON]
Type=Menu
Prompt=Condylar process (CON) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element MAN

[LandmarkMandibleCOR]
Type=Menu
Prompt=Coronoid process (COR) available?
Menu=No,Yes
Length=10
Condition1=Species NOT NID AND
Condition2=Element MAN

[I1L]
Type=Menu
Prompt=Enter value for sin I1 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side S,B,A
```

```
[I2L]
Type=Menu
Prompt=Enter value for sin I2 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side S,B,A

[I3L]
Type=Menu
Prompt=Enter value for sin I3 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side S,B,A

[CL]
Type=Menu
Prompt=Enter value for sin C please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side S,B,A

[P1L]
Type=Menu
Prompt=Enter value for sin P1 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side S,B,A

[P2L]
Type=Menu
Prompt=Enter value for sin P2 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side S,B,A

[P3L]
Type=Menu
Prompt=Enter value for sin P3 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side S,B,A

[P4L]
Type=Menu
```

```
Prompt=Enter value for sin P4 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side S,B,A

[M1L]
Type=Menu
Prompt=Enter value for sin M1 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side S,B,A

[M2L]
Type=Menu
Prompt=Enter value for sin M2 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side S,B,A

[M3L]
Type=Menu
Prompt=Enter value for sin M3 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side S,B,A

[I1R]
Type=Menu
Prompt=Enter value for (cf) D, cf S, or Indet I1 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side D,CfD,CfS,I,B,A

[I2R]
Type=Menu
Prompt=Enter value for (cf) D, cf S, or Indet I2 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side D,CfD,CfS,I,B,A

[I3R]
Type=Menu
Prompt=Enter value for (cf) D, cf S, or Indet I3 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
```

```
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side D,CfD,CfS,I,B,A

[CR]
Type=Menu
Prompt=Enter value for (cf) D, cf S, or Indet C please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side D,CfD,CfS,I,B,A

[P1R]
Type=Menu
Prompt=Enter value for (cf) D, cf S, or Indet P1 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side D,CfD,CfS,I,B,A

[P2R]
Type=Menu
Prompt=Enter value for (cf) D, cf S, or Indet P2 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side D,CfD,CfS,I,B,A

[P3R]
Type=Menu
Prompt=Enter value for (cf) D, cf S, or Indet P3 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side D,CfD,CfS,I,B,A

[P4R]
Type=Menu
Prompt=Enter value for (cf) D, cf S, or Indet P4 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side D,CfD,CfS,I,B,A

[M1R]
Type=Menu
Prompt=Enter value for (cf) D, cf S, or Indet M1 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side D,CfD,CfS,I,B,A
```

```
[M2R]
Type=Menu
Prompt=Enter value for (cf) D, cf S, or Indet M2 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side D,CfD,CfS,I,B,A

[M3R]
Type=Menu
Prompt=Enter value for (cf) D, cf S, or Indet M3 please
Menu=,XD,XX,SD,SX,?X,?D,FX
Length=10
Condition1=Species NOT NID AND
Condition2=Jaw L,U,I AND
Condition3=Side D,CfD,CfS,I,B,A

[WSP1L]
Type=Text
Prompt=Enter wear stage for sin P1 please
Length=30
Condition1=P1L XD,XX

[WSP2L]
Type=Text
Prompt=Enter wear stage for sin P2 please
Length=30
Condition1=P2L XD,XX

[WSP3L]
Type=Text
Prompt=Enter wear stage for sin P3 please
Length=30
Condition1=P3L XD,XX

[WSP4L]
Type=Text
Prompt=Enter wear stage for sin P4 please
Length=30
Condition1=P4L XD,XX

[WSM1L]
Type=Text
Prompt=Enter wear stage for sin M1 please
Length=30
Condition1=M1L XD,XX

[WSM2L]
Type=Text
Prompt=Enter wear stage for sin M2 please
Length=30
Condition1=M2L XD,XX

[WSM3L]
Type=Text
```

```
Prompt=Enter wear stage for sin M3 please
Length=30
Condition1=M3L XD,XX

[WSP1R]
Type=Text
Prompt=Enter wear stage for dex P1 please
Length=30
Condition1=P1R XD,XX

[WSP2R]
Type=Text
Prompt=Enter wear stage for dex P2 please
Length=30
Condition1=P2R XD,XX

[WSP3R]
Type=Text
Prompt=Enter wear stage for dex P3 please
Length=30
Condition1=P3R XD,XX

[WSP4R]
Type=Text
Prompt=Enter wear stage for dex P4 please
Length=30
Condition1=P4R XD,XX

[WSM1R]
Type=Text
Prompt=Enter wear stage for dex M1 please
Length=30
Condition1=M1R XD,XX

[WSM2R]
Type=Text
Prompt=Enter wear stage for dex M2 please
Length=30
Condition1=M2R XD,XX

[WSM3R]
Type=Text
Prompt=Enter wear stage for dex M3 please
Length=30
Condition1=M3R XD,XX

[CarnivoreModification]
Type=Menu
Prompt=Enter Cranivore Modification (0-3) please
Menu=0 - none,1- tooth mark/pit,2 - puncture/perforation,3 - gnawing
Length=30

[HumanModification]
Type=Menu
Prompt=Enter Human Modification (0-9) please
Menu=0 - none,1 - cutmark,2 - impact,3 - scraping,4 - percussion,5 - chopmark,6 - cutmark+impact,7 -
cutmark+scraping,8 - impact+scraping,9 - impact+percussion, 10 - cutmark?
```

```
Length=30

[PrimBreakage]
Type=Menu
Prompt= Enter primary breakage please
Menu=1 - green/fresh,2 - dry (ancient),3 - recent/curation,4 - not applicable
Length=19

[SecBreakage]
Type=Menu
Prompt= Enter secondary breakage please
Menu=1 - green/fresh,2 - dry (ancient),3 - recent/curation,4 - not applicable
Length=19

[Burning]
Type=Menu
Prompt=Enter a value for Burning
Menu=0 - unburned,1 - spot (<1/2) burnt,2 - slight carbonization (>1/2),3 - fully black,4 - calcined spot (<1/2),5 - very calcined (>1/2),6 - fully calcined = white,9 - indeterminate
Length=50

[Weathering]
Type=Menu
Prompt=Enter Weathering stage please
Menu=0 - none,1 - cracking (stage 1),2 - thin cortical flaking (stage 2),3 - cortical flaking,4 - small rectangular pcs,5 - flakes on cortical planes,6 - smoothed/rolled,7 - acid and/or digestion,8 - geological staining
Length=50
Condition1=Species NOT NID

[CorticalSurface]
Type=Menu
Prompt=Enter %visible cortical surface please
Menu=0 - 100%,1 - >75%,2 - 50-75%,3 - 25-50%,4 - <25%,5 - not applicable
Length=18

[Refit]
Type=Text
Prompt=Enter the cat. no. to which this specimens refit (pre-depostion) please
Length=50

[Conjoin]
Type=Text
Prompt=Enter the cat. no. to which this specimen Conjoins (post-deposition) please
Length=50

[Sampled?]
Type=Menu
Prompt=If the specimen is used for sampling insert for which purpose
Menu=None,AMS,Isotopes,ESR,TL
Length=10
Condition1=Species NOT NID

[Length]
Type=Instrument
Prompt=Insert length in mm please
Length=10
```

```
[Remarks]
Type=Text
Prompt= Enter any useful remarks please
Length=255
```

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Samenvatting

Minimaal vanaf de tweede helft van het Laat-Pleistoceen, rond 50–40 duizend jaar geleden, verspreidde Jong-paleolithische *Homo sapiens* zich vanuit Afrika naar Europa en Azië. De kolonisatie van Eurazië vond plaats in verschillende migratiegolven. Deze migratiegroepen bestonden vaak uit kleine populaties die zich verbreidden over grote gebieden. In tegenstelling tot sommige eerdere groepen, zoals die uit het vroegste Jong-paleolithicum (IUP) en Emerien, lijkt het erop dat latere vroeg Jong-paleolithische (EUP) of vroeg Ahmarien groepen meer succes hadden in het in stand houden van populaties in nieuw gebied. Dit lijkt gepaard te gaan met een toename in bevolkingsdichtheid gedurende het EUP. Wat waren de aanpassingen in gedrag die ten grondslag lagen aan deze toename en aan het succes van EUP-migraties naar Eurazië? Kunnen de eetgewoonten van EUP *Homo sapiens* bijgedragen hebben aan hun succes?

Dit proefschrift doet verslag van een studie naar het foerageergedrag van IUP en vroeg Ahmarien *Homo sapiens* in het oostmediterrane kustgebied, door het bestuderen van vertebraten en invertebraten gevonden in de abri Ksâr 'Akil (Libanon). Dit onderzoek wijst uit dat de EUP-bewoners een breder dieet hadden dan hun IUP-voorgangers. Dit is vooral te zien aan de toename in de exploitatie van kleinere diersoorten zoals gazellen, reeën en schildpadden, en het regelmatig verzamelen van zeevruchten en landslakken. Deze veranderingen in foerageergedrag leverden een veelzijdiger dieet op met een hoger percentage aan essentiële sporenelementen. Het is goed mogelijk dat dieetkeuzes bijgedragen hebben aan een betere volksgezondheid in het vroeg Ahmarien en geholpen hebben een grotere bevolkingsdichtheid in stand te houden.

Voor verder ingegaan kan worden op de precieze adaptaties in foerageergedrag en de mogelijke uitwerkingen daarvan op *Homo sapiens*-populaties, is het belangrijk om meer te weten te komen over het precieze tijdstip en de route van deze migratiegolven. De vindplaats Ksâr 'Akil speelt sinds lange tijd een belangrijke rol in de debatten rond de vroeg Jong-paleolithische migraties: aan de ene kant door zijn locatie in de zogenaamde "Levantijnse Corridor", die één van de mogelijke migratie routes voorstelt. En aan de andere kant door de verschillende menselijke resten die er gevonden zijn, geassocieerd met IUP en vroeg Ahmarien lagen. Recent onderzoek heeft op basis van radiocarbon dateringen, de validiteit van de Levant als een doorgangsroute voor Jong-paleolithische groepen van Afrika naar Eurazië in twijfel getrokken. Deze dissertatie stelt een nieuwe chronologie voor op basis van een multidisciplinair onderzoek dat radiocarbon dateringen combineert met zuurstofisotopen data, aminozuur racemisatie en andere chemische methoden om mogelijke diagenetische veranderingen in het bemonsterde schelpmateriaal te identificeren. Deze chronologie suggereert dat vroeg Jong-paleolithische *Homo sapiens*, zowel uit het IUP als EUP, eerder in Ksâr 'Akil aanwezig waren dan tot nu toe ergens anders bekend in Eurazië. Dit wijst erop dat de Levant toch als migratie route gebruikt lijkt te zijn gedurende het vroeg Jong-paleolithicum.

De eerste stap in het identificeren van foerageergedrag is het bestuderen van de taphonomische processen die een rol gespeeld hebben in de formatie van de fauna-assemblages. Botpreservatie is goed genoeg om modificaties gemaakt door dieren (bijvoorbeeld knaag- en bijt-sporen) en mensen (bijvoorbeeld snij- en slacht-sporen) te herkennen. Taphonomisch onderzoek in dit proefschrift wijst uit dat mensen het meest hebben bijgedragen aan de accumulatie van het botmateriaal en dat carnivoren vrij weinig invloed hebben gehad. De significante positieve relatie tussen identificeerbare botresten en het minimum aantal individuen per soort geeft aan dat post-depositionele taphonomische processen vergelijkbaar waren voor de botassemblages van verschillende lagen. Dit betekent dat het mogelijk is om de verschillen in soorten-compositie tussen lagen te vergelijken. Vergelijkbare resultaten zijn gevonden voor de invertebraten. Verder werden mollusken verzameld voor verschillende doeleinden. Schelpen werden op het strand verzameld om vervolgens gebruikt te worden als werktuigen (voornamelijk de tweekleppige *Glycymeris nummaria*) of als ornamenten zoals de slakken (bijvoorbeeld *Tritia gibbosula* en *Columbella rustica*). Sommige marine litorale soorten werden levend verzameld om gegeten te worden (bijvoorbeeld *Phorcus turbinatus* en *Patella rustica*). Ook de mortaliteitscurven van de landslak *Helix pachya* wijst op de selectieve verzameling van grote volwassen slakken, een patroon dat niet overeenkomt met dat van een normale levende populatie, maar met die van menselijk foerageergedrag.

De IUP en vroeg Ahmarien vertebraten assemblages worden beiden gedomineerd door Mesopotamisch damhert en, in mindere mate, wildzwijn en wilde geit. De exploitatiepatronen verschillen in de verspreiding van minder vaak voorkomende prooidieren zoals gazellen, schildpadden, en reeën, die gelijkmatiger verdeeld zijn in het vroeg Ahmarien. Alhoewel er incidenteel marine mollusken gegeten werden aan het einde van het IUP, komt de exploitatie van zeevruchten pas echt op gang in het vroeg Ahmarien. Deze vroeg Ahmarien marine exploitatie valt samen met de exploitatie van de bovengenoemde landslak. Deze veranderingen in foerageergedrag wijzen op een verbreding van het dieet en het aantal geëxploiteerde habitats gedurende het vroeg Ahmarien.

Zuurstofisotopenanalyse op schelpen van de gegeten litorale slak *Phorcus turbinatus* heeft uitgewezen dat in het vroeg Ahmarien deze zeevruchten gedurende het hele jaar werden gegeten, waarvan de meerderheid in de koudere maanden van het jaar. Aan de ene kant wijst dit erop dat het verzamelen van litorale zeevruchten een vrij normale bezigheid was die ten alle tijden kon plaatsvinden en niet seizoensgebonden was, zoals we bijvoorbeeld in het latere Atlitien zien. Aan de andere kant wijst de aanwezigheid van in alle seizoenen gevangen mollusken erop dat de locatie ook in alle seizoenen gebruikt werd.

De introductie van zeevruchten en landslakken, en de meer gelijk verspreide exploitatie van kleinere minder vaak gegeten prooidieren geven allemaal blijk van een verandering in foerageergedrag tussen het IUP en vroeg Ahmarien. Deze veranderingen laten zien dat de EUP *Homo sapiens* een groter beslag legde op de draagkracht van de ecosystemen in het oostmediterrane kustgebied dan hun IUP-voorgangers. Vanuit een *Optimal Foraging* oogpunt wordt dit fenomeen gezien als een indicatie van hogere druk op de voorhanden zijnde voedselbronnen, hetzij door een tekort aan voedsel door verslechterde klimaatomstandigheden, hetzij door een verhoogde bevolkingsdichtheid.

Vanuit een *Nutritional Ecology* oogpunt levert een breder aanbod aan voedselbronnen een meer gebalanceerd dieet met een grotere variëteit aan essentiële sporenelementen op. Zeevruchten bijvoorbeeld zijn rijk aan vitaminen A, B12, C, D, E, ijzer, foliumzuur, calcium, kalium en omega 3-vetzuren, waarvan sommige (bijvoorbeeld vitaminen B12, D, calcium en omega 3-vetzuren) moeilijk te verkrijgen zijn uit andere op het land levende voedselbronnen. Een beter gebalanceerd dieet zou bijgedragen kunnen hebben aan een gezondere populatie, een daling in kindersterfte en een hogere geboortefrequentie. Deze veranderingen zouden op hun beurt weer kunnen hebben bijgedragen aan een stijging in de bevolkingsdichtheid.

De veranderingen in foerageergedrag gezien in Ksâr ‘Akil lijken, in ieder geval deels, ook op te gaan voor andere EUP-vindplaatsen in het oostmediterrane kustgebied zoals in Üçağızlı I in Turkije. Hoe vallen de data van één of enkele vindplaatsen in te passen in grootschalige vragen over migratiepatronen? Hier biedt Gorodkov’s ecologische model van de verspreiding van diersoorten een aanknopingspunt. De verhoogde bevolkingsdichtheid in een ‘optimaal’ leefgebied kan dienen als pushfactor voor de verspreiding van de soort naar nieuwe minder optimale gebieden. Hoe hoger de druk op de bevolkingsdichtheid des de vaker zal zo’n migratiegolf plaatsvinden. Deze gemigreerde groepen kunnen of succesvol blijken in het nieuwe gebied of niet succesvol en uitsterven. Gezien de resolutie van de archeologische tijdschaal is het moeilijk om tussen deze twee mogelijkheden te differentiëren. De vindplaatsen met gerelateerde vuursteentechnologie, die we in steeds grotere getale zien opdagen in Eurazië gedurende het vroege Jong-paleolithicum zouden daarom het resultaat kunnen zijn van meerdere niet-continue migratie episodes en het ten onrechte doen lijken alsof EUP-*Homo sapiens* zich succesvol in nieuwe gebieden vestigde. Om daarachter te komen zouden we ons moeten richten op de vindplaatsen in Eurazië.

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Curriculum Vitae

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