Hunted gazelles evidence cooling, but not drying, during the Younger Dryas in the southern Levant

Gideon Hartman[a,b,1], Ofer Bar-Yosef[c], Alex Brittingham[a], Leore Grosman[d], and Natalie D. Munro[a]

[a]Department of Anthropology, University of Connecticut, Storrs, CT 06269; [b]Center for Environmental Science and Engineering, University of Connecticut, Storrs, CT 06269; [c]Department of Anthropology, Harvard University, Cambridge, MA 02138; and [d]Institute of Archaeology, The Hebrew University, Jerusalem, Israel 91905

Edited by Dolores R. Piperno, Smithsonian Institution, Fairfax, VA, and approved February 22, 2016 (received for review October 11, 2015)

The climatic downturn known globally as the Younger Dryas (YD; ∼12,900–11,500 BP) has frequently been cited as a prime mover of agricultural origins and has thus inspired enthusiastic debate over its local impact. This study presents seasonal climatic data from the southern Levant obtained from the sequential sampling of gazelle tooth carbonates from the Early and Late Natufian archaeological sites of Hayonim and Hilazon Tachtit Caves (western Galilee, Israel). Our results challenge the entrenched model that assumes that warm temperatures and high precipitation are synonymous with climatic amelioration and cold and wet conditions are combined in climatic downturns. Enamel carbon isotope values from teeth of human-hunted gazelle dating before and during the YD provide a proxy measure for water availability during plant growth. They reveal that although the YD was cooler, it was not drier than the preceding Bølling–Allerød. In addition, the magnitude of the seasonal curve constructed from oxygen isotopes is significantly dampened during the YD, indicating that cooling was most pronounced in the growing season. Cool temperatures likely affected the productivity of staple wild cereal resources. We hypothesize that human groups responded by shifting settlement strategies—increasing population mobility and perhaps moving to the warmer Jordan Valley where wild cereals were more productive and stable.

paleoclimate | stable isotopes | $\delta^{13}C$ | $\delta^{18}O$ | Natufian

This study measures the $\delta^{18}O$ and $\delta^{13}C$ isotopic values of gazelle tooth carbonates to address the controversy regarding water availability during the Younger Dryas (YD) climatic event in the eastern Mediterranean region. The YD was an abrupt, millennial-scale cooling event centered on the Northern Hemisphere between ∼12,900 and 11,500 BP (1). The weakening or possibly even the complete shutdown of the North Atlantic meridional overturning circulation caused dramatic cooling that reversed the post Last Glacial Maximum warming trend (2). Although the cooling phenomenon associated with the YD is clearly manifested in northern latitudes, contradictory data regarding the impact of this event in the eastern Mediterranean region is far from resolved (Fig. 1). Vastly disparate interpretations of the environmental and climatic impact of the YD on the southern Levant have been proposed with some arguing for xeric and others for opposing mesic conditions (3–10).

In the Mediterranean region of the Levant, the YD has been cited as a primary trigger for the transition to agriculture, a fundamental shift in human economic and social strategies that completely reconfigured human societies at the beginning of the Holocene (11–13). Clarifying regional impacts of the YD are essential for understanding the conditions that preceded this fundamental cultural change. In the Mediterranean Levant, the YD coincides with the Late Natufian (LN) cultural phase when the last hunter-gatherers occupied the region (11, 14).

In contrast to the Bølling–Allerød that was associated with unprecedented human sedentism in comparison with earlier periods, thinner site deposits and less investment in permanent architectural features reflect a reduction in site occupation intensity and an increase in population mobility coincident with the YD (12, 13, 15). The leading argument for the abandonment of a more or less sedentary lifestyle is an imbalance between human populations and their food resources related to a reduction in biomass production brought on by cool and dry conditions attributed to the YD (16, 17). Bar-Yosef and Belfer-Cohen (13) argue that experimentation with plant cultivation, triggered by the need to increase food production in response to declining resource abundance, ultimately lead to the beginning of agriculture at the onset of the Holocene. Other researchers recognize the importance of climatic change (18–20).

Multiple proxies have been used to reconstruct the climatic conditions of the YD. Oxygen isotope data from the Greenland ice core indicate clear evidence for a dramatic drop in temperature across the Northern Hemisphere (21) (Fig. 1*C*) when solar radiation approached its peak (22) (Fig. 1*B*). A local drop in sea surface temperature (SST) is also evident in the eastern Mediterranean Sea based on alkenone unsaturation ratios ($U^{k'}_{37}$) and positive shifts in the $\delta^{18}O$ values of foraminifera (23) (Fig. 1*E*) in deep sea cores. Despite general agreement on regional cooling during the YD, multiple proxies from the eastern Mediterranean conflict over the degree of aridity. In the Dead Sea Basin (DSB) for example, the shorelines of paleolake Lisan increase in elevation (Fig. 1*D*), suggesting higher water availability in the Mediterranean catchment area (9, 24). Based on a correlation between modern mean annual precipitation and the $\delta^{18}O$ values of meteoric water, Bar-Matthews et al. (3) interpreted a positive shift in cave speleothem $\delta^{18}O$ values as evidence for dry conditions during the YD [see also Orland et al. (25) for a modern cave carbonate analog]. However, following comparisons of the $\delta^{18}O$ data from

Significance

The Terminal Pleistocene Younger Dryas (YD) event is frequently described as a return to glacial conditions. In the southern Levant it has featured prominently in explanations for the transition to agriculture—one of the most significant transformations in human history. This study provides rare local measures of the YD by deriving gazelle isotopic values from archaeological deposits formed by Natufian hunters just prior to and during the YD. The results provide evidence for cooling, but not drying during the YD and help reconcile contradicting climatic reconstructions in the southern Levant. We suggest that cooler conditions likely instigated the establishment of settlements in the Jordan Valley where warmer, more stable conditions enabled higher cereal biomass productivity and ultimately, the transition to agriculture.

Author contributions: G.H. designed research; G.H. and A.B. performed research; O.B.-Y., A.B., L.G., and N.D.M. contributed new reagents/analytic tools; G.H. analyzed data; and G.H., O.B.-Y., L.G., and N.D.M. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence should be addressed. Email: gideon.hartman@uconn.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1519862113/-/DCSupplemental.

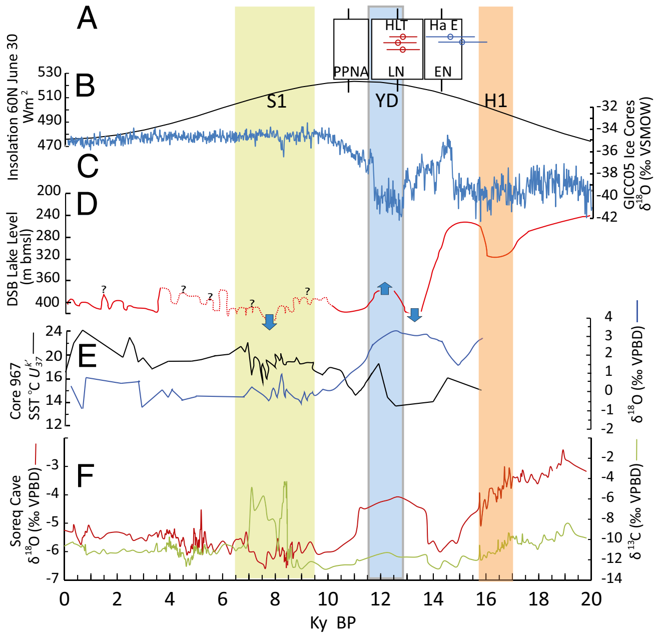

Fig. 1. Global and regional paleoclimate records for the past 20,000 y. (*A*) The chronology of EN, LN, and Prepottery Neolithic A (PPNA) cultures in the southern Levant based on calibrated ^{14}C dates (14); individual calibrated (OxCal13) radiocarbon dates of HLT (red symbols ± 1σ) and HC EN (blue symbols ± 1σ). (*B*) Calculated Northern Hemisphere insulation at 60°N (22). (*C*) Composite Greenland ice core oxygen isotope ($\delta^{18}O$) values provide a proxy for paleotemperature (21). (*D*) DSB lake level reconstruction (24). (*E*) Eastern Mediterranean reconstruction of SST using alkenone unsaturation ratio ($U^{k'}_{37}$) and *Globigerinoides ruber* $\delta^{18}O$ values (23). (*F*) Soreq Cave speleothem record (3). S2 is a sapropel formation event in the Eastern Mediterranean Sea; YD is the Younger Dryas; and H1 is a Heinrich Event.

deep sea cores and Lake Lisan carbonates, others interpret the speleothem $\delta^{18}O$ data as the result of a source effect, rather than a drop in precipitation (26, 27). Additional controversy revolves around the relative availability of arid-adapted plant families during the YD, with Rossignol-Strick (8) arguing for an increase in the arid-adapted plants recorded in deep sea cores, a shift that was not observed in lacustrine pollen diagrams (4). Gvirtzman and Wieder (5) argue that the YD was more arid based on their evaluation of coastal aeolian loess deposits. In addition, a study of Negev sand grains lead Roskin et al. (10) to argue that exceptionally windy rather than arid conditions are responsible for the formation of aeolian sand dunes.

The current study contributes to this debate by introducing $\delta^{18}O$ and $\delta^{13}C$ values of gazelle tooth carbonates to reconstruct climate conditions in the southern Levant during the Natufian cultural period, just before and during the YD. Seasonal carbon and oxygen isotope data recovered from gazelle teeth directly deposited by humans at archaeological sites are used to investigate the impact of climatic change at both local and regional scales. Reconstructing climate directly from archaeological material circumvents problems that arise when regional climatic datasets are applied to local archaeological sites dated using different techniques and/or situated in different environmental contexts. In this study, climatic conditions surrounding sampled archaeological sites are reconstructed based on $\delta^{13}C$ and $\delta^{18}O$ values from gazelle carbonates. We also aim to resolve sharply contrasting interpretations regarding regional patterns of aridity for this period. Because the primary controversy concerns water availability, which is also the major limitation on modern day biomass productivity in the eastern Mediterranean (28), we focus especially on this marker. Finally we discuss potential implications of the results on Natufian settlement and subsistence on the threshold of the transition to agriculture.

This study compares seasonal climatic conditions during the Early and Late Natufian (EN and LN, respectively) at the sites of Hayonim Cave (EN and LN) and Hilazon Tachtit (LN), Galilee, Israel (29–31). The $\delta^{18}O$ values are influenced by a number of climatic factors, and $\delta^{13}C$ provides an independent proxy for water availability (32–34), and is measured here to constrain the interpretation of $\delta^{18}O$ values. Carbon isotope values measured in gazelle teeth reflect water availability during the growth of C_3 vegetation consumed by gazelle and thus provide an indirect measure of how wet local conditions were when the C_3 plants were consumed (34). The site-based $\delta^{18}O$ and $\delta^{13}C$ values provided by gazelle tooth enamel carbonate are then directly compared with regional paleoclimate proxies to evaluate contrasting interpretations of climatic data.

Mountain gazelles (*Gazella gazella*) are the most ubiquitous hunted species in Natufian sites (15). Gazelle are ideal for paleoenvironmental and paleoclimatic reconstructions because the carbon isotope values ($\delta^{13}C$) of their body tissues reflect the carbon values of their plant diet. The carbon values mirror the amount of water available during the growth of C_3 plants in the diet and the proportion of C_4 vegetation consumed in steppic environments (34). Because tooth enamel forms incrementally, $\delta^{13}C$ values measured sequentially in tooth enamel carbonate provide valuable seasonal climatic and environmental information. Oxygen isotope values ($\delta^{18}O$) measured in gazelle teeth provide complementary information about the isotopic composition of the consumed meteoric water, and the animal's physiological condition, which changes under water stress (35, 36).

Hayonim Cave [HC; WGS84 32898277N 352689671W, 176 m above modern sea level (amsl)] and Hilazon Tachtit Cave (HTC; WGS84 32923617N 35216871W, 216 m amsl) are located about 10 km apart on the western slopes of the Mediterranean Hills, at the boundary between the Lower and Upper Galilee. They are situated at similar elevations, enjoy equal mean annual rainfall (~700 mm/y) and are surrounded by a mix of Mediterranean maquis and batha vegetation communities (*Supporting Information*; Fig. S1). Although the Natufian deposits at HC cover both the Early (15,000–13,600 Cal BP) and Late phases (13,640–11,540 Cal BP; ref. 30), the radiocarbon dates and cultural remains from HTC indicate a more limited occupation in the LN phase (12,744–12,674 OxCal13 BP) (14). Because the sites are environmentally similar, the isotopic samples can be combined to compare climatic and environmental conditions across the EN and LN boundary.

Results

General Trends between Early and Late Natufian Phases. The complete dataset of tooth enamel carbonate including unidentified gazelle molar fragments and lower third molars (M_3s) is detailed in Table S1. Before specific patterns are identified, it is important to note that mean $\delta^{18}O$ and $\delta^{13}C$ values from LN HC and LN HTC are statistically identical (two-tailed t test assuming unequal variance, $\delta^{18}O$ $P = 0.771$; $\delta^{13}C$ $P = 0.987$; Fig. 2). This result affirms that differences between the EN layer at HC and the LN layers at HC and HTC are the product of temporal changes in regional climate rather than site-specific microhabitat conditions or a change in gazelle hunting territories.

The mean $\delta^{18}O$ values measured in gazelle teeth from EN HC are significantly lower (negative) than those from LN HC and HTC (Table 1; Fig. 2). A similar relationship exists between the average most negative (minimum) and positive (maximum) measurements from each tooth cusp (Table 1; Fig. 2). Assuming that the lowest and highest $\delta^{18}O$ values measured in each tooth represent the wet and dry seasons respectively, the seasonal similarity between EN and LN samples indicates stability in Mediterranean climates over time. A more detailed examination of the seasonal data are provided for the M_3s below.

Table 1. Results summary

Site/period	EN HC	LN HC	LN HTC
$\delta^{13}C_{mean}$	−11.8 ± 0.7*	−12.2 ± 1.0	−12.2 ± 0.5*
$\delta^{13}C_{min}$	−12.4 ± 0.5†	−13.0 ± 1.2	−12.8 ± 0.6†
$\delta^{13}C_{max}$	−11.3 ± 0.8	−11.9 ± 0.9	−11.7 ± 0.6
$\delta^{18}O_{mean}$	−2.4 ± 1.5‡,§	−1.3 ± 1.5‡	−1.1 ± 1.5§
$\delta^{18}O_{min}$	−3.3 ± 1.6¶	−3.0 ± 0.9#	−2.1 ± 1.50¶,#
$\delta^{18}O_{max}$	−1.5 ± 1.4‖	−1.0 ± 1.1	−0.3 ± 1.5‖

One-tail *t* tests assuming unequal variance were performed on site mean, minimum, and maximum $\delta^{13}C$ and $\delta^{18}O$ values for EN HC–LN HC, EN HC–LN HTC, and LN HC–LN HTC pairs. Symbols mark the pairs with statistically significant results: *,†,§,¶,#,‖$P < 0.05$; ‡$P < 0.01$. Means are displayed with ±1σ (‰). For complete results, see Table S2.

The mean $\delta^{13}C$ values measured at LN HC and HTC are slightly negative [−0.42 – (−0.40) ‰] and significantly different from those measured at EN HC ($P < 0.05$; Table 1; Fig. 2). Because the ^{13}C in C_3 vegetation becomes enriched when annual precipitation drops (33), this result suggests similar albeit slightly wetter growth conditions during the LN. The magnitude of the seasonal difference indicated by the most negative (presumed wet season) and least negative (presumed dry season) $\delta^{13}C$ values is the same in the EN and LN periods (Table 1; Fig. 2).

Seasonal Isotope Patterns in M_3 Teeth. Plots of sequential $\delta^{13}C$ and $\delta^{18}O$ values from individual M_3s from EN HC and LN HTC provide seasonal data beginning at the time of tooth formation. The M_3 begins forming at parturition in the late spring (April–June; wet season), and continues forming until the following dry summer and fall seasons (July–November) (37, 38). The data presented in this section has been wiggle-matched to fit consensus regression lines (see Fig. S2 for unmatched data). The isotopic expression of the current Mediterranean climate is clearly observable in the combined $\delta^{13}C$ and $\delta^{18}O$ patterns of the Natufian gazelle. A similar difference between the wet and dry season is also recorded in the teeth of modern gazelle (34). Both EN HC and LN HTC $\delta^{13}C$ data form uniform and overlapping linear regression lines when plotted against time. Early in the tooth's formation, the values are consistently more negative than those measured later in the process (Fig. 3 *B*, *D*, *F*). The $\delta^{18}O$ patterns are similar to those for the gazelle molar fragment data (Fig. 2) showing more negative intercepts in the EN $\delta^{18}O$ value second-order polynomial regression curve compared with the LN (Fig. 3*E*; this difference is maintained when outlying specimen 44 is removed from the regression; Fig. S3). Differences in the seasonal pattern however, are visible in the amplitude of the evaporative dry season indicated by the curvature of wiggle-matched consensus regression lines. Although the EN HC sample shows a pronounced wet–dry–wet season shift, the hyperbolic curvature is shallower in the LN HTC data, implying weaker evaporative conditions during the dry season (Fig. 3 *A*, *C*, *E*).

Discussion

The results presented in this study clarify some ambiguities regarding the climatic effect of the YD on Natufian populations inhabiting the Mediterranean zone in the southern Levant. The interpretation of high-resolution cave speleothem oxygen isotope data (3) requires modern day analogs (25) and supporting oxygen isotope-based paleoclimate proxies (27, 39). The current study uses oxygen isotope values obtained through the sequential sampling of gazelle tooth enamel as a proxy for the seasonal composition of environmental water; this is made possible through comparison with data on water availability obtained from complementary carbon isotope data. A significant advantage of this proxy is that it derives directly from cultural remains, enabling direct association of human behavioral adaptations with climatic and environmental conditions.

Our results reveal no evidence for the aridification that has typically been associated with the YD. To the contrary, the carbon isotope values of the large dataset of tooth enamel cusps show that the water available to C_3 plants was similar to or even greater in the YD than the EN phase, which falls within the Bølling–Allerød period (Fig. 2; Table 1). Because the carbon data show that this change cannot represent a decrease in precipitation, the positive shift in oxygen isotope values from the EN to the LN ($^{18}\Delta_{EN\text{-}LN} = 1.32–1.14‰$) must reflect a change in the oxygen isotopic composition of Mediterranean seawater. This change would result from a drop in the temperature of the seawater—the source of Eastern Mediterranean precipitation (Fig. 1; refs. 23, 39). This result joins a growing body of evidence pointing to wet conditions during the YD including an abrupt rise in the Dead Sea Basin shore lakes (Fig. 1*D*; ref. 9) and the formation of a dark manganese and barium oxide desert varnish crust on the paleo-lakeshore pebbles (6). These results also help to resolve some discrepancies in recent reconstructions of the YD. For example, the increase in the presence of the arid-adapted plant genus *Artemisia* during the YD was originally interpreted as a marker of aridification (8). Given that vegetation was not water stressed during the YD, this is likely the result of the expansion of aeolian sand and loess sediments to which *Artemisia* is adapted (5, 10, 40) and thus a product of edaphic rather than climatic conditions.

The scale of seasonal change represented in the carbon and oxygen isotopes values from EN and LN gazelle carbonates reflects the typical modern Mediterranean climate pattern (wet and cool winter, hot and dry summer). Gazelles shift from protein-rich green herbaceous vegetation during the wet season to evergreen ligneous vegetation during the dry season (38). This dietary shift is manifested in the gradual increase in $\delta^{13}C$ values from early to late tooth formation (Fig. 4*D*; ref. 34). This period corresponds to a 6-mo period (37, 38) between the late spring, when most modern fawns are born, and the late fall, when the early rains begin but fresh green herbaceous vegetation has not yet sprouted. The oxygen isotope pattern fully agrees with the carbon pattern—negative oxygen values rise across the dry summer season and decline when temperature drops in the fall (Fig. 3 *A* and *C*). This seasonally cyclical transition from cold and rainy to hot and dry is measured locally in the $\delta^{18}O$ values of

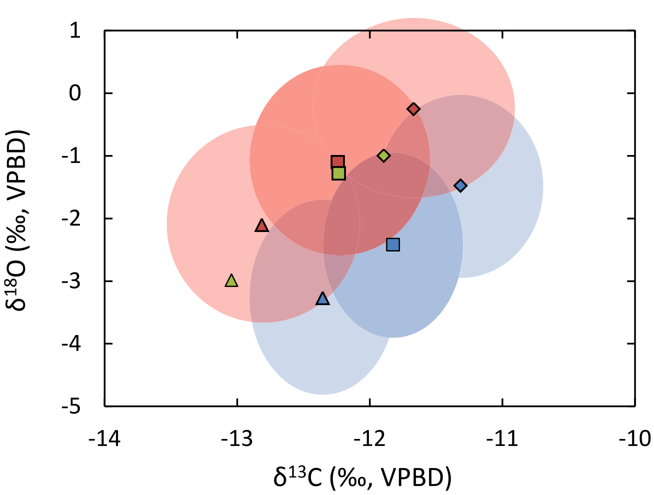

Fig. 2. Bivariate plot of all gazelle carbon and oxygen isotope enamel molar data (Table 1). Blue symbols and shaded spheres (±1σ): EN HC; green symbols: LN HC; red symbols and shaded spheres (±1σ) LN HTC; squares represent mean values; triangles represent the average minimal values measured in each tooth; diamonds represent the average maximal value.

ANTHROPOLOGY

EARTH, ATMOSPHERIC, AND PLANETARY SCIENCES

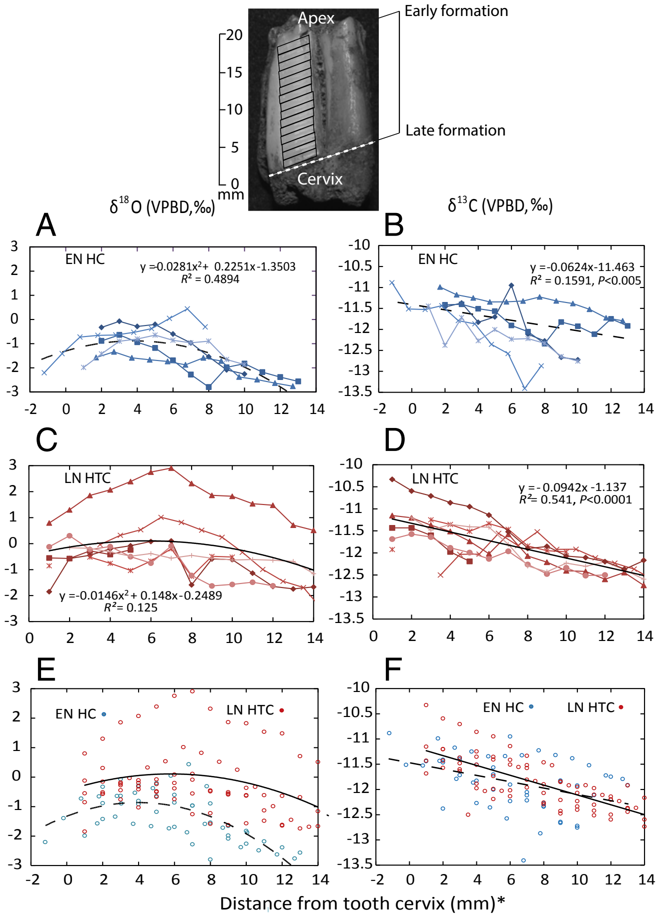

Fig. 3. Sequential sampling results of individual M_3 teeth from EN HC (blue-shaded plot lines) and Late LN HTC (red-shaded plot lines). The symbols in *A* ($\delta^{18}O$) correspond to those in *B* ($\delta^{13}C$) EN HC; and those from *C* ($\delta^{18}O$) correspond with *D* ($\delta^{13}C$) LN HTC; combined early and late Natufian sequential $\delta^{18}O$ (*E*) and $\delta^{13}C$ (*F*) data.

modern water vapor collected from Israel's seashore (Weizmann Institute) (41). Water vapor is an ideal analog for the oxygen isotope values of gazelle teeth because $\delta^{18}O$ values in plants and animals are determined by evaporation and transpiration during the dry season when measureable rainfall is absent. The consensus curve formed between $\delta^{18}O$ values and the distance from the tooth's apex in M_3s dated before the YD (EN HC) mirrors the curve of modern water vapor, and the curve of gazelle teeth deposited during the YD (LN HTC) is shallower (Fig. 4). Comparisons of the gazelle trend lines show that the smallest difference between the EN and LN occur in the dry season (June–September), and the largest differences occur in the wet season (December–April; Figs. 3 and 4). Although wet season differences reflect a change in water source oxygen isotope values, the dry season data indicate that evaporation was less pronounced during the YD than the EN. The typical Mediterranean pattern of wet winters and dry summers is not altered during the YD, but a drop in temperature would have decreased the evaporative regime. This would have increased the water available for plants even if rainfall remained constant in the wet season. The decrease in the magnitude of difference in $\delta^{18}O$ values between the wet and dry seasons during the YD is supported by high-resolution isotope and fluorescence patterns measured in this time period at Soreq Cave (speleothem N2; ref. 7).

If annual temperature dropped significantly during the YD and mean annual precipitation remained relatively constant, this alone could explain the modest negative shift in $\delta^{13}C$ values between the EN to LN phases (ref. 34; Fig. 2). Soil and air temperature during the YD are unknown, but sea surface temperature proxies (TEX_{86}, $U^{k'}_{37}$) indicate a drop of about 2–3 °C between the Bølling–Allerød and the YD (39). It is likely that seasonal and annual terrestrial temperature amplitudes would have been pronounced during a period of Mediterranean surface water cooling. Further work on carbonate temperature proxies (i.e., Δ_{47}) in cave speleothems might enable better reconstruction of terrestrial temperatures during the YD (42). Clarifying the speed of the onset of this climatic event is also important because it influences the ability of the local biome to adjust to changing climate conditions. Current data suggest that the cooling associated with the YD took place on a decadal scale (ca. 20 y) (43) and thus would have had a more profound effect on local biota and humans.

Other factors that could influence our carbon isotope data and mask increased aridity during the LN are a change in the relative balance of C_3 and C_4 plants in gazelle diets or a change in human hunting or gazelle foraging territories. In the Mediterranean Levant C_4 grasses are sporadic and available as a green food source only in summer when herbaceous C_3 vegetation is dry. Modern gazelles inhabiting these habitats in the Levant typically consume small quantities of C_4 grasses in the dry season (38). If conditions were much drier in the YD, then C_4 grasses may have been more abundant in Mediterranean habitats and potentially more important in gazelle diets, at least in the dry season. In this case, we would expect higher $\delta^{13}C$ values and a greater difference between dry and wet season values in LN than EN gazelles (34). Our data do not meet either of these expectations (Fig. 3; Table 1). If conditions were drier in the YD, humans or gazelles also could have adapted by foraging at higher elevations where rainfall was high enough to offset the drying impact of the YD. If gazelle foraged at higher elevations, their $\delta^{18}O$ values would be more negative (44); and again, our data contradict this expectation. Finally, the transport of near-complete gazelle carcasses (45) and tight clustering of both our within-group $\delta^{13}C$ and $\delta^{18}O$ values (Fig. 4; Table 1) suggest that humans foraged relatively close to home in both the EN and LN.

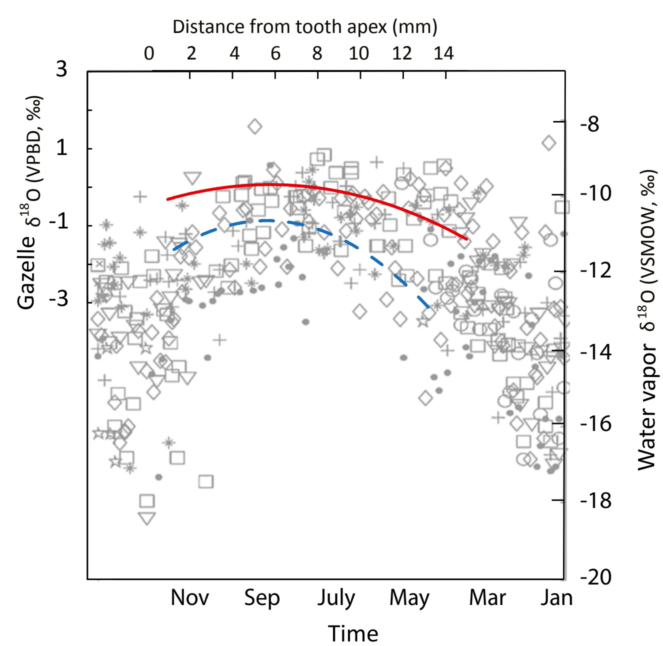

Fig. 4. Plot of seasonal near-surface water vapor $\delta^{18}O$ values (gray symbols; each symbol type relates to a specific year) measured between 1998 and 2006 on Israel's seashore overlain by gazelle M_3 tooth enamel regression lines. Pre-YD (EN HC): blue dashed line, YD (LN HTC): red line. Data from ref. 41.

Our results challenge the entrenched model that warm temperatures and high precipitation are synonymous with climatic amelioration and cold and wet conditions are combined in climatic downturns. Our results indicate that precipitation remained constant across the Natufian, and temperatures became colder in the Mediterranean zone. The relationship between this climatic and cultural change is complex, partially due to spatial variation in the scale of climatic change given the diverse topographies and environments of the southern Levant (i.e., climatic change may be more pronounced in the Mediterranean zone than the Jordan Valley) and partially due to the low resolution of Natufian chronologies, in particular the transition from the EN to the LN. The onset of the YD has traditionally been associated with the beginning of the LN, however absolute dates, especially those from the Mediterranean zone suggest that the LN may have begun up to 600 y before the onset of the YD (14, 20). Thus, many of the cultural markers of the LN, such as changes in lithic technology and burial practices likely emerged before the YD. The archaeological material in this study derives from well-dated LN contexts (30, 31), and thus the scale of the YD's impact can be detected in human subsistence and settlement strategies (15). Consequently, given evidence for a drop in temperature during the YD, we must now ask how this event might have affected the economy of highly sedentary Natufian societies?

Environmentally speaking, the answer probably lies in the ability of wild cereal species to maintain biomass productivity in a given stand at lower ambient temperatures. The discovery of sickle blades, ground stones, abraded tooth wear patterns, and increased abundance of grain phytoliths all point to the importance of grains in Natufian diets. Furthermore, grinding stones, and bedrock mortars are more common at LN than EN sites (11, 46, 47). Use wear analysis showed that these tools were used for grinding cereals and legumes typically associated with increasing dependence on cereals (46, 47).

The impact of lower growing season temperatures on cereal productivity is not well studied in semiarid Mediterranean environments because water availability rather than temperature is the primary factor determining crop biomass productivity today (48). Studies conducted on commercial and wild cold-adapted cereals reveal species-specific optimal temperature requirements for germination and growth (49). In a regionally relevant study from Israel the seeds of various wild barley (*Hordeum spontaneum*) populations were translocated into new environments (50). Seeds originating from warm climates showed high mortality when planted in a cool mountain plot where early growth temperatures range below freezing. Also, without exception all barley seeds sown in the cool location showed lower biomass productivity (<50% of optimal growth rate) after 2 mo of growth, although final reproductive size was not compromised (50). These results suggest the kind of impact that the YD could have had on wild grain growth. The rapid onset of the YD, may have caused an initial drop in grain production by killing seeds in winter frost events, and more importantly, delaying the germination and maturation of cereals and thus affecting the timing of the harvest. Although rapid natural selection for cold-adapted cereal variants likely took place, a delay in the germination and maturation of cereals would have been detrimental for human populations reliant on these seeds.

EN populations sustained their sedentary lifestyle by increasing environmental carrying capacity through the exploitation of abundant low-ranked foods such as cereal grains and small game animals, but this would have made them more sensitive to subtle compromises in food availability, especially of the low-ranked wild grasses that enabled sedentism in the first place. Thus, the YD may have disrupted the sedentary lifestyle of Natufian populations in the Mediterranean zone, which fits archaeological data suggesting that they adapted to new conditions by increasing population mobility (12, 15), and seeking more reliable grain stands in more climatically stable environments (e.g., the Jordan Valley; refs. 11, 51). Increased population mobility is evidenced by a significant decline in the scale and intensity of construction of architectural features and thickness of site deposits in EN versus LN sites (12). Some EN sites take on new primary roles as burial locales in the LN—at HC LN activity centered around burials interred toward the back of the cave. Only two insubstantial walls were constructed in the LN compared with several round structures, some with built hearths, slab-lined pits, and pavements in the EN (30). HTC also served primarily as a human burial site (29). Additionally, faunal indices of slow- and fast-moving small game reveal a significant drop in site occupation intensity during the LN in the Mediterranean zone (15). In contrast, the LN site of Nahal Ein Gev II indicates that the same is not true in the Jordan Valley. Excavations have revealed a substantial village with dense deposits and diverse architecture including the foundations of large structures, pits, and burials that reflect intensive occupation (52). Recent survey and testing at the site of Huzuq Musa farther south in the Jordan Valley also hint at large architectural features and dense archaeological deposits, although the site was only excavated to a limited extent (51).

Further work on the impact of cooling on wild cereal growth and productivity in Mediterranean environments is necessary to provide higher-resolution data on the potential affects of the YD on resource availability. Future work will also establish the degree of reliance of Jordan Valley residents on cereals during the LN.

Materials and Methods

Gazelle Tooth Sampling and Processing. Two groups of gazelle molars were available for study (n = 44 teeth) from clear stratigraphic contexts at HC and HTC (Table S2). The first group includes lower third molars (M_3) from EN and LN contexts (n = 12). M_3s were chosen for analysis because unlike the M_1 and M_2 they are easy to identify to element when recovered in isolation (37). The seasonal signal created by sequentially sampling the M_3 can be directly compared to detect seasonal differences between the EN and LN phases. The second group includes molar cusp fragments from secure EN and LN contexts that were not sufficiently diagnostic to be assigned to a specific molar (n = 32). This sample was predominantly used to provide more robust climate data and to improve the confidence levels of the mean $\delta^{13}C$ and $\delta^{18}O$ values.

The external surfaces of the teeth were cleaned by manually removing adhering debris and sediment and were then mounted on a carrying glass. The teeth were microsampled using a micromilling system (New Wave Research). After mounting, the sampling area was mechanically cleansed using the micromill drill by removing 5 μm of enamel from the tooth's surface. Sampling took place sequentially on a single labial tooth cusp starting from the tooth cervix and advancing toward that tooth enamel apex in 1-mm intervals. Each sample was drilled to an average depth of 450 μm. This strategy ensured comparability among specimens and allowed the seasonal signal from multiple teeth from a single cultural context to be aligned so that statistically significant results could be produced. The drill head was cleaned with 0.5 N hydrochloric acid and then dried with 100% ethyl alcohol after each sequential sample was extracted to eliminate potential contamination.

The enamel powder (~3 mg per sample) was treated to remove organic remains and unbound exogenous carbonate following Balasse et al.'s (53) protocol. The samples were first treated with 2 mL of 2% NaOCl (sodium peroxide) in reaction tubes to remove organic remains. The samples were agitated and then left to react with the NaOCl solution for 24 h and then washed and agitated 3 times with Milli-Q H_2O (MΩ.cm 18.2 Milli-Q; Millipore). Later the samples were reacted with highly diluted 0.1 N pH 3 CH_3COOH (acetic acid). The acid reaction was limited to 4 h, and was terminated by repeated washing and centrifuging until the solution reached neutrality (pH 7). Water was decanted from the reaction tubes after the final centrifuging cycle and left in the desiccating oven to dry at 50 °C overnight.

The birth of modern mountain gazelle can vary within the spring season (March–May) in accordance with peak biomass productivity (38). Thus, the timing of initial tooth formation should not be fully synchronized among individuals. Wiggle-matching over minute distances (<3 mm) was used to align the seasonal patterns in individual teeth when both the carbon and oxygen isotope data from a tooth lined up with the average trend lines.

Stable Isotope Analysis. The samples were analyzed at the stable isotope facility of the Department of Écologie et Gestion de la Biodiversité, at the Muséum National d'Histoire Naturelle, Paris, France. Approximately 600 μg of treated enamel powder was reacted for 240 s with 100% phosphoric acid

ANTHROPOLOGY

EARTH, ATMOSPHERIC, AND PLANETARY SCIENCES at 70 °C in individual vessels in a Kiel IV carbonate device (Thermo Scientific). The evolving CO_2 was transferred by vacuum to a Delta V Advantage isotopic ratio mass spectrometer (Thermo Scientific) where *m/z* 45, 46, 47 were converted to isotopic ratios using the following equation:

$$\delta\, sample\ (‰) = \left(\frac{R\ sample - R\ standard}{R\ standard}\right) - 1 \times 1{,}000,$$

where *R* is the ratio of $^{13}C/^{12}C$ to $^{18}O/^{16}O$ normalized against the Vienna Pee Dee Belemnite (VPDB) standard.

The analytical precision of $\delta^{13}C$ and $\delta^{18}O$ values determined by repeated measurement of in house carbonate standard MarberLM ($n = 53$; $\delta^{13}C_{VPDB}$ = 2.130‰ and $\delta^{18}O_{VPDB} = -1.830‰$) were 0.026‰ (1σ) and 0.044‰ (1σ) respectively. The MarberLM in house standard was calibrated against IAEA NBS 19 (NIST).

ACKNOWLEDGMENTS. This study was supported by the University of Connecticut (G.H.) and the Israel Science Foundation (ISF 459/11 to L.G.). Archaeological sample export permit for detractive analysis was granted by the Israel Antiquities Authority (No. 14114).

1. Muscheler R, et al. (2008) Tree rings and ice cores reveal C-14 calibration uncertainties during the Younger Dryas. *Nat Geosci* 1(4):263–267.
2. Broecker WS, et al. (2010) Putting the Younger Dryas cold event into context. *Quat Sci Rev* 29(9-10):1078–1081.
3. Bar-Matthews M, Ayalon A, Gilmour M, Matthews A, Hawkesworth CJ (2003) Sea-land oxygen isotopic relationships from planktonic foraminifera and speleothems in the Eastern Mediterranean region and their implication for paleorainfall during interglacial intervals. *Geochim Cosmochim Acta* 67(17):3181–3199.
4. Bottema S (1995) The Younger Dryas in the Eastern Mediterranean. *Quat Sci Rev* 14(9):883–891.
5. Gvirtzman G, Wieder M (2001) Climate of the last 53,000 years in the eastern Mediterranean, based on soil-sequence stratigraphy in the coastal plain of Israel. *Quat Sci Rev* 20(18):1827–1849.
6. Liu T, Broecker WS, Stein M (2013) Rock varnish evidence for a Younger Dryas wet period in the Dead Sea basin. *Geophys Res Lett* 40(10):2229–2235.
7. Orland IJ, et al. (2012) Seasonal resolution of Eastern Mediterranean climate change since 34 ka from a Soreq Cave speleothem. *Geochim Cosmochim Acta* 89:240–255.
8. Rossignol-Strick M (1995) Sea-land correlation of pollen records in the Eastern Mediterranean for the glacial-interglacial transition: Biostratigraphy versus radiometric time-scale. *Quat Sci Rev* 14(9):893–915.
9. Stein M, Torfstein A, Gavrieli I, Yechieli Y (2010) Abrupt aridities and salt deposition in the post-glacial Dead Sea and their North Atlantic connection. *Quat Sci Rev* 29(3-4): 567–575.
10. Roskin J, Tsoar H, Porat N, Blumberg DG (2011) Palaeoclimate interpretations of Late Pleistocene vegetated linear dune mobilization episodes: Evidence from the northwestern Negev dunefield, Israel. *Quat Sci Rev* 30(23-24):3364–3380.
11. Bar-Yosef O (1998) The Natufian culture in the Levant, threshold to the origins of agriculture. *Evol Anthropol* 6(5):159–177.
12. Goring-Morris N, Belfer-Cohen A (1997) The articulation of cultural processes and Late Quaternary environmental changes in Cisjordan. *Paéorient* 23(2):71–93.
13. Bar-Yosef O, Belfer-Cohen A (2002) Facing environmental crisis. Societal and cultural changes at the transition from the Younger Dryas to the Holocene in the Levant. *The Dawn of Farming in the Near East, Studies in Early Near Eastern Production, Subsitence, and Environment*, eds Cappers RTJ, Bottema S (Ex Oriente, Berlin), Vol 6, pp 55–66.
14. Grosman L (2013) The Natufian chronological scheme - New insights and their implications. *Natufian Foragers in the Levant. Terminal Pleistocene social changes in Western Asia, Archaeological Series*, eds Bar-Yosef O, Valla FR (International Monographs in Prehistory, Cambridge), Vol 19, pp 622–637.
15. Munro ND (2004) Zooarchaeological measures of hunting pressure and occupation intensity in the Natufian - Implications for agricultural origins. *Curr Anthropol* 45: S5–S33.
16. Sherratt A (1997) Climatic cycles and behavioural revolutions: The emergence of modern humans and the beginning of farming. *Antiquity* 71:271–287.
17. Byrd BF (2005) Reassessing the emergence of village life in the Near East. *J Archaeol Res* 13(3):231–290.
18. McCorriston J, Hole F (1991) The ecology of seasonal stress and the origins of agriculture in the Near East. *Am Anthropol* 93(1):46–69.
19. Rosen AM, Rivera-Collazo I (2012) Climate change, adaptive cycles, and the persistence of foraging economies during the late Pleistocene/Holocene transition in the Levant. *Proc Natl Acad Sci USA* 109(10):3640–3645.
20. Maher LE, Banning B, Chazan M (2011) Oasis or mirage? Assesing the role of abrupt climate change in the prehistory of the Southern Levant. *Camb Archaeol J* 21(1):1–30.
21. Rasmussen SO, et al. (2006) A new Greenland ice core chronology for the last glacial termination. *J Geophys Res*, 10.1029/2005JD006079.
22. Berger A, Loutre MF (1991) Insolation values for the climate of the last 10,000,000 years. *Quat Sci Rev* 10(4):297–317.
23. Emeis KC, et al. (2000) Temperature and salinity variations of Mediterranean Sea surface waters over the last 16,000 years from records of planktonic stable oxygen isotopes and alkenone unsaturation ratios. *Palaeogeogr Palaeoclimatol Palaeoecol* 158(3-4):259–280.
24. Torfstein A, Goldstein SL, Stein M, Enzel Y (2013) Impacts of abrupt climate changes in the Levant from Last Glacial Dead Sea levels. *Quat Sci Rev* 69:1–7.
25. Orland IJ, et al. (2014) Seasonal climate signals (1990-2008) in a modern Soreq Cave stalagmite as revealed by high-resolution geochemical analysis. *Chem Geol* 363: 322–333.
26. Frumkin A, Ford DC, Schwarcz HP (1999) Continental oxygen isotopic record of the last 170,000 years in Jerusalem. *Quat Res* 51:317–327.
27. Kolodny Y, Stein M, Machlus M (2005) Sea-rain-lake relation in the Last Glacial East Mediterranean revealed by $\delta^{18}O$ - $\delta^{13}C$ in Lake Lisan aragonites. *Geochim Cosmochim Acta* 69(16):4045–4060.
28. Sternberg M, Shoshany M (2001) Aboveground biomass allocation and water content relationships in Mediterranean trees and shrubs in two climatological regions in Israel. *Plant Ecol* 157(2):173–181.
29. Grosman L, Munro ND, Belfer-Cohen A (2008) A 12,000-year-old Shaman burial from the southern Levant (Israel). *Proc Natl Acad Sci USA* 105(46):17665–17669.
30. Bar-Yosef O (1991) The archaeology of the Natufian layer at Hayonim Cave. *The Natufian Culture*, eds Bar-Yosef O, Valla FR (International Monographs in Prehistory, Ann Arbor, MI), pp 81–92.
31. Grosman L (2003) Preserving cultural traditions in a period of instability: The Late Natufian of the hilly Mediterranean zone. *Curr Anthropol* 44(4):571–580.
32. Kohn MJ, Cerling TE eds (2002) Stable isotope compositions of biological apatite. *Rev Mineral Geochem* 48: 455-488.
33. Hartman G, Danin A (2010) Isotopic values of plants in relation to water availability in the Eastern Mediterranean region. *Oecologia* 162(4):837–852.
34. Hartman G (2012) Impacts of environmental deterioration on the carbon isotope values of modern vegetation and gazelles in the southern Levant: Predicting the severity of the Younger Dryas. *Palaeogeogr Palaeoclimatol Palaeoecol* 321:55–64.
35. Kohn MJ, Schoeninger MJ, Valley JW (1996) Herbivore tooth oxygen isotope compositions: Effects of diet and physiology. *Geochim Cosmochim Acta* 60(20):3889–3896.
36. Levin NE, Cerling TE, Passey BH, Harris JM, Ehleringer JR (2006) A stable isotope aridity index for terrestrial environments. *Proc Natl Acad Sci USA* 103(30):11201–11205.
37. Munro ND, Bar-Oz G, Stutz AJ (2009) Aging mountain gazelle (Gazella gazella): Refining methods of tooth eruption and wear and bone fusion. *J Archaeol Sci* 36(3): 752–763.
38. Mendelssohn H, Yom-Tov Y, Groves CP (1995) Gazella gazella. *Mamm Species* 490: 1–7.
39. Castañeda IS, et al. (2010) Millennial-scale sea surface temperature changes in the eastern Mediterranean (Nile River Delta region) over the last 27,000 years. *Paleoceanography*, 10.1029/2009PA001740.
40. Danin A (2004) *Distribution Atlas of Plants in the Flora Palaestina Area* (Israel Academy of Science and Humanities, Jerusalem).
41. Angert A, Lee J-E, Yakir D (2008) Seasonal variations in the isotopic composition of near-surface water vapour in the eastern Mediterranean. *Tellus* 60B:674–684.
42. Affek HP, Bar-Matthews M, Ayalon A, Matthews A, Eiler JM (2008) Glacial/interglacial temperature variations in Soreq cave speleothems as recorded by 'clumped isotope' thermometry. *Geochim Cosmochim Acta* 72(22):5351–5360.
43. Brauer A, et al. (1999) High resolution sediment and vegetation responses to Younger Dryas climate change in varied lake sediments from Meerfelder Maar, Germany. *Quat Sci Rev* 18(3):321–329.
44. Hartman G, Hovers E, Hublin J-J, Richards M (2015) Isotopic evidence for Last Glacial climatic impacts on Neanderthal gazelle hunting territories at Amud Cave, Israel. *J Hum Evol* 84:71–82.
45. Munro ND, Bar-Oz G (2005) Gazelle bone fat processing in the Levantine Epipalaeolithic. *J Archaeol Sci* 32:223–239.
46. Dubreuil L (2004) Long-term trends in Natufian subsistence: A use-wear analysis of ground stone tools. *J Archaeol Sci* 31(11):1613–1629.
47. Wright KI (1994) Ground-stone tools and hunter-gatherer subsistence in Southwest Asia: Implications for the transition to farming. *Am Antiq* 59(2):238–263.
48. Tambussi EA, Bort J, Araus JL (2007) Water use efficiency in C_3 cereals under Mediterranean conditions: A review of physiological aspects. *Ann Appl Biol* 150(3): 307–321.
49. Nyachiro JM, Clarke FR, DePauw RM, Knox RE, Armstrong KC (2002) Temperature effects on seed germination and expression of seed dormancy in wheat. *Euphytica* 126(1):123–127.
50. Volis S, Mendlinger S, Ward D (2002) Differentiation in populations of *Hordeum spontaneum* along a gradient of environmental productivity and predictability: Life history and local adaptation. *Biol J Linn Soc Lond* 77:479–490.
51. Nadel D, Rosenberg D (2013) The final Epipaleolithic/PPNA site of Huzuq Musa. *Natufian Foragers in the Levant*, eds Bar-Yosef O, Valla FR (International Monographs in Prehistory, Ann Arbor, MI), pp 382–398.
52. Grosman L, et al. (2016) Nahal Ein Gev II, a Late Natufian community at the Sea of Galilee. *PLoS One* 11(1):e0146647.
53. Balasse M, Ambrose SH, Smith AB, Price TD (2002) The seasonal mobility model for prehistoric herders in the south-western Cape of South Africa assessed by isotopic analysis of sheep tooth enamel. *J Archaeol Sci* 29:917–932.