



Possible paleohydrologic and paleoclimatic effects on hominin migration and occupation of the Levantine Middle Paleolithic[☆]

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ABSTRACT

This paper explores the impact of major glacial/interglacial paleohydrologic variations in the Middle-Paleolithic Levant on hominin migration and occupation. The climatic reconstruction is based primarily on the most straight-forward paleohydrologic records recently published. These terrestrial proxies convey direct paleoenvironmental signals of effective precipitation and aquifer recharge. The two main proxies are temporal changes of terminal lake levels in the Dead Sea basin and periods of deposition or non-deposition of speleothems. Other records, such as stable isotopes, if interpreted correctly, correspond well with these two direct proxies. All the records consistently indicate that the last two glacial periods in the central Levant were generally wet and cool, while the last two interglacials were dry and warm, so more water was available for the ecosystem and thus hominins during glacial periods than during interglacials. Some proxies indicate that the higher precipitation/evaporation ratio during glacial periods involved higher precipitation rather than only reduced evaporation. Beyond the general mean glacial/interglacial climate suggested here, variations occurred at all temporal scales throughout glacial or interglacial periods. In the Sahara-Negev arid barrier, moister conditions occurred during Marine Isotope Stage (MIS) 6a–5e, when Anatomically Modern Humans apparently migrated out of Africa. We suggest that this migration, as well as the later Neanderthal expansion from Southeast Europe or the Anatolian plateau into the Levant during early MIS 4, could be facilitated by the observed major climatic variations.

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Introduction

The question of whether or not climatic changes modified the patterns of human evolution has gained new interest because of recent environmental change (Hay and Beniston, 2001; McLeman and Smit, 2006). Dispersal of modern humans and possible sympatry with Neanderthals in the Levant have been continuously debated (e.g., Hovers, 2006; Hublin and Pääbo, 2006; Mellars, 2006; O'Connell, 2006; Zilhao, 2006; Shea, 2008). The tectonic evolution of the Levant during the last 200 kyr is assumed to be of second order importance relative to climatic change, i.e., there was no dramatic modification of catchments, lakes or land bridges due to tectonics (Horowitz et al., 2001). The ongoing subsidence of the Dead Sea basin affected the long term (~1 Myr) levels of water bodies within the basin, but climatic factors appear to be dominant

in the glacial/interglacial cycles within the last 200 kyr (Frumkin, 2001; Lisker et al., 2009). Here we address possible climatic impacts on the hominin migrations and occupations in the Levant, augmenting similar impacts suggested in the literature (e.g., Bar-Yosef et al., 1992; Rak, 1993; Tchernov, 1998; Finlayson, 2004; Shea and Bar-Yosef, 2005; Shea, 2008).

Hominins extended their home range during the Pleistocene from Africa to Eurasia or vice versa and had to move through the Levant, a relatively narrow terrestrial “corridor,” rendering it the main ‘Out of Africa’ corridor. The Levant is bounded in the north by the Taurus mountains, in the west by the Mediterranean Sea, and on the south and east by deserts (Fig. 1a), roughly encompassing the present areas of Lebanon, Israel, Syria, Jordan, and Sinai. The central Levant is referred to here as the Jordan river catchment and the area between it and the Mediterranean.

Past studies in the central Levant often dealt with local aspects of climate (e.g., Issar, 1980; Moshkovitz and Magaritz, 1987; Avigour et al., 1992). One hypothesis postulated that glacial periods in the Levant were generally drier than interglacials (e.g., Bar-Matthews et al., 1997; Shea, 2003; Finlayson, 2004; Hovers, 2006; Robinson

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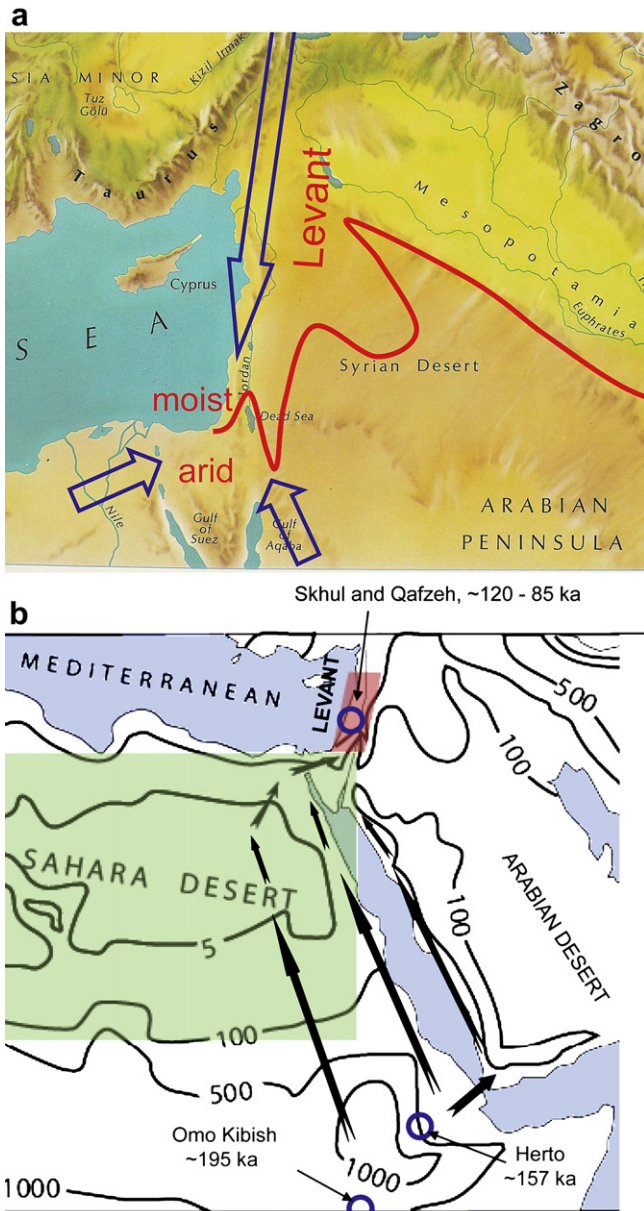


Fig. 1. Physiographic and climatic barriers of the Levant and associated possible hominin migrations. (a) The Levant physiographic borders: on the north the Taurus and Zagros mountain chains, on the west the Mediterranean Sea, which supplies its moisture, and on the south and east the deserts. Arrows indicate possible hominin invasion routes discussed in the text. (b) The Saharo-Arabian Desert – the southern climatic boundary of the Levant, with isohyets (mm/y) and possible “Out of Africa” migration routes. Increased precipitation during MIS 6a–5e rendered it traversable to Anatomically Modern Humans (see text). Sites of Anatomically Modern Human fossils are shown with their age. The Levant Mediterranean zone was relatively dry during MIS 5.

et al., 2006; Shea, 2008), implying that the last interglacial period (marine isotope stage MIS 5, and especially substage 5e) in the Levant was humid (Bar-Matthews et al., 2003). Another suggestion was that the Levant was at least as arid as it is today during much of the Late Pleistocene (Shea, 2008).

In this paper we challenge these hypotheses, and suggest an alternative paleoclimatic model. This re-evaluation is based on recent studies of cave and lake deposits in Israel, using straightforward paleoclimatic records whose chronology is based on hundreds of radiometric dates (e.g., Bartov et al., 2002; Vaks et al.,

2003, 2006, 2007; Bookman et al., 2006; Stein and Goldstein, 2006; Lisker et al., 2009).

Building on the new paleoclimatic evidence, we explore the impact of major environmental changes on hominin migration and occupation of the Levant. The main hypothesis of this paper is that environmental conditions facilitated hominin occupation within, and migration routes in and out of, the Levant. We show that although the archaeological evidence is limited, it does indicate that hominins were influenced by climatic change along the ‘Out of Africa’ route.

Scope

This paper explores two basic questions. First, what was the nature of the dominant glacial/interglacial climatic change in the Levant and along its borders? Second, did these climate fluctuations affect hominin migration and occupation of the Levantine Middle Paleolithic? The paleoclimatic evaluation presented here is based upon records that indicate the amount of excess water available for the ecosystem; its chronology is well established by several hundreds of accurate radiometric dates, and it covers entire glacial cycles, allowing deduction of paleohydrologic shifts between glacial and interglacial periods.

Using our suggested paleoclimatic reconstruction, we compare the glacial/interglacial climatic variations with shifts in the nature of hominin populations as inferred from available dated archaeological remains and the few hominin fossils that have been recovered from this region. Thus, we try to explore possible connections between hominin migrations and occupations, and climate. We do not attempt to resolve the issue of short climatic fluctuations within the glacial/interglacial cycles (e.g., Bartov et al., 2003), although they may affect hominin societal evolution (e.g., d’Errico and Sanchez Goñi, 2003; Shea, 2008). One of the present goals is to set the general climatic baseline, in terms of glacial/interglacial time scale, for future study of short-term deviations and their impact on hominins. The implication of these short-term events on human prehistory depends on the resolution of dating techniques in both paleoclimate proxies and archaeological remains. Despite major progress in the accuracy and precision of radiometric dating techniques commonly used in Paleolithic archaeology (e.g., TL, ESR OSL), their resolution when compared to U–Th, or calibrated radiocarbon dates during the last 20 kyr, leaves some room for doubt that these coarse-grained correlations can be interpreted as a solid base for causation.

Our principal paleoclimatic conclusion is that, contrary to some earlier interpretations, the last glacial periods in the central Levant were generally wetter than interglacials. Secondly, such long-term climatic fluctuations in the Levant and particularly in its barrier regions could influence the dispersal of Anatomically Modern Humans and the arrival of Neanderthals.

Present rainfall and environmental conditions

Rainfall, mostly provided by the eastern Mediterranean, decreases from roughly >1000 mm/y in the northern Levant mountains to <50 mm/y in the southern Levant deserts (Fig. 1b) (Dayan, 1986). Although precipitation is the major factor controlling water balance and terrestrial productivity, additional environmental factors control local evaporative water loss, such as vegetation cover, temperature, winds, clouds, temporal distribution of precipitation (season of precipitation, number of wet and dry periods, duration of wet periods), geology and topography. The water available for recharge and runoff is the difference between precipitation and total losses to the atmosphere. It is impractical to estimate past variations of each factor individually because some

can hardly be measured even today. Instead, the “downstream” is estimated here; this is the ultimate excess of water in the environment, which we will term *effective precipitation*. It includes both underground recharge of aquifers (the major fraction) and subaerial runoff (a much smaller fraction; see below). The problem of equifinality exists in this case (i.e., does more available water reflect higher precipitation or lower evaporation?); it is not in the focus of this paper, although we mention some indicators that could aid in resolving this problem.

High-intensity rainfall and rapid percolation through cracks, fissures, or solution channels are typical for the karstic Mediterranean hills of the Levant. Annual potential evaporation exceeds rainfall, ranging from 1400 to 2800 mm/y in northern and southern Israel, respectively. While the annual water budget seems to provide no effective precipitation, the excess of water is more evident on a monthly basis. Rainfall during the rainy winter months in northern Israel exceeds evapotranspiration, but in the semi-arid to arid zones monthly evapotranspiration exceeds rainfall. An average evapotranspiration of ~70% of the rainfall is estimated for the entire area of Israel (Gvirtzman, 2002). Following evaporation losses, the remaining water under moister Mediterranean climate nourishes plants, infiltrates into caves forming speleothems, recharges aquifers, resurges in springs and/or flows as surface runoff, eventually reaching the sea or inland lakes. Groundwater recharge averages ~25% of precipitation, and runoff average is ~5% (Gvirtzman, 2002). Most recharge and runoff follow periods of heavy rainfall, when the available water exceeds the capacity of soil and epikarst (uppermost layer of carbonate rock). As a baseline for paleohydrologic reconstruction we use the recent mean annual

precipitation (P) (Fig. 2a) to estimate the associated recharge (R) using the empiric equations of Zukerman (1999):

$$R = 0.45(P - 180) \text{ for } 200 < P \leq 650$$

$$R = 0.88(P - 140) \text{ for } 650 < P \leq 1000$$

Calculations of these equations show complex patterns of recharge (R , Fig. 2b).

The Mediterranean has been the dominant humidity source of the central Levant not only today (Alpert et al., 1990) but also throughout the last glacial cycles (e.g., Gat and Magaritz, 1980; Kolodny et al., 2005; Vaks et al., 2006). A steep transition between the moister Mediterranean and the Negev arid zones demonstrates the effects of the Mediterranean Cyprus Lows. This interface, with its high north-south gradient of precipitation (falling from 400 to 200 mm/y over 30 km or less), forms a virtual continuation of the south Mediterranean coastline eastward in the northern Negev Desert (Fig. 2a). The storms moving from west to east carry little humidity south of this line, because they do not pass over the humid, warm sea (Enzel et al., 2008). Further south, the present climate ranges from arid to extremely arid, forming part of the Saharo-Arabian Desert belt. Speleothem studies (e.g., Vaks et al., 2006, 2007) indicate that the geo-climatic border of the northern Negev was important also during the last glacial cycles, moving only slightly in response to climatic change (Fig. 2c).

Instrumental measurements of precipitation in the Levant cover only the last ~150 years. Therefore, when studying paleoclimate we must use climatic proxies. These provide a climatic signal, but

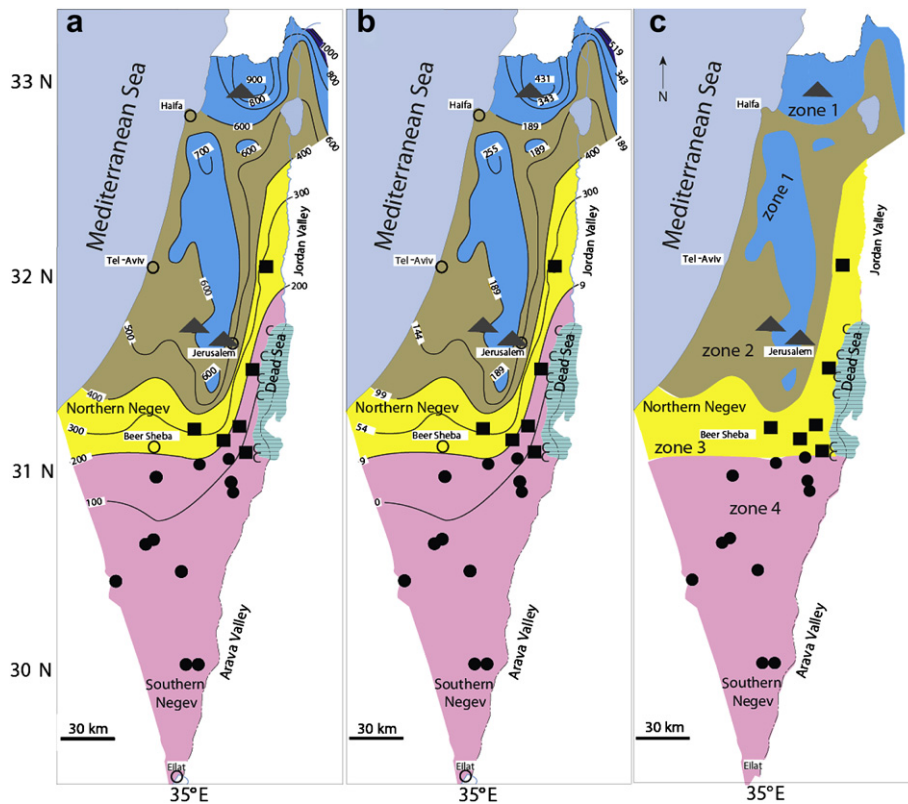


Fig. 2. Studied cave locations and the hydrological perspective of this paper. (a) Present mean annual rainfall (mm/y) map for 1961–1990. (b) Mean annual recharge to the aquifer (mm/a) 1961–1990, calculated by empiric equations (Zukerman, 1999). (c) Four paleoclimatic zones defined by past speleothem deposition (see text). Full triangles, Zones 1 + 2: Caves with continuous deposition during the last glacial cycles; Full rectangles, Zone 3: caves with last intensive deposition during MIS 4–2; Full circles, Zone 4: Arid zone caves where last speleothem deposition occurred during MIS 6a–5e (Negev). Open circles are modern cities.

sometimes act as filters, transforming climatic conditions into a complex record that we must interpret properly.

Depending on present climate, the distribution of plants in the Levant ranges from dominant oak woodland within the northern-central Mediterranean part, to absence of plants in the arid zone interflaves where no concentration of runoff occurs. The basic control on biological productivity in the east Mediterranean/arid ecotone region is the availability of water (Gvirtzman, 2002). This contrasts with higher latitude temperate regions where water is generally more abundant, so temperature is the limiting factor during Pleistocene climatic shifts. There is no doubt that water balance changed significantly in the Levant during the last 200 kyr, encompassing two full glacial/interglacial cycles (e.g., Vaks et al., 2003, 2006; Enzel et al., 2008).

Caves and rockshelters

The majority of the Levant hilly zone bedrock comprises carbonate rocks, particularly limestone and dolomite. This contrasts with some other regions south and north of the Levant, where carbonate outcrops are less common. Low relief and tectonic stability during the early-mid Cenozoic favored the development of chamber caves along the watertable (Frumkin and Fischhendler, 2005). Renewed late Cenozoic tectonic activity favored higher relief, stream downcutting, higher erosion rates, and breaching of caves by surface erosion (Frumkin et al., 2009). Shallow caves or rockshelters, usually with lateral (rather than vertical) entrances were commonly exposed. These have become favorable (but not the only) sites for evidence of hominin occupation since the Mid-Pleistocene. Thick archaeological deposits in some caves (e.g., Tabun) demonstrate that these caves attracted humans recurrently or continuously for long periods.

Simple paleohydrologic proxies

An important pair of paleohydrologic proxies, levels of terminal lakes reconstructed by geomorphic and geologic methods and dated by U–Th and radiocarbon and speleothem growth periods dated by U–Th, both yield concordant results. These paleohydrologic proxies are relatively easy to interpret, and thus differ from complex proxies (e.g., oxygen isotopes) which integrate several effects, sometimes causing misinterpretations (Frumkin et al., 1999). Lake levels can be reconstructed where geomorphic indicators of paleo-shorelines can be found and dated. In principle, speleothems provide a continuous record unless there is cessation of deposition which is largely dictated by hydrology/climate. Therefore, bracketed periods of non-deposition can be constrained. These records are important for the discussion of possible barriers to hominin migrations and occupation.

The paleohydrologic evidence reviewed here reflects the amount of effective precipitation, or water available for the ecosystem. This is a major determinant of the local types of flora and fauna and, to some extent, human populations, all of which depend on available water. Although the precise transformation of the records into climatic variables, such as precipitation, is not possible, the final result is clear: high amounts of excess water under relatively warm (compared with northern latitudes) Levant environments promote productive ecosystems.

Lake levels

The level of an arid terminal lake is the closest analogue of a regional rain gauge, integrating the effective precipitation over the catchment (Street-Perrott and Harrison, 1985). The Dead Sea and its Pleistocene predecessors, Lisan, Samra, and Amora lakes are

excellent examples of such lakes (Stein et al., 1997; Frumkin et al., 2001; Enzel et al., 2003; Torfstein et al., 2009). The level of these lakes fluctuated dramatically as a result of their high sensitivity to climate change (Fig. 3).

The Dead Sea basin catchment area is 43,000 km², and covers climatic regimes from moister Mediterranean to extremely arid (Fig. 4). The wetter northern part of the catchment (Fig. 2), contributes most of the lake water. Consequently the lake levels are strongly reflective of water availability in this wetter region today, and presumably also in the last 200 kyr. The precipitation trajectories of the northern part of the catchment pass over the coastal zone where the sites of Kebara, Skhul, and Tabun all experience similar precipitation regimes (Alpert et al., 1990; Enzel et al., 2008).

Dead Sea and Lake Lisan levels have been studied and dated in detail (Supplementary Online Material (SOM) Tables 1, 2; Fig. 5a) (e.g., Kaufman et al., 1992; Frumkin, 1997; Bartov et al., 2002; Enzel et al., 2003; Bookman et al., 2004; Haase-Schramm et al., 2004; Stein and Goldstein, 2006). Most recently the Dead Sea escarpment has been thoroughly screened to identify and date paleo-lake deposits (Frumkin, 2001; Lisker et al., 2010). Relict aragonite lake stromatolites are preserved in shallow caves and rock shelters (Lisker et al., 2009), indicating the minimum lake stand at each site, with Th/U age ranging from 75 to 17 ka (SOM Table 2). The last glacial period experienced the highest lake levels, which started ~70 ka, earlier than suggested by previous studies (e.g., Bartov et al., 2002, 2003). This resulted in a considerably larger lake surface area, reaching an equilibrium state 200–300 m higher than the Holocene Dead Sea (Fig. 4). Note that the level of a terminal lake is determined by the balance between water input (stream, runoff and spring discharge) and evaporation (Street-Perrott and Harrison, 1985). The lake's evaporation rate is influenced by salinity, humidity, temperature, and wind speed. During periods of high rainfall associated with high lake levels, reduced temperature, as well as higher air humidity could both contribute to lower evaporation rates. On the other hand, the heavy rainfall produced by deep Cyprus Lows is associated with higher wind speed. High-intensity or high-frequency of strong winds is associated with increased evaporation rates (e.g., Asmar and Ergenzinger, 1999). The contrasting effect of wind speed and other factors on evaporation, on both the lake and catchment scale, reduces the overall



Fig. 3. The north basin of the Dead Sea at approximately -420 m msl level. The horizontal lake terraces on the western escarpment indicate the retreating Lake Lisan during deglaciation, late MIS 2.

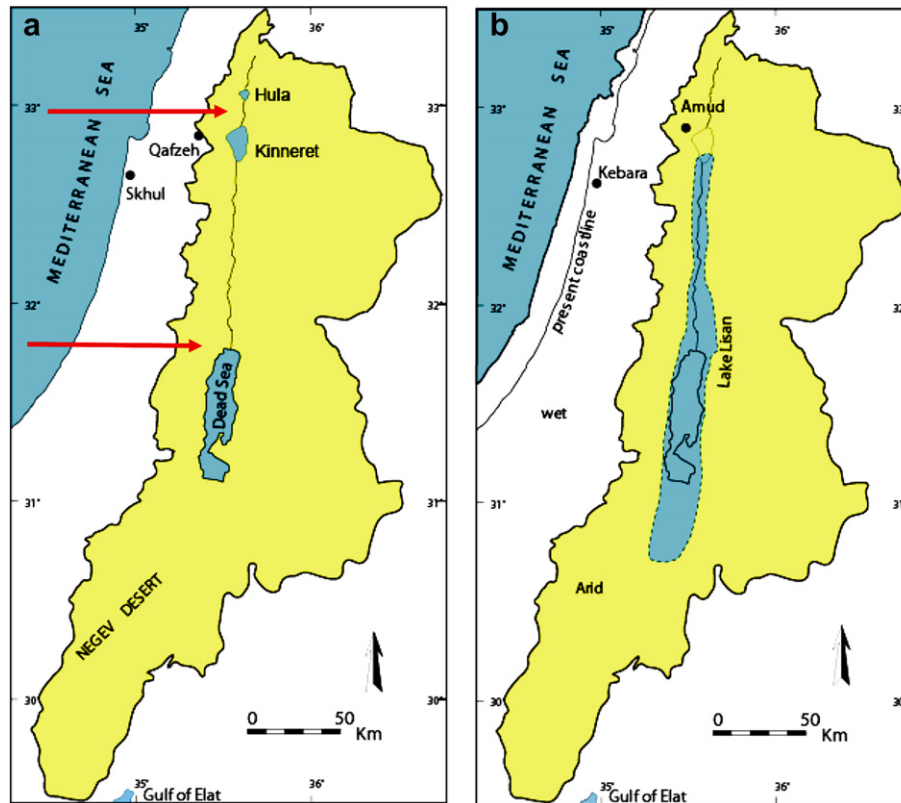


Fig. 4. The catchment area of the Dead Sea basin (shaded) with the Jordan River flowing from north to south, and the main water bodies: (a) interglacial situation, represented by 1950 water bodies: small disconnected lakes in the Jordan – Dead Sea valley, and high Mediterranean level. Arrows represent mean rain trajectories of the common Cyprus Lows. Skhul and Qafzeh Caves, with MIS 5 Anatomically Modern Human fossils are shown; (b) 24 ka, with Lake Lisan (final high stand period) and low glacial period Mediterranean levels. The Gulf of Eilat is slightly smaller than today.

effect of evaporation variation on lake levels. In general, the lake levels depend primarily on precipitation (Enzel et al., 2003). High Lisan levels during the last glacial period correspond to a significantly wetter climate than today.

Additional indirect paleoclimate evidence has been derived from aragonite and gypsum lake deposits (Stein et al., 1997). These inorganic evaporites required substantial input of bicarbonate and sulfate, respectively. Bicarbonate was supplied by the incoming fresh water, which would have formed a less saline layer on top of the underlying brine. Aragonite saturation was reached in the upper layer when the lake obtained a stratified configuration and appropriate concentrations of Ca and bicarbonate (Stein et al., 1997; Kolodny et al., 2005). Lake Lisan sediments show that the carbon flux entering the lake during the glacial period was approximately fivefold larger than the carbon flux entering the Holocene Dead Sea, implying considerably higher runoff during the glacial period compared with the Holocene (Barkan et al., 2001). Significant lake level drops occurred during late Pleistocene cold Heinrich events (Bartov et al., 2003), suggesting that reduced temperatures alone without rainfall increase cannot sustain high lake levels. Enzel et al. (2008) estimated a twofold modern rainfall increase during the last glacial period at the north-central headwaters of the lake.

Lake sediments older than those of Lake Lisan offer some clues to earlier paleolimnology and associated paleoclimate, although lake levels are not well constrained. The MIS 5 lake seems to indicate drier climate, compared with Lake Lisan (Fig. 5a, following Waldmann et al., 2007). The MIS 6 lake experienced an enhanced long-term supply of freshwater. The high fraction of primary minerals implies that MIS 6 probably represents the longest wet stage in the recorded history of Lake Amora, the predecessor of Lake

Lisan. The sedimentary record of Lake Amora extends back at least to ~800 ka (Torfstein et al., 2009), allowing a possible connection between data presented here and earlier periods marked by hominin dispersals (e.g., Bar-Yosef, 1987; Goren-Inbar et al., 2000; Bar-Yosef and Belfer-Cohen, 2001; Barkai et al., 2003; Rightmire et al., 2006).

Speleothem growth periods

While lakes integrate a regional paleohydrologic signal of their catchment, speleothems can serve as excellent local paleohydrologic proxies. Water availability is generally the most important control on speleothem growth rate (Fairchild and McMillan, 2007). Therefore speleothem growth is a direct proxy of effective rainfall and aquifer recharge (Fig. 2b). About 100 mm/y rainfall at the beginning of the wet season is needed to wet the soil and trigger cave dripping in the east Mediterranean karstic caves today. This was demonstrated by both direct observations under natural conditions and artificial sprinkling of water above a cave (Sheffer, 2009). We can therefore use the existence of speleothems as indicators that rainfall at deposition time exceeded the minimum level needed for speleothem growth. In addition, speleothem deposition is enhanced by biogenic activity above the cave, which supplies the CO₂ necessary for limestone dissolution/deposition process (Ford and Williams, 2007), so speleothem growth periods provide a direct record of paleo-vegetation in presently unvegetated areas (Fig. 6).

Although some individual speleothems have been dated at multiple points, the density of dated points is seldom sufficient to extract information about secular changes in growth rates at

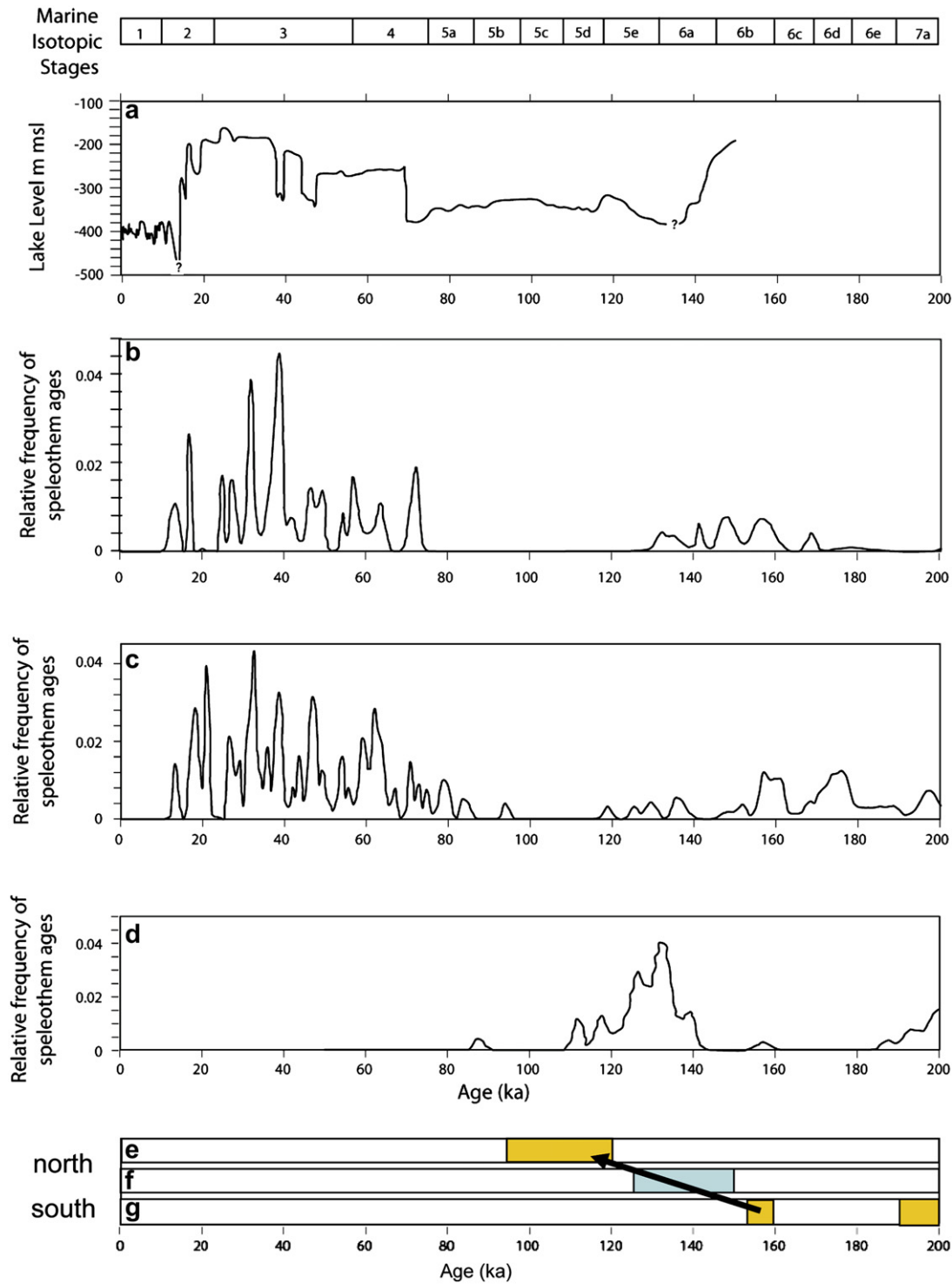


Fig. 5. Paleoclimatic records of lake levels and speleothem deposition periods in Israel during the last 200 kyr. The relative frequency diagrams were drawn using Isoplot 3 software (Ludwig, 2003). They show running average relative frequency of all ages, indicating the probability distribution of the dated samples. Marine isotopic stages and substages are marked at the top of the figure. (a) composite lake level curve of Samra-Lisan-Dead Sea lakes (Frumkin, 1997; Bartov et al., 2002; Bookman et al., 2004; Migowski et al., 2006; Waldmann et al., 2007; Lisker et al., 2009); (b) speleothems from the western Dead Sea and Jordan valley rain-shadow deserts (northern rectangles in Fig. 2c) (Vaks et al., 2003; Lisker et al., 2010); (c) northern Negev speleothems (southern rectangles in Fig. 2c) (Vaks et al., 2006); (d) central-southern Negev speleothems (filled circles in Fig. 2c) (Vaks et al., 2007; Vaks et al., in press); (e) approximate occupation period of Skhul and Qafzeh by Anatomically Modern Humans (Schwarcz, 1980; Schwarcz et al., 1988; Valladas et al., 1988; Stringer et al., 1989; Mercier et al., 1993; Grün et al., 2005); (f) mean Saharan wet period (composite representation of: Miller et al., 1991; McKenzie, 1993; Schwarcz and Grün, 1993; Szabo et al., 1995; Rohling et al., 2002; Osmond and Dabous, 2004; Smith et al., 2004b; Kieniewicz and Smith, 2007; Smith et al., 2007). (g) Ethiopian occupation periods by Anatomically Modern Humans (White et al., 2003; McDougall et al., 2005). Arrow indicates the suggested “Out of Africa” northward migration chronology utilizing the wet Saharan climate of MIS 6a-5e.6. Speleothems (indicated by arrow) dated to MIS 6a-5e in a partly destroyed cave at the southern Negev (Ktora Cracks, Vaks et al., 2007). Present mean precipitation is ~30 mm/y and there is no recharge on alluvial surfaces. No vegetation grows at the site today and no speleothems are deposited.



Fig. 6. Speleothems in the presently hyperarid southern Negev, Israel, deposited during late MIS 6 to MIS 5e.

individual drip sites, let alone regional differences in these rates. However, when many dates are available across tens of speleothems from many caves, the regional frequency distribution of the dates relate to climatic fluctuations (e.g., Gascoyne et al., 1983; Baker et al., 1993). While the general paleoclimatic picture is clear, individual highs or lows in the frequency curve may relate to sampling bias and not necessarily indicate detailed climatic fluctuations.

Our present knowledge of thousands of caves over the climatic gradient of the Levant reveals the climatic constraints on speleothem deposition under present conditions (Frumkin et al., 1998; Frumkin and Fischhendler, 2005; Vaks et al., 2006; Verheyden et al., 2008; Frumkin et al., 2008; Frumkin, unpublished data). Present deposition of speleothems in caves clearly reflects the present hydrology of the cave site, which can be divided into climatic regions as follows (Fig. 2a and b):

- 1) Intensive speleothem deposition occurs where rainfall exceeds 600 mm/y (recharge >190 mm/y), evidenced by active deposition in most caves. Modern deposition occurs at all or most drip sites where speleothem growth ever occurred.
- 2) Partial deposition is observed today in some caves receiving 400–600 mm/y rainfall (recharge 100–190 mm/y). Deposition occurs in at least some points in many caves, but dry speleothems are also common.
- 3) Almost no present deposition is observed in caves receiving 200–400 mm/y rainfall (recharge 10–100 mm/y), although some speleothems date to previous Holocene phases. Speleothems are not ubiquitous, and most of them are dry today.
- 4) Speleothems are relatively rare in areas receiving <200 mm/y rainfall (recharge <10 mm/y). No speleothem deposition occurs today; rare drip sites occur, but do not produce speleothems.

This present-day hydrologic subdivision is used to determine what recharge or effective precipitation level was required to achieve past deposition during the last glacial cycles. Thus we use the distribution of dated speleothems as integrators of the effects of several climatic factors, including rainfall and temperature, inferring the available water in the environmental system which influenced the entire ecosystem, including humans. Speleothems have been dated in dozens of caves, mainly in Israel (e.g., Schwarcz, 1980; Frumkin et al., 1999; Bar-Matthews et al., 2003; Vaks et al., 2003, 2006; Lisker et al., 2010), and some in Lebanon (Verheyden et al., 2008) and Jordan (Frumkin et al., 2008).

The geographic distribution of dated speleothems shows that the studied region can be divided into four zones according to past deposition periods in the caves (Fig. 2c). These are roughly similar to the present-day subdivision (Fig. 2a and b).

Continuous speleothem deposition is apparent in Zone 1 through the last glacial cycle, including the Holocene and MIS 5. Deposition is ubiquitous and continuous in most speleothems that have been analyzed. Random depositional hiatuses are attributed to local conditions rather than regional climate, because, on a regional scale, deposition is observed during all periods of the last glacial cycles. This zone is roughly similar to the region with >190 mm/y recharge today. This zone is the main supplier of water to the Dead Sea basin. The continuous deposition in this region renders speleothem growth periods less sensitive as climate proxies compared with drier regions.

Zone 2 had a somewhat less continuous deposition of speleothems, but their widespread spatial and chronological distribution indicates that the last glacial cycles were as wet or wetter than today. This zone is roughly similar to the region with present recharge from 100 to 190 mm/y.

Zone 3 includes the region with present recharge from 10 to 100 mm/y, as well as the rain-shadow desert along the western side of the Dead Sea where present recharge is <10 mm/y. Today, and during the entire Holocene, no speleothems have been deposited in this zone. Past deposition has been restricted to some wet periods separated by major hiatuses. Significantly, deposition was extensive in these caves during the glacial periods, MIS 6, 4, 3, and 2 (Vaks et al., 2003, 2006; Lisker et al., 2010). Almost no speleothems were recorded in the Jordan valley–Dead Sea area dating to interglacial MIS 5 (SOM Table 3, Fig. 5b). This pattern of clear glacial/interglacial difference is the main reason for treating the last 200 kyr in units of glacial/interglacial periods. In the northern Negev, slight deposition did occur during MIS 5 (SOM Table 4, Fig. 5c) (Vaks et al., 2006), associated with the last moist episode in the central - southern Negev, as described below (Vaks et al., 2007).

Zone 4 covers the central - southern Negev Desert, where present recharge is <10 mm/y. During the mid-late Pleistocene, speleothem deposition was restricted to thin laminae with intermediate hiatuses, indicating episodic moister events (Vaks et al., 2007). The last clear deposition period here was MIS 6a-5e (SOM Table 5, Figs. 5d and 6). Recharge estimates for these episodes are from 10 to 100 mm/y (similar to the northern Negev today). The lack of calcic horizons in old terraces in southern Negev soils (Amit et al., 2006) also indicates that these episodic moister events were not very intense or prolonged.

Following the above observations, we suggest that continuous deposition indicates a period with local recharge >190 mm/y. Episodic speleothem deposition indicates local recharge <190 mm/y (assuming other variables are constant), while regional lack of deposition indicates recharge <10 mm/y (Fig. 2). This simple gauge for local effective precipitation is most sensitive within the semi-arid belt of the southern Levant. The wetter region of the central Levant is less adequate for this method due to continuous speleothem deposition. As noted above, studied speleothems used here reflect the effective precipitation directly above the cave site. In order to construct a regional picture which is not distorted by local effects, a large number of speleothems from several caves across the region have been dated recently (Fig. 5) (Vaks et al., 2003, 2006, 2007; Lisker et al., 2010).

Deciphering isotopic records of the terrestrial Levant

Stable isotopes of speleothems have been commonly used as paleoclimatic indicators for the Levant, although they are complex proxies (e.g., Frumkin et al., 2000; Bar-Matthews et al., 2003; Vaks

et al., 2006; Verheyden et al., 2008). Stable carbon isotopes ($\delta^{13}\text{C}$) of speleothems seem to present a promising index of effective rainfall. Large shifts in $\delta^{13}\text{C}$ values of speleothem calcite in the Levant have been ascribed to climate-driven changes in vegetation density and C_3 versus C_4 dominated plant assemblages (e.g., Frumkin et al., 2000). The $\delta^{13}\text{C}$ record is remarkably consistent over the Mediterranean zone of the Levant, demonstrated by its similarity in different caves (Bar-Matthews et al., 2003), and indicating dominance of regional climatic factors over local factors (McDermott, 2004; Fairchild et al., 2006). The $\delta^{13}\text{C}$ record is more sensitive to effective rainfall close to the Mediterranean – semi-arid border, where mixed C_3/C_4 vegetation and overall biologic production is highly dependent upon water excess in the ecosystem (Frumkin et al., 2000). Such arid conditions, reflected in extremely high $\delta^{13}\text{C}$ values, penetrated the Mediterranean climatic zone rarely, in particular during MIS 5e. The unprecedented jump of $\delta^{13}\text{C}$ during this period indicates intensive drying and destruction of the ecosystem followed by extensive soil stripping.

Unlike $\delta^{13}\text{C}$, the oxygen isotopic composition of speleothem calcite is more complex, reflecting climatically controlled variables (temperature and $\delta^{18}\text{O}$ of precipitation) which may have contrasting effects on $\delta^{18}\text{O}$ values of calcite (Schwarcz, 1986; Gascoyne, 1992; McDermott, 2004; Fairchild et al., 2006).

Issar and Bruins (1983) suggested that glacial precipitation in the Negev was depleted in ^{18}O compared with the Holocene values. However, speleothem calcite studies in Israel show that glacial values are enriched in ^{18}O compared with interglacials (e.g., Frumkin et al., 1999; Vaks et al., 2006). Under present conditions, $\delta^{18}\text{O}$ of speleothem calcite increases with decreased rainfall as a result of the so-called “amount effect” (Dansgaard, 1964; Bar-Matthews et al., 1997). Bar-Matthews et al. (1997) concluded that higher glacial period $\delta^{18}\text{O}$ values of speleothems indicate drier glacial conditions compared with interglacials. Consequently, increasing $\delta^{18}\text{O}$ values of speleothems during the MIS 5/4 transition (interglacial to glacial) was suggested to indicate decreasing rainfall which was interpreted as marking a drop in terrestrial productivity (Shea, 2008). This argument was based on the assumption that past $\delta^{18}\text{O}$ fluctuations directly reflect rainfall amounts, as is the case during wet/dry years today. However, a close resemblance of the $\delta^{18}\text{O}$ records of Israeli speleothems and the East Mediterranean marine records (proxies of sea surface water) has been observed by Frumkin et al. (1999) and further demonstrated by Bar-Matthews et al. (2003). Frumkin et al. (1999) showed that the $\delta^{18}\text{O}$ variations in speleothem calcite at glacial/interglacial transitions reflect mainly the “source effect,” (i.e., changes in the isotopic composition of surface waters of the east Mediterranean Sea, rather than glacial/interglacial variations of local rainfall amounts). Kolodny et al. (2005) examined this source effect further, demonstrating that it is transmitted from the evaporating Mediterranean water by rainfall, not only to speleothems but also ultimately to the Dead Sea basin lacustrine sediments. This is particularly significant over glacial/interglacial periods with substantial variations in the isotopic values of Mediterranean Sea surface water, the source of precipitation in the Levant. These variations are dominated by global, rather than local climate change. Almogi-Labin et al. (2009) attempted to eliminate the dominant, first-order source effect by carefully subtracting the speleothem record from two marine records. After removing the source effect ($\Delta\delta^{18}\text{O}$), the residual $\delta^{18}\text{O}$ curves show that speleothems were more depleted in ^{18}O during glacial periods than during interglacials. The similarity between the Soreq (Bar-Matthews et al., 2003) and the Jerusalem (Frumkin et al., 1999) speleothem $\delta^{18}\text{O}$ records indicates that the topographic and sea–land distance effects are less significant than the amount effect which is dominant today when the source (Mediterranean) water is constant. Thus, the amount effect was probably the main factor that

determined the second order glacial/interglacial $\Delta\delta^{18}\text{O}$ fluctuation revealed by Almogi-Labin et al. (2009, their Fig. 10). The depleted second order glacial ^{18}O compared with interglacial values (after removing the source effect) indicate higher precipitation during glacial periods compared with interglacials.

It is therefore concluded through several lines of evidence that the isotopic terrestrial record is consistent with the direct paleo-hydrologic proxies such as lake levels and speleothem growth periods. (Frumkin et al., 1999; Vaks et al., 2003, 2006; Kolodny et al., 2005; Enzel et al., 2008).

The $\delta^{18}\text{O}$ records of speleothems can also be used to reconstruct paleotemperatures. McGarry et al. (2004) demonstrated that it may be possible to derive terrestrial paleotemperatures from $\delta^{18}\text{O}$ of cave-deposited calcite by analyzing fluid inclusions and comparisons with alkenone-derived temperatures from Mediterranean sediments. Using this method they calculated a drop of about 10°C during the last glacial maximum. Affek et al. (2008), used measurements of “isotope clumping” to obtain similar temperature shifts at selected points in the speleothem record.

In an independent study, $\delta^{18}\text{O}$ analyses of sequential samples of enamel from goat teeth from the archaeological site of Amud (Fig. 4) show that during glacial stages MIS 4–3 rain fell throughout the year, including the summer, whereas at the interglacial MIS 5b site of Qafzeh, rain fell dominantly during the winter as at present. Vegetation of Qafzeh region during MIS 5b included significant amounts of C_4 grasses (Hallin et al., in preparation).

Isotopic marine records of the east Mediterranean

A large glacial/interglacial amplitude of $\delta^{18}\text{O}$ of the epipelagic foraminifer *Globigerinoides ruber* in the eastern Mediterranean indicates a large glacial/interglacial amplitude of surface water $\delta^{18}\text{O}$ (e.g., Vergnaud-Grazzini et al., 1977; Tucholka et al., 1987; Fontugne and Calvert, 1992; Almogi-Labin et al., 2009). This results from the large, anomalous glacial/interglacial changes in $\delta^{18}\text{O}$ of surface waters of the eastern Mediterranean sea. Shifts in $\delta^{18}\text{O}$ of the eastern Mediterranean (and Red Sea) are parallel to the global ice volume effect, but have a larger amplitude. The amplification in these quasiclosed basins results from excess evaporation (Thunell and Williams, 1989), advection (Bigg, 1995), and limited water circulation (Assaf, 1977) during glacial low sea levels. In addition, influx of isotopically depleted water into the eastern Mediterranean during deglaciations and from the Nile River during enhanced monsoon periods significantly increases the glacial/interglacial offset of sea surface $\delta^{18}\text{O}$.

Almogi-Labin et al. (2009) analyzed two cores in the Mediterranean sea, showing that the Nile River has a major effect on sea water, in addition to glacial melt water input. Variations in these inputs, coupled with input from the west Mediterranean modulated by sea level changes, as well as variable output through evaporation, all contribute to the east Mediterranean chemistry, sediments, and isotopic record. The Nile River delivered the bulk of the southeast Mediterranean sediments (Almogi-Labin et al., 2009). Water contribution from local rainfall and central Levant rivers flowing to the east Mediterranean is several orders of magnitude smaller than the Nile.

Glacial/interglacial paleohydrology in the Levant

Following the above discussion, the long-term, glacial/interglacial paleohydrological cycle of the Levant can be reconstructed from direct proxies such as speleothem growth periods and lake levels, corroborated by more complex ones, such as stable isotopes. All of them lead to similar general conclusions. As noted above, only major climatic fluctuations are discussed here, on a glacial/

interglacial time scale. Short-term episodes of climatic fluctuation that occurred during the glacial periods (e.g., Ayalon et al., 2002; Bartov et al., 2003) and more modestly during interglacials (e.g., Bar-Matthews et al., 1997; Frumkin, 1997; Bookman et al., 2006) are beyond the scope of this paper. Glacial terminations and early interglacial periods were particularly unstable and marked by intermittently falling lake levels.

Interglacial periods in the Levant

The terrestrial hydrology of the Levant during the Holocene is relatively well known, as a result of abundant instrumental, historical and geological records. For the present discussion it is imperative to note the lack of deposition of Holocene speleothems in the arid and semi-arid zone (Fig. 5b and c) (Vaks et al., 2003, 2006; Frumkin et al., 2008; Lisker et al., 2010), and low natural Dead Sea levels, approximately -400 ± 30 m above sea level (Frumkin, 1997; Bookman et al., 2006; Migowski et al., 2006), both attributed to the low effective precipitation (low rainfall and high evaporation rates). In general, the Holocene climate exemplifies the dry, warm conditions typical of interglacial climate (which is modulated by small fluctuations).

The last interglacial, MIS 5, generally had a similar, albeit not identical, dry, warm character. Speleothem deposition rate in the semi-arid zone was very low during MIS 5 (Vaks et al., 2003, 2006; Frumkin et al., 2008; Lisker et al., 2010). Following the beginning of MIS 5, no interglacial deposition of speleothems is observed in the semi-arid and arid zones of the Dead Sea and Jordan River valley, indicating a dry interglacial climate. Sporadic deposition did occur in the northern Negev Desert during MIS 5 (Vaks et al., 2006), but at a significantly lower rate than local glacial period deposition (Fig. 5c).

In the arid central-southern Negev, however, MIS 5e was the last deposition period (Vaks et al., 2007), indicating a different climatic regime (Figs. 2c and 5d). Some of this region's groundwater ultimately flows to Arava valley springs, where MIS 5 also appears to be the last major deposition period (Livnat and Kronfeld, 1985), compared with only slight deposition during the last glacial periods.

Lake Samra, the MIS 5 predecessor of Lake Lisan in the Dead Sea basin, seems to reflect a negative water balance with lower groundwater input, compared to glacial Lake Lisan (Waldmann et al., 2007; Torfstein et al., 2009). This corroborates the dry climate of the central Levant during MIS 5.

Glacial periods in the Levant

All of the records seem to be mutually consistent in that they demonstrate the last two glacial periods had higher effective precipitation than the Holocene and MIS 5 interglacial in the central Levant (Zones 1–3, Fig. 2c). The last glacial period (MIS 4 to 2) experienced the most intensive speleothem deposition in the presently semi-arid zone, from the northern Negev northward (Vaks et al., 2003, 2006; Lisker et al., 2010). In addition, Lake Lisan commonly experienced high levels of -260 to -150 m (Bartov et al., 2002; Lisker et al., 2009) and high bicarbonate influx, arriving at its maximum stand approximately 26–24 ka. The levels were generally high throughout the last glacial period, albeit with large fluctuations (Bartov et al., 2003). Spring carbonates were also deposited for the last time during the last glacial period in the northern highlands of the Negev (Schwarcz et al., 1979, 1980).

Approaching the end of the last glacial, during the latest part of MIS 2, the region experienced increasingly drying climate with fluctuations, reflected by low (16–13 ka) to absent (13–10 ka) speleothem deposition in the semi-arid zone, and rapid fall of Lake

Lisan levels. Lake Lisan had already started falling about 24 ka, indicating that the second half of MIS 2 became increasingly drier compared with early MIS 2. Similar unstable drying seems to have occurred at MIS 6/5 transition (Frumkin et al., 2000). The unstable climate during deglaciation is in agreement with records on a global scale (e.g., Barker et al., 2009).

Enzel et al. (2008) argued that under any climatic conditions, it will be difficult to deposit speleothems in the presently semi-arid zone caves without a rainfall increase compared with today. Evaporation reduction alone, associated with lower glacial period temperatures, will not suffice for such deposition. Presently, semi-arid regions along the rain-shadow of the central mountains of Israel suffered from similar physiographic limitations for rain penetration during glacial periods, as they do today. The northward retreat of the Mediterranean coastline of Sinai reduced the chance for eastern Mediterranean cyclones to bring precipitation to the northern Negev. Yet the intensive speleothem deposition during glacial periods in both the northern Negev (Vaks et al., 2006) and rain-shadow desert (Vaks et al., 2003; Lisker et al., 2010) suggest increase of precipitation. This indicates that the entire region, from the northern Negev northward, enjoyed increased precipitation during glacial periods. This includes not only the presently semi-arid zone but also the Mediterranean zone, which must have been wetter than today (Frumkin et al., 2000; Kolodny et al., 2005; Enzel et al., 2008). The rainy season seems to have also lasted longer than today (Hallin et al., in preparation). All these features contrast with the Holocene and MIS 5.

Overall, the last glacial period in the central Levant was generally wet, characterized by high precipitation, high lake stands, high rate of inorganic carbon influx into the lake, and high atmospheric humidity. This scenario is also reflected in speleothem $\delta^{13}\text{C}$ (Frumkin et al., 2000).

Similarly, the penultimate glacial period (MIS 6) in the central Levant also experienced a generally wet climate, reflected by intensive speleothem deposition in the presently semi-arid zone, although there are fewer dates than for the last glacial. The lower abundance of dates can be partly attributed to sampling bias, because normal sampling practice usually favors younger speleothems which are more exposed and easier to collect. Significantly more speleothems grew in MIS 6 than in MIS 5 in the semi-arid zone (Zone 3, Fig. 2c) (Vaks et al., 2003, 2006; Lisker et al., 2010). Lake deposits of MIS 6 are far less exposed and less studied than the last glacial Lake Lisan, yet, Lake Amora lithology indicates that MIS 6 glacial period was wetter than MIS 7 and MIS 5 interglacials (Torfstein et al., 2009). Although the exact amount of paleoprecipitation cannot be determined, the available knowledge discussed above indicates that rainfall was higher during glacial periods relative to interglacials (Frumkin et al., 2000; Barkan et al., 2001; Kolodny et al., 2005; Enzel et al., 2008).

The wetter climate of the central Levant during glacial periods is associated with high atmospheric pressure over Europe, and the glacial ice sheet (e.g., Issar et al., 1985; Horowitz, 1987). This high pressure zone pushed high-latitude climatic belts southward, funneling Mediterranean cyclones into the central Levant and replacing the moister and semi-arid Mediterranean zone with a wetter temperate climate. Wetter conditions are generally observed during glacial periods down to the northern Negev. Exceptions occurred during episodes of high freshwater influx into the Mediterranean, causing stratification of the eastern Mediterranean water column, and reducing its effect as a solar energy reservoir and the associated Mediterranean cyclones.

The lack of speleothem deposition in the central-southern Negev (Vaks et al., 2007) indicates that, contrary to previous suggestions (e.g., Issar et al., 1985; Horowitz, 1987), the wetter conditions of the glacial periods hardly penetrated south of the

northern Negev. The general west-east direction of the Mediterranean cyclones, as well as the mountain range of the Negev effectively blocked the rainfall from reaching the southern Negev (Amit et al., 2006).

As part of the global marine system, the Mediterranean level dropped and the coastal shelf became exposed during glacial periods. The width of the exposed shelf decreased northward where bathymetric topography becomes steeper. This retreating sea influenced the terrestrial hydrologic system (streams, water table, springs) which must have adjusted to the changing base level. The moisture-source area for precipitation was thus somewhat reduced during the glacial maximum, especially at the southern Mediterranean coast (Enzel et al., 2008), possibly reducing precipitation during late MIS 2. From northern Israel northward, the mountains often reach the Mediterranean coast, leaving only intermittent coastal plains. In this region, the effect of falling base level was environmentally more important than that of reduced sea area. Mountains are even steeper along the Red Sea – Gulf of Elat, where the coastline rarely retreated more than few hundred meters during glacial periods.

Climatic and physiographic barriers

Physiographically, the Levant is the land bridge between Africa and Eurasia. However, the terrestrial Levant is circumscribed by deserts and mountains that act as barriers to migrations (Fig. 1), depending on their environmental conditions (Tchernov, 1988; Tchernov and Belmaker, 2004). Therefore, the Levant may become isolated from its neighboring continents, rendering it a biogeographic peninsula or almost a physio-climatic island. The climates of the barrier land areas were probably more important determinants than the climate of the Levant itself for human migrations. Therefore, hominin turnovers and adaptations in the Levant can only be assessed if we consider the climatic situation of these barrier areas and their influence on migrating populations.

As a result of the barriers, areas which may become climatically suitable for some species remain remote from their distribution regions, and beyond their dispersal capacity. Consequently, species with low adaptability, low dispersal capacity or both may be “caught by the dilemma” of climate-forced range change and low likelihood of finding distant habitats to colonize, ultimately resulting in increased local extinction rates (Walther et al., 2002). Alternatively, such species can migrate to new regions when climate at the barriers becomes favorable, allowing easy invasion of a new range. The climatic barriers around the Levant had been relatively traversable during the Lower and Middle Pleistocene (Bar-Yosef, 1987; Goren-Inbar et al., 2000; Bar-Yosef and Belfer-Cohen, 2001). They were intermittently penetrable during the late Pleistocene, first with the arrival of the Anatomically Modern Humans (Skhul-Qafzeh group) and later with the arrival of the Neanderthals from the north and the Modern humans from the south. The Negev Desert was intermittently much wetter in the early-mid Pleistocene than in the late Pleistocene (e.g., Ginat et al., 2003; Vaks, 2008) and was part of the dispersal routes from Africa during the early-mid Pleistocene. Late Pleistocene populations probably used the coastal route or the Jordan Rift Valley. It seems that their technology enabled them to negotiate these routes and their presence later in Eurasia is substantiated by a wealth of archaeological evidence.

Although the major late Pleistocene terrestrial barrier of the Levant is the large Saharo-Arabian Desert, which could effectively block hominin crossing, it hardly blocked prehistoric migrations during climatically favored periods (Fig. 1b) (McBrearty and Brooks, 2000; Stringer, 2000; Vermeersch, 2001; McDougall et al., 2005). Currently, the Saharo-Arabian desert is the largest global hyperarid

region, with almost no precipitation at its core (Fig. 1b). Because it is generally a formidable barrier, alternate routes, including spatial routes like the Nile valley, or wetter periods which eliminated the need to traverse the hyper-arid zone (Derricourt, 2005), should be considered.

The northern barrier of the Levant comprises the Taurus-Zagros mountain chains. These high mountains must have been harder to traverse during glacial periods, with abundant glaciers and harsh conditions. This barrier could be more easily traversed through valleys or during warmer periods.

Barriers could be partly crossed via coastlines. The East Mediterranean coastline would have extended somewhat further to the west during the low sea-stands of the Pleistocene glacial stages, and the resultant exposed coastal plain could have served at some places as a convenient passage for movement both to the north and south. However, undersea topography of the northern Levant is occasionally steep due to active tectonics and low sedimentation rates (Hall et al., 1994, their Fig. 1.13), rendering these coastlines less favorable for human passage. A coastal passage along the Red Sea was also suggested (Stringer, 2000), but similar topographic problems occur there, associated with steeper terrain.

Possible climatic effects on human migration and occupation

Hominins were predictability dependent on food resources and water availability and accessibility in their environments, but were subject to environmental factors causing contraction and expansion of ecological niches. Shifts between wet and arid climate in the relatively dry Levant constrained the availability of water, although food was probably always abundant. Fallow deer (*Dama mesopotamica*) and mountain gazelles (*Gazella gazella*) dominated the faunal assemblages of hominins during the mid-late Pleistocene in the central Levant (Belmaker, 2008a), however, sites located in the more northern, rocky area indicate an increase of wild goat (*Capra aegagrus*) and sites in the semi-arid region are dominated by gazelle and ass (*Equus*), suggestive of regional variability (Tchernov, 1988; Rabinovich, 2003).

It is hard to imagine that a slight change in annual precipitation in the Mediterranean zone, say, from 600 mm to 400 mm would cause an environmental disaster. The stability of the vegetational composition and the faunal associations along the hilly coastal ranges of the Levant did not significantly change. A slight decrease in biomass productivity, given the mobility of foragers in this belt, would not result in major site abandonment. The situation would be different in the semi-arid areas, but Anatomically Modern Humans coped with this by intensification and technological improvements.

The dispersal of Anatomically Modern Humans from Africa during MIS 5

The “Out of Africa” hypotheses imply several migrations from Africa, colonizing the other parts of the world as well as the potential for movements back into North Africa (Stringer and Andrews, 1988; Goren-Inbar et al., 2000; Bar-Yosef and Belfer-Cohen, 2001; Barkai et al., 2003; Finlayson, 2004; Forster, 2004; Olivieri et al., 2007; Shea, 2008). It also means that we can only ascertain the presence of hominins when they are found. This does not mean that the hominins did not arrive in the region at an earlier time, so the uncovered fossils are not necessarily the first pioneers. In the course of the migrations through the Levant, this region was unquestionably occupied by various hominins, probably starting at ca.1.8 Ma (e.g., Rightmire et al., 2006). Within the Pleistocene, the Middle Stone Age/Middle Paleolithic is unique in terms of extreme climatic changes and abundant hominin remains in the Levant.

The Ethiopian sites of Omo Kibish Formation, dating back to 195 ± 5 ka (McDougall et al., 2005), and Herto-Bouri, 160–154 ka (White et al., 2003) (Fig. 1b) produced some of the earliest fossils attributed to archaic Anatomically Modern Humans, indicating that our species originated in East Africa. It is yet unknown whether the first wave of migrants arrived in the Levant at the onset of the Mousterian, some 250–200 ka, due to the absence of fossils from the Early Mousterian or the Tabun D-type (Bar-Yosef, 1998; Shea, 2008; Hovers, 2009; Fig. 7).

The main archaeological presence of archaic Anatomically Modern Humans in the Levant (the Skhul-Qafzeh fossils) is reasonably well dated to 140 ± 10 through 92 ± 5 ka, mainly within MIS 5, but not without certain ambiguities (Schwarcz, 1980; Schwarcz et al., 1988; Valladas et al., 1988; Stringer et al., 1989; Mercier et al., 1993; Grün et al., 2005). Notably, Tabun C2 mandible, morphologically attributed to the same population of Skhul-Qafzeh, was found below the top of layer C. TL dates are spread from 190 ka through 144 ka (Mercier et al., 1995). The average date for the readings attributed to Layer C was recalculated from 171 ± 17 to 165 ± 16 ka (Mercier and Valladas, 2003, and compare Mercier et al., 1993; Bar-Yosef, 1998, 2007; Mercier and Valladas, 2003; Grün et al., 2005).

The group of Skhul-Qafzeh came from Africa (McBrearty and Brooks, 2000; McDougall et al., 2005), but their exact migration routes are poorly known (Fig. 1b) (Petraglia and Alsharekh, 2003). Although few human remains were discovered in Ethiopia, none were found in the eastern Sahara or in the Arabian Peninsula. Their presence is inferred from lithic assemblages that were found along presumed routes (Vermeersch, 2001; Petraglia and Alsharekh, 2003; Smith et al., 2004a, 2007).

The expansion of early Anatomically Modern Humans into the Levant could be facilitated by the relatively high Saharan humidity during MIS 6a-5e. (Smith et al., 2007). This is indicated by various proxies that suggest relatively more favorable ecosystems for mobile foragers across the Sahara-Negev Desert, compared with earlier and later periods (Miller et al., 1991; McKenzie, 1993; Schwarcz and Grün, 1993; Szabo et al., 1995; Rohling et al., 2002; Osmond and Dabous, 2004; Smith et al., 2004b, 2007; Kieniewicz and Smith, 2007).

Indeed, the widespread distribution of Middle Stone Age assemblages across the Sahara at MIS 5 (Garcea, 2004; Stringer and Barton, 2008) suggests that the northward dispersal of Anatomically Modern Humans took place at this period.

The Negev speleothem evidence demonstrates that a moister period also occurred in this region during MIS 6a-5e (Fig. 5d) (Vaks et al., 2007). The pluvial conditions occurred when a northward shift of the African monsoon resulted from displacement of the Inter-tropical Convergence Zone due to increased orbital insolation (Prell and Kutzbach, 1987; de Noblet et al., 1996; Kutzbach and Liu, 1997).

The wetter conditions over Sahara-Negev Desert during MIS 6a-5e could provide a generally continuous semi-arid corridor into the Levant. This corridor supported the availability of drinking water across presently arid barriers, such as the Arava valley. The heterogeneous environments of the Levant, which included Mediterranean forest (even during dry periods such as MIS 5), coupled with variable ecological niches including caves and rock-shelters, tempted the Anatomically Modern Humans to remain in this region.

Another migration route could also have occurred along the Red Sea coastline as suggested by hominin occupations at some coastal

Marine Isotope Stage	Ka B.P.	ENTITIES	HOMININS	Combined TL and ESR chronology	Africa	Sahara	Levant	Taurus-Zagros	Europe
3	38/36	Early Ahmariyan Emiran	"Egbert" Ksar Akil	Upper Paleolithic		warm arid	cool wet		
	46/47								
4	50	"Tabun B-type"	Dederiyeh Amud Kebara Tabun Woman	Tor Faraj Amud Tor Sabiha	Dederiyeh ? Kebara Tabun B	warm arid	cool wet N	cold wet	cold wet
	100								
5	100	"Tabun C-type"	Qafzeh Skhul Tabun II (jaw)	Skhul Tabun C	Qafzeh Quneitra ?	warm moist	warm dry Hs	cool wet	N cool wet
	150								
6	150	"Tabun D-type"		Douara IV? Tabun D	Hayonim E upper	Hs warm moist			N
	200								
7	200	Hummalian		Rosh Ein Mor Yabrud I (1-10)	Hayonim E lower Hayonim F	Hs			N
	250								
8	250	Acheulo-Yabrudian In the northern and central Levant	fragments in Tabun E Zuttiyeh	Tabun E Qesem Cave	Hayonim G				
	300								
9	300	Upper or Late Acheulian		Tabun F	Upper Acheulian in the Southern Levant				
	350								

Fig. 7. Chronological chart indicating the main sites and position of units within the Late Acheulian and Middle Paleolithic in the Levant. Technological and typological similarities between the stone assemblages and their stratigraphic position are taken as the main measure, and ambiguities of ESR dates are indicated by question marks. The main sites with hominin fossils are indicated by Hs (Anatomically Modern Humans/Skhul-Qafzeh group), and N (Neanderthals).

locations (Fig. 1b) (Van Peer et al., 1996; Stringer, 2000; Walter et al., 2000; Petraglia and Alsharekh, 2003). The Arabian coast could also serve for such migration if the hominins crossed the Babel-Mandab Straits (Rose, 2004). Thus, it seems improbable that humans were prompted to cross an extremely arid belt by slight drying of tropical Africa. The moister Saharan period of MIS 6a–5e seems a better candidate for this migration.

Population history during the Last Glacial in the Levant

The lack, up to now, of Anatomically Modern Human fossils in the Levant during MIS 4 (compared with several sites of Neanderthal fossils) suggests a local extinction during early MIS 4. It is unlikely that environmental change in the Levant was the sole cause for the local extinction of the Skhul-Qafzeh group, as indicated by the spatial availability and reliability of seasonally available food resources (Bar-Yosef et al., 1992; Hovers, 2009). Competitive exclusion between the two populations was suggested as an alternative interpretation (Shea and Bar-Yosef, 2005; Shea, 2008), associated with the Neanderthal invasion from the north.

Only Neanderthal fossils have been clearly dated in the Levant to MIS 4—early MIS 3 (Valladas et al., 1987; Schwarcz et al., 1989; Solecki and Solecki, 1993; Valladas et al., 1999; Rink et al., 2001; Akazawa and Muhesen, 2002; Shea, 2008). Among the best-known fossils are those uncovered in Dederiyeh Cave (northern Syria) and Amud and Kebara caves (Israel). In addition, the Tabun C1 fossil is considered a Neanderthal. Its ambiguous stratigraphic position was already noted by Garrod, the excavator (Bar-Yosef and Callander, 1999; Grün and Stringer, 2000), and thus it is considered a burial dug into layer C from Layer B. ESR dates for this layer are post-90 ka (Coppa et al., 2005; Fig. 7), and the resemblance of the industry to other Late Mousterian assemblage across the entire Levant (Shea, 2008), supports this conclusion.

Neanderthal environments in south-eastern Europe and the Anatolian plateau became drier and colder during MIS 4 and increasingly frequent environmental fluctuations may have prompted the southward expansion into the Levant and the Zagros valleys (e.g., Bar-Yosef et al., 1992; Finlayson, 2004). The wet, cool MIS 4 climate of the Levant was somewhat similar to their previous (Eurasian) environment, as evidenced by the presence of a rich fauna and flora (Belmaker, 2008b). Both the Levant and the valleys in the Zagros (Shanidar and other caves) favored ecological systems for hunter-gatherers with a relatively mild, wet climate and abundant food resources. The Neanderthals could easily traverse the mountain barriers of the Anatolian plateau through the valleys under MIS 4 conditions. They may have migrated along the widening coastal plain which existed at that time in some places, associated with a range of intermittently wet habitats. Near-coastal Neanderthal sites such as Kebara and Tabun caves must have been attractive localities for foragers seeking well sheltered places.

The later replacement of Neanderthals by Upper Paleolithic modern humans in the Levant is beyond the scope of this paper. However, Shea (2008) suggested that the Levant settlement of both Anatomically Modern Humans and Neanderthals was possibly terminated by abrupt short-term drying events. While this could be a plausible hypothesis, it appears that it is not yet possible to verify it from the current available proxies coupled with both the ambiguities and large standard deviations of the available radiometric dates. The intense speleothem deposition since the end of MIS 5 until MIS 2 suggests a continuous, more or less wet glacial period in the central Levant until MIS 2, even during climatic fluctuations. The Lake Lisan level fluctuated at a relatively high level compared with the Holocene, even during the short drier episodes of the last glacial period, suggesting that the Mediterranean ecosystem

enjoyed conditions that were wetter than any of the Holocene millennia.

Summary

Paleohydrologic evidence from the Levant and its barrier regions was reviewed, concentrating on straight-forward proxies that directly register the available water in the terrestrial system. The levels of terminal lakes in the Dead Sea basin and periods of deposition/non-deposition of speleothems convey direct paleo-environmental signals of major dry vs. wet periods in semi-arid regions of the central Levant. We also present an up-to-date interpretation of the isotopic records. All the summarized records consistently indicate that, contrary to previous studies, within the central Levant, glacial periods were wet and cool, while interglacials were dry and warm. Beyond the general character of the glacial/interglacial climate suggested here, variations occurred at all temporal scales throughout these periods.

The arrival of two successive waves of hominins into the Levant may be associated with the demonstrated paleoclimate conditions. Anatomically Modern Humans could have utilized the moister MIS 6–5 Saharan climatic corridor, moving northward from East Africa across northeast Africa or Arabia into the Levant. Paleoclimatic evidence for this favorable corridor up to the Levant seems well established, but human remains along the migration route are still scarce.

In the same way, the evidence presented here implies that ecogeographic similarities made it relatively easy and appropriate for groups of Neanderthals to disperse into the Levant from the north during early MIS 4. They could have crossed the Taurus-Zagros mountain range exploiting milder conditions in the valleys, or migrated along expanding parts of the coastal plain.

We only have limited archaeological windows into the past, so there is no continuous archaeological sequence, unlike speleothems or deep sea cores. Consequently, while there is no perfect congruence between climatic conditions and hominin movement or presence, we suggest that the arrival of successive waves of hominins into the Levant were facilitated by climatic conditions. The subsequent local extinction of the Neanderthals in the Levant who were facing modern humans, bearers of Upper Paleolithic technologies, is unclear and beyond the scope of this paper.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jhevol.2010.03.010.

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