Younger Dryas – early Holocene transition in the south-eastern Iberian Peninsula: insights from land snail shell middens

YURENA YANES,1* MAGDALENA GÓMEZ-PUCHE,2,4 MARCO A. ESQUEMBRE-BEBIA and JAVIER FERNÁNDEZ-LÓPEZ-DE-PABLO4,5

1Department of Geology, University of Cincinnati, Cincinnati, OH 45221, USA
2Dept. de Prehistoria y Arqueología, Unitat d’Evolució i Paleopuntualitat, Universitat de València, València, Spain
3Arpa Patrimonio S.L., San Vicente del Raspeig, Alicante, Spain
4Institut Català de Paleoecologia Humana i Evolució Social, Tarragona, Spain
5Àrea de Prehistoria, Universitat Rovira i Virgili, Tarragona, Spain

ABSTRACT: The land snail Sphincterochila candidissima from archaeological records in Villena (SE Spain) was studied isotopically to estimate the Younger Dryas (YD)–early Holocene transition in the western Mediterranean. Live-collected individuals exhibited body (~21.8 ± 1.6‰) and shell (~5.8 ± 1.4‰) δ13C values typical of a C3 plant diet, probably combined with carbonate ingestion. Calculations of a carbon flux balance-mixing model suggest that living specimens experienced similar metabolic rates, with comparable ratio of input and output fluxes of bicarbonate from the snail hemolymph. All fossil shells showed comparable δ13C values among each other, but values were ~2‰ higher than living specimens. This may be explained by higher water stress at the YD–Holocene transition or by the Suess effect. YD shells δ18O values averaged +1.3 ± 0.8‰ for living individuals, ~0.5 ± 0.8‰ for Holocene (8.4–10.2 cal ka BP) specimens and +0.4 ± 0.6‰ for YD (12.0–12.4 cal ka BP) snails. An oxygen flux balance-mixing model suggests that YD shells precipitated during relative humidity (RH) values of ~79–82%, after which RH increased gradually reaching maximum values of ~87–88% at ~8.4–8.6 cal ka BP and, from there, RH eventually declined to present values of ~82%. Comparisons with other snail data suggest that the xerophilous Sphincterochila records different environmental signatures fro other contemporaneous taxa.

KEYWORDS: land snails; shell middens; stable isotopes; western Mediterranean; Younger Dryas.

Introduction

Some prehistoric human groups used to collect and consume edible (i.e. medium to large size: >10–15 mm in length) land snails as a complementary food resource. After consumption, snail shells were frequently discarded in well-filled shell middens (sites containing shells and other remains consumed or used by humans accumulated over time). In other cases, shells were discarded to combustion areas. Prehistoric accumulations of shells reflect past socio-economic activities and human-induced ecological and landscape modifications (Burney et al., 2001). Moreover, the isotopic composition of aragonitic land snail shells recovered from archaeological sites offers insights into past environmental conditions during ancient human occupation. The carbon isotopic composition (δ13C) of the shell is principally affected by the δ13C values of the oxidized vegetation consumed and assimilated by the snail (Stott, 2002; Metref et al., 2003). The oxygen isotopic composition (δ18O) of the shell is mainly influenced by four environmental variables: liquid water δ18O values, water vapor δ18O values, air temperature and relative humidity (Yapp, 1979; Balakrishnan and Yapp, 2004; Balakrishnan et al., 2005a, 2005b). Hence, the δ13C and δ18O values of archeological shells have been increasingly used as paleovegetation and paleoatmospheric proxies, respectively (Balakrishnan et al., 2005b; Colonese et al., 2007, 2010a, 2010b, 2011, 2013a, 2013b; Yanes et al., 2011, 2012, 2013). However, the relationship between the isotopic composition of the shell and the environment can be complicated by other less well-understood factors. For example, the δ13C values of the shell may in part be affected by the δ13C values of limestone on which snails live (Goodfriend and Hood, 1983; Goodfriend, 1987; Goodfriend et al., 1999), and further complications may arise if contemporaneous snails experience differing metabolic rates (Balakrishnan and Yapp, 2004). The δ18O values of the shell are influenced by multiple atmospheric factors operating jointly (Balakrishnan and Yapp, 2004). The δ18O values of the snail body fluid (and, in turn, the shell) are several per mil richer in 18O with respect to environmental water. Balakrishnan and Yapp (2004) explained mathematically this process by a steady-state flux balance model in which water from the snail body fluid is lost through evaporation only. The aforementioned complexities can be minimized by the study of local modern analogs of the same taxa. Thus, establishing local modern snail isotopic baselines are essential to better interpret the environmental significance of the stable isotopes extracted from ancient shells.

While the isotopic compositions of aquatic shells recovered from shell middens have been used intensively over decades to deduce past climatic conditions and the season of shellfish collection (see a recent review and publications by Andrus, 2011; Andrus and Thompson, 2012; Surge and Barrett, 2012; and numerous references therein), land snail shells have been relatively much less well studied. However, the recent growing body of isotopic studies on land snail shells preserved in archaeological sites suggests that they are promising paleoenvironmental archives that complement other marine and continental proxies (Balakrishnan et al., 2005b; Colonese et al., 2007, 2010a, 2010b, 2011, 2013a, 2013b; Yanes et al., 2011, 2012, 2013). Land snail shell middens are quite abundant in the Mediterranean region, both in southern Europe and in northern Africa (Lubell, 2004a, 2004b). In the Iberian Peninsula, the southernmost part of Europe, human-
induced land snail shelly accumulations are common (Gutiérrez-Zugasti, 2011; Fernández-López-de-Pablo et al., 2011a, 2011b; Lloveras et al., 2011). Quaternary shell middens are abundant in several sites of the upper Vinalopó Valley in Villena, Alicante (Fig. 1), in the south-east of Spain (Fernández-López-de-Pablo et al., 2011a, 2011b). These shells provide an excellent opportunity to explore Lateglacial–Holocene environmental shifts in the westernmost part of the Mediterranean using an alternative continental proxy not commonly exploited in the region. In the present study, live-collected specimens were analysed isotopically to establish the first modern isotopic baseline for the xerophilous snail Sphincterochila candidissima (Draparnaud, 1801). Secondly, the carbon and oxygen stable isotope compositions of ancient land snail shells and the sediment matrix where shells were preserved were analysed to elucidate the latest Pleistocene–early Holocene transition in south-eastern Spain. New radiocarbon analyses are also reported to better constrain the chronological context of these archaeological sites.

Materials and methods

Climate and vegetation

The Villena basin, Alicante (Fig. 1), exhibits a Mediterranean-type climate, with warm, dry summers and cool, wet winters (Fig. 2), but with continental influence. Local climatic data are available in Torre-García and Alías-Pérez (1996) and the meteorological station for Alicante for the recording period 1971–2000 (Agencia Estatal de Meteorología: www.aemet.es). Average air temperature ranges from 22.8 °C in July–August to 6.4 °C in January (Fig. 2A). The mean annual temperature is 14 °C. Temperature during spring and fall (March–May and September–November) is also 14 °C. Precipitation ranges from a minimum of 5.5 mm in July to a maximum of 55.8 mm in October (Fig. 2A). Total annual precipitation is 373 mm. During spring and fall only, precipitation is 232 mm, which reveals the current semi-arid nature of the study area. Average relative humidity (RH) is quite stable throughout the year in Alicante, ranging from 62% in April to 69% in October (Fig. 2B). Mean annual RH is 66%. This average value remains the same if only rainy months are considered. Maximum RH values were not available. Air moisture content is probably strongly influenced by the short distance to the Mediterranean Sea. The weighted annual mean oxygen isotopic composition of current precipitation in Alicante, SE Spain, is $-7.0‰$ vs. SMOW (Araguás-Araguás and Díaz-Teijeiro, 2005). If only fall and spring rain $\delta^{18}O$ values are considered, the average $\delta^{18}O$ value of rainfall in Alicante remains equivalent to the annual value.

The study area is characterized by an open-vegetation cover adapted to dry conditions dominated by vascular plants that follow a C₃ photosynthetic pathway. Native C₄ and CAM plants are not present in the sampling locality. The vegetation cover is dominated by pine tree forests of the species Pinus halapensis and P. pinea, and by shrubs and herbs of species such as Rosmarinus officinalis and Ulex parviflorus (Torre-García and Alías-Pérez, 1996).

Land snail species

Although many land snails are hygrophilous or favored under wetter conditions because they are highly sensitive to dehydration, some species are xerophilous, i.e. taxa well adapted to arid conditions through behavioral, physiological or morphological mechanisms (Moreno-Rueda, 2007). This is the case of Sphincterochila candidissima, which is abundant in arid environments of the western Mediterranean (Martínez-Ortí, 1999; Martínez-Ortí and Robles, 2003). The species exhibits a white and thick shell, which allows it to reduce water loss during estivation (Moreno-Rueda, 2008). Moreno-Rueda and Collantes-Martin (2007) observed that S.
includes two hearths and the filling sediment of a burial pit grave from the Casa Corona site (UE166, UE142 and UE128), and a hearth from the Arenal de la Virgen site (ARVIR-IV), about 6 km south from Casa Corona (Fig. 1A). The study area is located at 500 m above sea level (a.s.l.) on the upper course of the Vinalopó river (Fig. 1A). Shells were preserved together with lithic artifacts and bone remains. Archeological evidence suggests all these deposits are early Mesolithic in age, apart from the UE142 site, which yielded an Epipaleolithic radiocarbon age (Table 1). Land snails are associated with either habitation structures (Fig. 1B,C) or the filling sediments of a burial structure (UE128). Thousands of shells were found on each site and are presently deposited in the Institut Català de Paleoecologia Humana i Evolució Social (IPHES).

Thirty-two entire shells (eight from each archeological structure) were selected for stable isotope analyses. In addition, aliquots of the bulk sediment matrix in which shells were preserved were collected to evaluate the isotopic signature of surrounding carbonates. To establish the first isotopic baseline for S. candidissima, nine live specimens from the Arenal de la Virgen region were also collected for subsequent isotopic analyses of the shell and body tissue. The carbon isotope composition of the body tissue was measured as a second proxy for plant diet in addition to the shell. Although surrounding plants were not available for isotopic analyses, the body tissue is a reliable vegetation proxy because it is influenced by the carbon isotopes derived from assimilated plants only (DeNiro and Epstein, 1978) with no contribution from ingested limestone. Bootstrap simulations show that the isotopic measurement of five shells per locality is sufficient to estimate the central tendency and available isotopic variability of both isotopes ($\delta^{18}$O and $\delta^{13}$C). Hence, the measured number of shells per archeological structure ($n = 8$) and the modern sample ($n = 9$) should offer meaningful average values, regardless of isotopic variance.

The chronological context was determined by accelerator mass spectrometry radiocarbon dating of two charcoal samples recovered from ARVIR-IV (Fernández-López-de-Pablo et al., 2011a, 2011b) and UE166, and two land snail shells from UE142 and UE128 (Table 1). Samples were analysed in the Beta Analytic Radiocarbon Dating Laboratory using standard procedures. Due to the potential ingestion of limestone by Sphincterochila throughout its lifespan, the shell aperture was selected for radiocarbon dating because it is likely to have been less affected by carbonate ingestion (Goodfriend et al., 1999). To test this hypothesis, the shell aperture of a live-collected land snail from the region was also radiocarbon dated (Table 2). Radiocarbon results were calibrated using the CALIB 6.1 program and the IntCal09 isotopic baseline for additional radiocarbon dating.

Shell preservation
Before stable isotope analysis, three shells from ARVIR-IV were selected to evaluate their preservation status via X-ray diffraction. Analyses were made using a Bruker-AXS D8-Discover diffractometer equipped with parallel incident beam (Göbel mirror), vertical 0-0 goniometer, XYZ motorized stage and with a GADDS (General Area Diffraction System) in the IPHES. The X-ray diffraction results demonstrated that shells contained only aragonitic crystals and therefore recrystallization or secondary overgrowths are considered insignificant. The shell material studied here is thus suitable for geochemical analyses and paleoenvironmental reconstruction.
**Table 1.** Radiocarbon results of archeological sites from Villena, Alicante, SE Spain.

<table>
<thead>
<tr>
<th>Sample ID</th>
<th>Locality</th>
<th>Laboratory no.</th>
<th>Sample type</th>
<th>Species</th>
<th>δ¹³C (‰ PDB)</th>
<th>¹⁴C age (a BP)</th>
<th>Corrected age (a BP)</th>
<th>2σ calibrated age (cal a BP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ARVIR-IV</td>
<td>Arenal Virgen</td>
<td>Beta-243772</td>
<td>Charcoal</td>
<td>Quercus sp.</td>
<td>−25.8</td>
<td>7750 ± 40</td>
<td>8590–8430</td>
<td></td>
</tr>
<tr>
<td>UE166</td>
<td>Casa Corona</td>
<td>Beta-323497</td>
<td>Charcoal</td>
<td>Quercus sp.</td>
<td>−24.2</td>
<td>8520 ± 50</td>
<td>9550–9450</td>
<td></td>
</tr>
<tr>
<td>UE128</td>
<td>Casa Corona</td>
<td>Beta-330865</td>
<td>Land snail shell lip</td>
<td>Sphincterochila candidissima</td>
<td>−6.1</td>
<td>9110 ± 40</td>
<td>8900 ± 40</td>
<td>10 190–9900</td>
</tr>
<tr>
<td>UE142</td>
<td>Casa Corona</td>
<td>Beta-330866</td>
<td>Land snail shell lip</td>
<td>Sphincterochila candidissima</td>
<td>−5.5</td>
<td>10 520 ± 40</td>
<td>10 310 ± 40</td>
<td>12 380–11 980</td>
</tr>
</tbody>
</table>

*Data adapted from Fernández-López-de-Pablo et al. (2011a, 2011b). ¹⁴C ages from the shell lip were corrected by the expected age anomaly of 210 a associated with dead carbon ingestion during the oldest ontogenetic stage (Table 2 and text).

**Stable isotope analysis**

Samples were prepared and analysed in the Stable Isotope Laboratory of the Department of Earth and Environmental Sciences, University of Kentucky. The snail body was separated manually from the shell, rinsed with deionized water, oven-dried at 40°C overnight and homogenized using an electric blender. About 1.5 mg of each organic sample was weighed in a tin capsule, crimped and combusted in a Costech Elemental Analyzer (ESC 4010). The CO₂ and N₂ produced after combustion were analysed using a Finnigan Deltaþ XP isotope ratio mass spectrometer. Analytical uncertainty was ±0.1‰ based on the periodic measurements of in-house standards dispersed periodically throughout each run sequence (n = 10).

Adult shells were cleaned mechanically in distilled water with ultrasonication, and subsequently oven-dried at 40°C overnight. Entire shells were finely ground by hand using an agate mortar and pestle. Whole-shell analyses of numerous individuals per age interval were preferred over intra-shell analyses of a few specimens because the goal of this study was to estimate the average (dominant) environmental conditions rather than seasonal variations. The analysis of a reasonably high number of whole shells should portray a representative average environmental signature despite potential differences in seasonal behaviors among individuals. About 150 μg of carbonate was placed in a 6-mL Exetainer™ vial that was subsequently flushed with helium. The carbonate was converted to CO₂ gas by adding 0.1 mL of 100% H₃PO₄ at 25°C. The CO₂ was analysed after 24 h using the GasBench II connected to the isotope ratio mass spectrometer. Stable isotope results are reported in δ notation relative to the international standard Pee Dee Belemnite (PDB). The δ values are defined as:

\[ δ^{13}C = \left[ \frac{R_{sample}}{R_{standard}} - 1 \right] \times 1000 \text{‰} \]

where \( R = \frac{^{13}C}{^{12}C} \) or \( \frac{^{18}O}{^{16}O} \). Analytical uncertainty was ±0.1‰ based on the periodic measurements of in-house and international standards throughout each sequence (n = 18).

**Results**

**Radiocarbon results**

The shell aperture of a live-collected Sphincterochila specimen from Arenal de la Virgen exhibited a ¹⁴C age of 102 ± 0.30 (percentage modern carbon, pMC), which indicates that fossil specimens probably exhibit an age anomaly of about 210 a in the shell lip (Table 2). This result points to a minimal limestone ingestion by Sphincterochila at the oldest ontogenetic stage. Such age anomaly estimates were used to correct the ages obtained from archeological shells. Radiocarbon analyses of the shell aperture of two fossil Sphincterochila shells indicate an age of 12.0–12.4 cal ka BP for the UE142 site, coinciding with the Younger Dryas (YD) period of the northern hemisphere (e.g., Rasmussen et al., 2011), and an age of 9.9–10.2 cal ka BP for the UE128 site (Table 1). Two samples of charcoal of oak (Quercus sp.) from two hearths of Casa Corona (UE166) and Arenal de la Virgen (ARVIR-IV) exhibited an age of 9.5–9.6 and 8.4–8.6 cal ka BP, respectively (Table 1). It is assumed that these four radiocarbon ages (Table 1) represent the chronological context of all shells and sediments analysed isotopically in this work.

**Stable isotopes of land snail tissues**

Bulk body tissue samples of live-collected Sphincterochila shells from Villena, Alicante (SE Spain), ranged in δ¹³C values from −23.9 to −19.6‰ (Table 3; Fig. 3A), and averaged −21.8 ± 1.6‰ (n = 9). Shell δ¹³C values of living specimens ranged from −7.2 to −3.2‰ (Table 3; Fig. 3A), averaging −5.8 ± 1.4‰ (n = 9). The δ¹³C values of snail body and shell correlated positively (r = 0.80, P = 0.0089, n = 9; Fig. 3A).

The δ¹³C values of all fossil shells ranged from −5.0 to −1.6‰ (Table 4; Fig. 4A), averaging −3.5 ± 1.0‰ (n = 32). Shells recovered from each archeological site (UE142, UE128, UE166 and ARVIR-IV) showed respective average δ¹³C values of −3.1 ± 1.2‰ (n = 8), −2.7 ± 1.0‰ (n = 8), −4.2 ± 0.4‰ (n = 8), and −3.7 ± 0.9‰ (n = 8). Overall, YD–early Holocene (~8.4–12.5 cal ka BP) shells were, on

**Table 2.** Radiocarbon analysis of a live-collected Sphincterochila candidissima shell from the Arenal de la Virgen locality, Villena, Alicante.

<table>
<thead>
<tr>
<th>Sample ID</th>
<th>Locality</th>
<th>Collection year</th>
<th>Laboratory no.</th>
<th>Sample type</th>
<th>Species</th>
<th>δ¹³C (‰ PDB)</th>
<th>Shell ¹⁴C (pMC)</th>
<th>Contemporary ¹⁴C (pMC)</th>
<th>Age anomaly (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>AVIR-0</td>
<td>Arenal Virgen</td>
<td>2011</td>
<td>Beta-347475</td>
<td>Land snail shell lip</td>
<td>Sphincterochila candidissima</td>
<td>−5.1</td>
<td>102.4 ± 0.30</td>
<td>105</td>
<td>210</td>
</tr>
</tbody>
</table>

pMC, % modern carbon. Contemporary ¹⁴C value for comparison was taken from extrapolation of data in Levin and Hesshaimer (2000).
average, ~2.3% higher in $\delta^{13}C$ than living specimens (Fig. 4A).

The $\delta^{18}O$ values of modern snail shells ranged from +0.3 to +2.7% (Table 3; Fig. 4B), and averaged +1.3 ± 0.8% ($n = 9$). In contrast, fossil shells exhibited an average value of $-0.3 ± 0.9\%$ ($n = 32$), ranging from −2.8% to +1.1% (Table 4; Fig. 4B). Fossil shells were, on average, ~1.6% lower in $\delta^{18}O$ than live individuals (Fig. 4B). Shells recovered from each archeological site (UE142, UE128, UE166 and ARVIR-IV) displayed average $\delta^{18}O$ values of +0.4 ± 0.6% ($n = 8$), $-0.2 ± 0.6\%$ ($n = 8$), −0.6 ± 0.8% ($n = 8$) and −0.8 ± 1.0% ($n = 8$), respectively.

**Stable isotopes of bulk sediments**

Modern carbonates from sediments in the study area showed a $\delta^{13}C$ value of −4.5% (Table 5). Ancient carbonate-rich sediment samples in which shells were preserved showed an average $\delta^{13}C$ value of −5.5 ± 0.4% ($n = 4$), ranging from −6.0% in ARVIR-IV to −5.1% in UE166 (Table 5). The carbon isotopic signature of modern and ancient bulk sediments was significantly different from that of modern and fossil land snail shells (Fig. 5).

Bulk modern soil sediment showed a $\delta^{18}O$ value of −4.9% (Table 5). Bulk sediment samples from the YD site and various early Holocene sites exhibited an average $\delta^{18}O$ value of −6.1% ($n = 4$), ranging from −8.3% in UE166 to −5.2% in ARVIR-IV (Table 5). The oxygen isotopic composition of bulk sediment samples and measured *Sphincterochila* shells was notably different (Fig. 5).

**Discussion**

**Comparison among modern pulmonate land snail species**

Modern *S. candidissima* shells from Villena, Alicante (SE Spain), showed average carbon and oxygen isotope values of −5.8 ± 1.4 and −1.3 ± 0.8%, respectively. In contrast, published data of other modern land snail species from various localities in Spain show minimal isotopic differences among each other, but significantly different values from those obtained from living *Sphincterochila* shells here (Fig. 6). The herbivorous *Cernuella virgata* (Da Costa, 1778) from Granada and Jaén, southern Spain ($n = 32$), exhibit respective average $\delta^{13}C$ and $\delta^{18}O$ values of −9.3 ± 1.0% and −0.6 ± 0.9% (Yanes et al., 2011, 2013). The omnivorous *Rumina decollata* (Linnaeus, 1758) from Granada ($n = 4$) shows average values of −9.8 ± 0.5 and −1.5 ± 0.3%, respectively (Yanes et al., 2012). The herbivorous *Cepaea nemoralis* (Linnaeus, 1758) from Cantabria, northern Spain ($n = 12$), exhibits respective average values of −10.3 ± 1.1 and −1.1 ± 0.7% (Yanes et al., 2012). Thus, *Sphincterochila* shells are, on average, ~4% higher in $\delta^{13}C$ values and ~2% higher in $\delta^{18}O$ values than other species collected from modern ecosystems in southern and northern Spain (Fig. 6). Interestingly, carbon and oxygen isotope values of *Sphincterochila* correlate positively, whereas they do not correlate for the other species (Fig. 6). This distinctive isotopic signature of modern *Sphincterochila* may be explained by ethological and physiological mechanisms different from those shown by other taxa not as well adapted to dry conditions. As Moreno-Rueda (2007) observed in field surveys, *Sphincterochila* is adapted to arid to semi-arid conditions and may withstand

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**Table 3.** Carbon and oxygen stable isotope values of live-collected *Sphincterochila candidissima* specimens from Casa Corona, Villena, Alicante, SE Spain.

<table>
<thead>
<tr>
<th>Sample ID</th>
<th>Body tissue $\delta^{13}C$ (% PDB)</th>
<th>Shell $\delta^{13}C$ (% PDB)</th>
<th>Body tissue $\delta^{18}O$ (% PDB)</th>
<th>Shell $\delta^{18}O$ (% PDB)</th>
<th>$\Delta\delta^{13}C_{\text{shell-body}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>ARVIR-0-snail-1</td>
<td>−19.6</td>
<td>−3.5</td>
<td>1.9</td>
<td>16.1</td>
<td></td>
</tr>
<tr>
<td>ARVIR-0-snail-2</td>
<td>−23.9</td>
<td>−6.3</td>
<td>0.3</td>
<td>17.7</td>
<td></td>
</tr>
<tr>
<td>ARVIR-0-snail-3</td>
<td>−19.9</td>
<td>−3.2</td>
<td>2.7</td>
<td>16.7</td>
<td></td>
</tr>
<tr>
<td>ARVIR-0-snail-4</td>
<td>−20.5</td>
<td>−5.7</td>
<td>1.3</td>
<td>14.7</td>
<td></td>
</tr>
<tr>
<td>ARVIR-0-snail-5</td>
<td>−22.4</td>
<td>−5.8</td>
<td>2.2</td>
<td>16.6</td>
<td></td>
</tr>
<tr>
<td>ARVIR-0-snail-6</td>
<td>−21.4</td>
<td>−6.4</td>
<td>1.7</td>
<td>15.0</td>
<td></td>
</tr>
<tr>
<td>ARVIR-0-snail-7</td>
<td>−22.5</td>
<td>−7.2</td>
<td>0.4</td>
<td>15.2</td>
<td></td>
</tr>
<tr>
<td>ARVIR-0-snail-8</td>
<td>−23.7</td>
<td>−6.9</td>
<td>0.4</td>
<td>16.8</td>
<td></td>
</tr>
<tr>
<td>ARVIR-0-snail-9</td>
<td>−22.3</td>
<td>−6.7</td>
<td>1.1</td>
<td>15.6</td>
<td></td>
</tr>
</tbody>
</table>

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**Figure 3.** Carbon stable isotope values of live-collected land snails from Villena, Alicante, SE Spain. (A) Continuous line depicts the relationship between the $\delta^{13}C$ values of body and shell from cultured experiments by Stott (2002) with negligible limestone influence into the shell. Continuous line depicts the relationship between the $\delta^{13}C$ values of body and shell of live-collected *Sphincterochila candidissima* individuals. (B) Calculations of the carbon flux balance mixing model by Balakrishnan and Yapp (2004). Lines represent model calculations assuming a temperature of calcification of ~14°C and variable ratios of input and output fluxes of bicarbonate from the snail body fluid. Solid dots depict measured snails in the present study.
Dry episodes better than other sympatric species. *Sphincterochila* seems to be capable of a retarded rate of water loss through evaporation from the body fluid (Moreno-Rueda, 2007 and references therein). This physiological mechanism may result in snail body fluids (and shells) with significantly higher $\delta^{18}O$ values than those from other species. As water is lost by evaporation from snail body fluids, the light isotopes would evaporate preferentially, whereas the heavy isotopes would remain in the body fluid, resulting ultimately in $^{18}$O-enriched shells. Also, *Sphincterochila* is capable of being active at warmer/drier times and may feed upon plants at times of higher water stress than other contemporaneous snails. Moreover, *Sphincterochila* shells are relatively thick and large, which suggests that this species may require higher carbonate intake to promote shell growth than other species with thinner and smaller shells such as *Cernuella* and *Rumina*. This could also explain the observed higher $\delta^{13}C$ values of modern *Sphincterochila* shells. While some previous studies have suggested that multiple land snail species often show similar isotopic values (e.g. Yanes et al., 2009), the results here suggest that the carbon and oxygen isotopic signature of *Sphincterochila* shells is not directly comparable with other contemporaneous snail taxa (see also Goodfriend and Magaritz, 1987).

**Paleovegetation estimates**

The $\delta^{13}C$ values of the shell and the body tissue correlated significantly, which indicates that both proxies record similar environmental information (Fig. 3A, B). Assuming that snail body is $\sim$1% higher than plant diet (DeNiro and Epstein, 1978), living specimens in the study area should have consumed plant matter with an average $\delta^{13}C$ value of $-22.9\%$. This value overlaps with the natural range of $\delta^{13}C$ values for C$_3$ plants. However, the relatively high $\delta^{13}C$ values observed in snail body tissues suggest that consumed C$_3$ plants were $13C$-enriched possibly due to greater water stress (Dawson et al., 2002). This seems reasonable considering that the study site is semi-arid and local plants and animals may experience water deficiency. The regression line computed for the $\delta^{13}C$ values of *Sphincterochila* shell and body tissue shows a slope of 0.7 (Fig. 3A), which differs from the slope of 1 observed in cultured snails by Stott (2002). This is possibly explained by the effect of limestone ingestion into the shell $\delta^{13}C$ values. The $\delta^{13}C$ values of the shell are, on average, 16% higher than the body tissue (Table 3). This large $\delta^{13}C$ offset between shell and body may be explained by limestone ingestion (Yanes et al., 2008).

The carbon snail flux balance-mixing model proposed by Balakrishnan and Yapp (2004) can be used to evaluate potential variations in metabolic rates among contemporaneous specimens and also estimate potential effects from carbonate ingestion. Model calculations were carried out assuming that temperature of calcification was $\sim14\,^\circ C$, on average. Other choices of temperature did not change model assumptions from the snail body fluid was the same among measured individuals. Thus, live-collected snails experienced comparable metabolic rates. Specimens that plotted directly on the line for $\Phi=0.00$ or to the left possibly reflect that some

<table>
<thead>
<tr>
<th>Sample ID</th>
<th>Sample type</th>
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<th>Age (2σ cal a BP)</th>
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<th>$\delta^{13}C$ (‰ PDB)</th>
</tr>
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</tr>
<tr>
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<td>Shell</td>
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<td>12 380–11 980</td>
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</tr>
<tr>
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<td>Shell</td>
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<td>-3.8</td>
</tr>
<tr>
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<td>Shell</td>
<td>Casa Corona</td>
<td>12 380–11 980</td>
<td>0.1</td>
<td>-3.4</td>
</tr>
<tr>
<td>UE 142-6</td>
<td>Shell</td>
<td>Casa Corona</td>
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</tr>
<tr>
<td>UE 142-7</td>
<td>Shell</td>
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<td>-4.9</td>
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<tr>
<td>UE 142-8</td>
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<td>-4.0</td>
</tr>
<tr>
<td>UE 128-1</td>
<td>Shell</td>
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<td>-4.1</td>
</tr>
<tr>
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</tr>
<tr>
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</tr>
<tr>
<td>UE 128-4</td>
<td>Shell</td>
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<tr>
<td>UE 128-5</td>
<td>Shell</td>
<td>Casa Corona</td>
<td>10 190–9 990</td>
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<tr>
<td>UE 128-6</td>
<td>Shell</td>
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<tr>
<td>UE 128-7</td>
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<tr>
<td>UE 128-8</td>
<td>Shell</td>
<td>Casa Corona</td>
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<tr>
<td>UE 166-1</td>
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<td>Casa Corona</td>
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<tr>
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</tr>
<tr>
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<td>Shell</td>
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<td>-4.5</td>
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<tr>
<td>UE 166-5</td>
<td>Shell</td>
<td>Casa Corona</td>
<td>9 550–9 450</td>
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<td>-4.6</td>
</tr>
<tr>
<td>UE 166-6</td>
<td>Shell</td>
<td>Casa Corona</td>
<td>9 550–9 450</td>
<td>0.0</td>
<td>-3.9</td>
</tr>
<tr>
<td>UE 166-7</td>
<td>Shell</td>
<td>Casa Corona</td>
<td>9 550–9 450</td>
<td>-0.9</td>
<td>-4.8</td>
</tr>
<tr>
<td>UE 166-8</td>
<td>Shell</td>
<td>Casa Corona</td>
<td>9 550–9 450</td>
<td>-0.9</td>
<td>-4.2</td>
</tr>
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<td>-3.7</td>
</tr>
<tr>
<td>ARVIR-IV-2</td>
<td>Shell</td>
<td>Arenal Virgen</td>
<td>8 590–8 430</td>
<td>-0.8</td>
<td>-4.1</td>
</tr>
<tr>
<td>ARVIR-IV-3</td>
<td>Shell</td>
<td>Arenal Virgen</td>
<td>8 590–8 430</td>
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<td>-3.1</td>
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<tr>
<td>ARVIR-IV-4</td>
<td>Shell</td>
<td>Arenal Virgen</td>
<td>8 590–8 430</td>
<td>-0.5</td>
<td>-5.0</td>
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<tr>
<td>ARVIR-IV-5</td>
<td>Shell</td>
<td>Arenal Virgen</td>
<td>8 590–8 430</td>
<td>-0.4</td>
<td>-2.2</td>
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<tr>
<td>ARVIR-IV-6</td>
<td>Shell</td>
<td>Arenal Virgen</td>
<td>8 590–8 430</td>
<td>-1.8</td>
<td>-4.6</td>
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<td>ARVIR-IV-7</td>
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<td>ARVIR-IV-8</td>
<td>Shell</td>
<td>Arenal Virgen</td>
<td>8 590–8 430</td>
<td>-2.8</td>
<td>-4.2</td>
</tr>
</tbody>
</table>
individuals ingested other carbon sources besides C3 plants, such as limestone (Balakrishnan and Yapp, 2004).

The δ13C values of modern and fossil sediments, which range from −8.3 to −4.9‰ (Table 4), reflect the influence of continental rather than marine carbon sources into the bulk carbonate-rich sediment matrix analysed. The δ13C values of fossil snail shells are significantly higher than those from the sediment matrix (Fig. 5). This suggests that fossil shells are reasonably free of sediments and exhibit distinctive isotopic populations. While YD shells showed similar δ13C values to early Holocene shells, all fossil shells were significantly higher in δ13C (−3.5 ± 1.0‰; n = 32) than living individuals (−5.8 ± 1.4‰; n = 9) (Fig. 4). This pattern may be explained by several compelling hypotheses. (1) C3 plants ingested by snails may have experienced stronger water-stress conditions in the transition from the YD to the early Holocene than today. Drought conditions induce plants to persist for longer with closed stomata to prevent water loss. This physiological mechanism causes 13C-enriched tissues in C3 plants (Dawson et al., 2002), which in turn will be recorded in the snail shell. (2) Modern shell δ13C values may be affected by the Suess effect, i.e. isotopic depletion of surface carbon reservoirs due to the burning of fossil fuels, and therefore they are anomalously lower in δ13C values by about 1.6‰ (Marino and McElroy, 1991). If modern snails are corrected for the Suess effect, then fossil and modern snails show comparable shell δ13C values. (3) Specimens during the YD and the early Holocene ingested more limestone or carbonates with higher δ13C values than at present. (4) Fossil snails consumed some C4 or CAM plants, whereas today snails consume C3 plants exclusively. This last hypothesis is not convincing because pollen studies indicate that native C4 and CAM plants have not been present in the study area throughout the late Quaternary (Carrión et al., 2001, 2010). The snail δ13C results presented here can be explained more simply by higher water-stress among C3 plants in the YD–Holocene transition, and/or by the effects of the Suess effect upon modern plants and snails. A pending challenge in snail research investigations is to quantify if and how carbonates ingested by the snail affect the δ13C values of the shell. Also, to the best of our knowledge, the potential relationship between shell size and thickness and the proportion of carbonate ingested has not been assessed.

**Paleoatmospheric estimates**

The δ18O of land snail shells showed an average value of +0.4 ± 0.6‰ during 12.0–12.4 cal ka BP. This then declined gradually to the lowest average value of −0.8 ± 1.0‰ at 8.4–8.6 cal ka BP. Consecutively, shell δ18O values may have fluctuated but ultimately increased to the modern average value of +1.3 ± 0.8‰. This fluctuation in shell δ18O values of over ~2‰ suggests that atmospheric conditions during the Lateglacial–Holocene transition in SE Spain were different from today. The snail evaporative steady-state flux balance model of Balakrishnan and Yapp (2004) is combined with published proxy data to quantitatively evaluate the environmental significance of these temporal fluctuations in shell δ18O values (Fig. 7A). Balakrishnan and Yapp (2004) observed that it is reasonable to assume that liquid water ingested by the snail and water vapor are in isotopic equilibrium. They also showed that it is useful to assume that water loss from snail body fluid occurred exclusively by evaporation. Both assumptions are adopted in the present study for model calculations. This model suggests that the most important environmental controls upon shell δ18O values are the δ18O values of the rain and the water vapor,

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**Table 5.** Carbon and oxygen stable isotope values of bulk sediment samples in which fossil shells were immersed. Modern surrounding bulk sediments were also analysed for comparison.

<table>
<thead>
<tr>
<th>Sample ID</th>
<th>Sample type</th>
<th>Locality</th>
<th>Age (cal a BP)*</th>
<th>δ13C (%) PDB</th>
<th>δ18O (%) PDB</th>
</tr>
</thead>
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<td>Sediment</td>
<td>Casa Corona</td>
<td>12 380–11 980</td>
<td>−5.4</td>
<td>−5.5</td>
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<tr>
<td>UE128-sed</td>
<td>Sediment</td>
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<td>10 190–9900</td>
<td>−5.4</td>
<td>−5.6</td>
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<td>UE166-sed</td>
<td>Sediment</td>
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<td>9550–9450</td>
<td>−5.1</td>
<td>−8.3</td>
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<td>ARVIR-IV-sed</td>
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<td>Arenal Virgen</td>
<td>8590–8430</td>
<td>−6.0</td>
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</tr>
<tr>
<td>ARVIR-mod-sed</td>
<td>Sediment</td>
<td>Casa Corona</td>
<td>Modern</td>
<td>−4.5</td>
<td>−4.9</td>
</tr>
</tbody>
</table>

*It is assumed that sediments have similar age to shells and charcoal samples used for radiocarbon dating.
the ambient temperature and RH as a decimal fraction (see Balakrishnan and Yapp, 2004 for further details).

Live-collected land snails deposit shell material under current environmental conditions, i.e. air temperatures of ∼14°C and rain δ18O values of −7.0‰ (SMOW) (Araguás-Araguás and Díaz-Teijeiro, 2005). Outputs of the model by Balakrishnan and Yapp (2004), constrained with observed environmental data, suggest that living specimens, with a measured average shell δ18O value of −1.3‰, can only be explained if calcification occurred at RH values of ∼82%, on average (Fig. 8A). This predicted RH value by the model is 16% higher than the observed average annual value for the study area. However, considering that snails can only be active at RH values above 70–75%, and that they tend to be active during the wettest times, principally at night, a predicted value of 82% seems reasonable. Even though the study area is considered semi-arid today (<380mm of annual precipitation), RH values can be high due to the close proximity to the Mediterranean Sea, especially at the soil–air interface, at night and during the rainy season, when snails are more active and grow shell material. Consequently, this model seems useful for the target species and the study area and can be used to infer credible paleoclimatic scenarios in the western Mediterranean.

To infer possible paleoclimatic scenarios in the western Mediterranean, calculations of the snail model should first be constrained by independent proxy data. It is broadly accepted that the environmental variable that most affects the δ18O values of precipitation is the air temperature at mid-to-high latitudes (Dansgaard, 1964). Spatial studies on present precipitation illustrate that temperature is the main environmental factor controlling seasonal variations in rain δ18O values at localities with a Mediterranean-type climate of the northern hemisphere (Bowen, 2008). Recent studies, however, suggest that other atmospheric variables (e.g. vapor condensation height, raindrop re-evaporation and storms trajectories) could also influence the δ18O values of the precipitation at mid-latitudes, especially at sub-hourly, weekly, seasonal and inter-annual scales (Buennning et al., 2013). However, air temperature is probably the main environmental variable that affects the δ18O values of the precipitation at the multi-millennial scale in mid latitudes. This assumption is adopted in the present study.

The δ18O values of the precipitation in the Greenland Ice Core (GRIP) were several per mil lower during the latest glacial than during the Holocene (Fig. 7B) as a response of lower temperatures (Dansgaard et al., 1989, 1993; GRIP Members, 1993; Grootes et al., 1993; Johnsen et al., 1997). Several published marine and continental proxies repeatedly suggest that at mid-to-high latitudes of the northern hemisphere, precipitation was several per mil lower in δ18O than at present, linked to lower air temperatures (e.g. Verbruggen et al., 2010; Rasmussen et al., 2011). In contrast, during the early Holocene, δ18O values of the precipitation in the northern hemisphere were largely comparable to present values associated with subdued variations of temperature throughout the Holocene.

Alkenone proxies of marine deep sea cores in the western Mediterranean (Fig. 7C) reveal that the sea surface temperature was ∼6°C lower during 12.0–12.4 cal ka BP than today, whereas during the early Holocene temperatures were comparable to present values (Martrat et al., 2004, 2007).

Rain δ18O values decrease ∼0.58‰ every ∼1°C of temperature decrease (Rozanski et al., 1993). If around 12.0–12.4 cal ka BP air temperatures were ∼6°C lower than today in the study area, as suggested by alkenone proxies in the western Mediterranean (Cacho et al., 2001; Martrat et al., 2004, 2007; Moreno et al., 2005), then rain δ18O values possibly showed an average value of ∼−10.5‰ (SMOW). During the early Holocene (∼8.4–10.2 cal ka BP), rain δ18O values were probably similar to present-day values, considering that temperature (as inferred from alkenone proxies) has been comparable as well (Cacho et al., 2001; Martrat et al., 2004, 2007; Moreno et al., 2005).

Calculations of the model of Balakrishnan and Yapp (2004) constrained with the aforementioned paleoenvironmental data from published proxies (Fig. 7) suggest that shells during the YD, with a measured shell δ18O value of +0.4‰, possibly deposited carbonate when temperatures were ∼8°C (i.e. ∼6°C lower than today, as suggested by the alkenone proxy by Martrat et al., 2004, 2007), average rain δ18O values were ∼−10.5‰ (SMOW) (assuming a temperature effect of
~0.58‰/1 °C; Rozanski et al., 1993) and RH values of ~0.79 (Fig. 8B). From there, shell δ¹⁸O values declined gradually to a minimum of ~0.8% at 8.4–8.6 cal ka BP, as a response to a progressive increase in temperature from ~8 to ~14 °C (Fig. 7C), an increase in rain δ¹⁸O values from ~−10.5% (SMOW) to ~−7.0% (SMOW), and an increase in RH from ~0.79 to ~0.87 (Fig. 8B). Finally, shell δ¹⁸O values may have shifted throughout the Holocene but finally increased to present values of ~+1.3‰ (Fig. 7A). Modern shells precipitated at temperatures of ~14 °C, rain δ¹⁸O values of ~−7.0‰ (SMOW) and RH values of ~0.82, on average (Fig. 8A, B). In general, snail data, in the context of this model, suggest that calcification occurred at drier conditions during the YD, at wetter times during the early Holocene, and ultimately returned to drier conditions at present, but not as dry as during the YD (see arrows in Fig. 8B).

An alternative plausible paleoenvironmental scenario may be inferred if we consider that seawater δ¹⁸O values may have influenced rain δ¹⁸O values at the Lateglacial–Holocene transition in the study locality (Fig. 8C). Seawater displayed higher δ¹⁸O values during the latest glacial (Fig. 7D), as reflected in the benthic foraminifera data from deep sea cores in the western Mediterranean (Martrat et al., 2004, 2007). Seawater was ~1‰ higher in δ¹⁸O during 12.0–12.4 cal ka BP than today, whereas no significant differences can be deduced between the early Holocene and the present

(Fig. 7D). If higher seawater δ¹⁸O values during the latest glacial influenced the rain δ¹⁸O values, then around the YD, rain δ¹⁸O values could have been ~−9.5‰ (SMOW), on average, whereas early Holocene rain plausibly showed comparable δ¹⁸O values to today (Fig. 7D). In this alternative paleoenvironmental scenario, the following pattern is inferred (Fig. 8C). On average, YD snails deposited shell material at temperatures of ~8 °C, rain δ¹⁸O values of ~−9.5‰ (SMOW) and RH values of ~0.82. Thereafter, RH increased to maximum values of ~0.87 at 8.4–8.6 cal ka BP and consecutively declined to present values of ~0.82 (Fig. 8C). This second scenario suggests that conditions in the western Mediterranean were noticeably drier during the YD, became wetter around the early Holocene, and eventually returned to the current drier setting (see arrows in Fig. 8C). In this case, snails suggest that the YD was as dry as today.

Both possible paleoatmospheric scenarios proposed here (Fig. 8B, C) point to overall drier conditions during the latest glacial and wetter conditions during the early Holocene. The documented lower RH values here during the YD in the western Mediterranean could be explained by a decrease in net precipitation, as observed in published records from northern Africa and Europe (see recent review by Carlson, 2013). This paleoenvironmental scenario inferred from land snails agrees with published paleoclimatic studies from mid to high latitudes of the northern hemisphere that have used
Figure 8. Calculations of the snail evaporative steady-state flux balance mixing model by Balakrishnan and Yapp (2004). (A) Oxygen stable isotope values of live-collected specimens as a function of relative humidity, assuming that calcification occurred at average temperatures of 14°C and rain water values of −7‰ (SMOW). (B, C) Plausible paleoatmospheric conditions in SE Spain during the YD–early Holocene. Arrows depict hypothetical trajectories of shell δ¹⁸O values as a function of relative humidity, constrained by published proxy data (see text for explanation).

Conclusions

The xerophilous land snail Sphincterochila candidissima records valuable local and regional environmental aspects in the isotopic composition of its shell. Due to its affinity for and tolerance to dry conditions, Sphincterochila shells exhibit a significantly higher carbon and oxygen isotopic fingerprint than other contemporaneous snail species. This is probably associated with differing ethological and physiological mechanisms: (1) Sphincterochila is capable of being active at warmer and/or drier times of the day than other snail taxa from the same habitat; and (2) Sphincterochila follows different physiological mechanisms to fight aridity than other contemporaneous snails. While some published studies suggest that multi-taxa snail proxies are reliable because no significant isotopic differences among species are observed, this study shows that Sphincterochila is not directly comparable isotopically to other sympatric species. The δ¹³C values of all fossil shells were ~2‰ richer in ¹³C than live-collected shells. This suggests that during the YD–early Holocene, the δ¹³C values of consumed plants were significantly higher than at present because of higher water stress. Alternatively, modern snail shells are anomalously lower in δ¹³C values than fossils due to the Suess effect. The δ¹⁸O values of measured northern European land snails from the Last Glacial Maximum show higher shell δ¹⁸O values than at present (Kehrwald et al., 2010). During glacial conditions, lower temperatures favor longer snail hibernation periods and therefore snails are more active during warmer seasons. Thus, Kehrwald et al. (2010) proposed that ¹⁸O-enriched summer rains might explain the higher shell δ¹⁸O values observed among glacial shells. In Alicante, SE Spain (38°N), Lateglacial temperatures are estimated to have been ~8°C (Cacho et al., 2001; Martrat et al., 2004, 2007; Moreno et al., 2005). Thus, snails possibly did not have to hibernate as long as northern European snails. Although higher rain δ¹⁸O values of summer seasons may have affected the snail data here, we propose that variations in RH also played an important role in shell δ¹⁸O values of snails.

Early Holocene snail records from Granada, southern Spain (Yanes et al., 2011), and eastern pre-Pyrenees, north-east Spain (Colonese et al., 2013a), also suggest prevailing wetter conditions than at present, with Holocene snails from the eastern Iberian Peninsula overall recording comparable regional moisture regimes. Sphincterochila shells appear to record convincingly well local and regional environmental conditions in the oxygen isotope composition of the shell. However, considering its distinctive ecological behavior and isotopic signature, Sphincterochila shells should not be mixed with other snail species in paleoenvironmental studies. Thus, fossil Sphincterochila shells should only be compared with modern shells of the same species.

The results presented here also have important implications for archeologists. Ancient human groups that inhabited the south-eastern Iberian Peninsula throughout the late Quaternary have experienced significantly different moisture regimes. The inferred changing environment from snail shells probably influenced the degree of water availability, and the presence and abundance of different plants and animals. The archeological record of the Villena basin shows that Epipaleolithic and Mesolithic human communities were resilient to these environmental changes, for example by broadening their diets with the incorporation of alternative food resources such as land snails.
Younger Dryas et al. Balakrishnan M, Yapp CJ, Theler JL, PDB, Pee Dee Belemnite; RH, relative humidity; YD, greatly appreciated.

Associate Editor Antony Long and two anonymous reviewers are University of Kentucky. Detailed and insightful comments by the analyse all samples from this study in the stable isotope facility of the this work. Additional thanks go to Chris Romanek who allowed us to analyse all samples from this study in the stable isotope facility of the University of Kentucky. Detailed and insightful comments by the Associate Editor Antony Long and two anonymous reviewers are greatly appreciated.

Abbreviations. PDB, Pee Dee Belemmitte; RH, relative humidity; YD, Younger Dryas

References


