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Oxygen isotopes of land snail shells in high latitude regions

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ABSTRACT

The present study investigates the environmental significance of the oxygen isotopic composition of several modern land snail species collected along two north-to-south transects in Alaska and Scandinavia at latitudes between 60 and 70 °N. We tested the hypothesis that land snail shell $\delta^{18}O$ values primarily track precipitation $\delta^{18}O$. The results show that shell $\delta^{18}O$ values from Scandinavia were ~5.1‰ enriched in ^{18}O with respect to snails from Alaska, equivalent to differences in precipitation $\delta^{18}O$ values between the two regions. Within the Alaskan transect, shell $\delta^{18}O$ values increased with observed increasing air temperature and precipitation $\delta^{18}O$, whereas shell $\delta^{18}O$ values from Scandinavia did not correlate to instrumental climate data because of a reduced climatic gradient across the locations sampled. In addition, shell $\delta^{18}O$ values differed significantly among sympatric species, with larger species consistently exhibiting higher $\delta^{18}O$ values, which implies that species-level isotopic variations should be considered at the local and microhabitat scale. However, when snail shell $\delta^{18}O$ values from this study are combined with previously published data from North America and Europe, we see evidence that shell $\delta^{18}O$ values track precipitation $\delta^{18}O$ across latitudes, even when different species are combined because climate gradients are greater than variations among taxa.

1. Introduction

High-latitude regions (>60°) are arguably at the highest risk of climate change because of fast-rising temperatures and accelerated melting of ice. For example, Alaska specifically has warmed twice as rapidly as the rest of the continental United States over the past 60 years (Stewart et al., 2013). Moreover, polar regions harbor vast groups of plants and animals well adapted to cold environments that are likely to struggle in future warmer scenarios (Clark et al., 2010). To better understand the tempo and mode of climate change and its effect on the biosphere, it is essential to consider a geohistorical perspective that captures the entire range of climate variability and better identifies the long-term response of living things to climate change. Accordingly, generating new data on climate change over multimillennial time scales is an urgent task that scientists need to develop, especially for highly climate-sensitive areas like polar regions.

Paleoclimate in polar regions has been heavily investigated by ice core drilling projects (e.g., Hurrell, 1995; Steig et al., 1994; Yiou et al., 1997) and a few studies on tree rings (e.g., Overpeck et al., 1997; D'Arrigo et al., 2005; Grudd, 2008) and terrestrial and marine sediment cores (e.g., Fronval and Jansen, 1997; Overpeck et al., 1997; Thomas et al., 2012). Although these proxies are informative, they exhibit limitations with respect to the climate parameter inferred, time resolution, and geographical distribution. Thus, the development, calibration, and application of novel proxies can offer new and complementary environmental information that can augment our knowledge and predictions of climate change in polar regions and provide additional empirical data to test and validate climate models.

Land snails are invertebrate animals that have been incredibly successful in an evolutionary sense, as they have colonized almost all environments within the continental realm, apart from hyper-

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arid deserts and Antarctica (Yanes et al., 2019). Land snails grow a calcium carbonate shell that is often durable in the recent (Quaternary) geologic record (Rech et al., 2011), and as ectothermic organisms with low migratory ability, they are highly sensitive to variations in the local environment and climate change (Yanes et al., 2019). Therefore, snails have the potential to be a useful paleoclimate proxy because the oxygen isotope values of their shells appear to track the conditions of the environment in which snails grew (Balakrishnan and Yapp, 2004).

Since the seminal work of Yapp (1979) a large number of studies (>60) have been published on the calibration and application of the oxygen isotopes of land snails to infer environmental conditions. However, the application of land snail oxygen isotopes as a paleoclimate proxy has remained challenging due to multiple environmental variables that seem to influence the shell $\delta^{18}O$ values. The oxygen isotope composition ($\delta^{18}O$) of the shell has been shown to capture different aspects of the environment, including precipitation $\delta^{18}O$, water vapor $\delta^{18}O$, air temperature, and relative humidity (Balakrishnan and Yapp, 2004). However, the contribution of each variable into the shell $\delta^{18}O$ remains difficult to quantify and is expected to vary across species and locales. Moreover, whether different sympatric land snail species record environmental conditions in an equal matter is unclear. Some of these uncertainties may be improved by collecting new isotope data from modern land snails of different species and diverse geographic areas. In the most recent review on the topic, Yanes et al. (2019) identified a lack of empirical data from equatorial and high latitudes, which limits our ability to use and apply this proxy at extreme environments. The present work aims to fill this geographical gap by measuring the oxygen isotope composition of several land snail species living in high latitude regions of Alaska and Scandinavia and identifying the main environmental drivers of the resulting isotopic patterns. Specifically, we tested the hypothesis that, similar to what has been observed at middle latitudes, high-latitude snail shell $\delta^{18}O$ values primarily reflect precipitation $\delta^{18}O$ during the growing period (active period) of land snails. Our results also provide comprehensive modern oxygen isotopic baseline data for land snails living in these under-investigated cold regions, which is necessary before fossil land snails preserved in permafrost soils and loess deposits can be utilized for Quaternary paleoclimate reconstruction.

2. Background

Most terrestrial mollusks (except slugs) secrete a shell composed of a single layer of aragonite, $CaCO_3$ (Balakrishnan and Yapp, 2004). Some species, however, exhibit multiple layers of aragonite (Pavat et al., 2012). Aragonite shells of land snails are durable in most depositional environments, and accordingly, they are often present in Quaternary sedimentary sequences. When shell aragonite is present in its original form, the oxygen isotopic composition can be used to study the environmental conditions during shell diagenesis (Sharp, 2015). However, aragonite is easily altered to form the more stable calcium carbonate polymorph of calcite, which is commonly observed in shells preserved in older rocks. Isotopic measurement of shells containing calcite are difficult to interpret and are usually avoided in paleoenvironmental studies.

Oxygen isotope composition ($\delta^{18}O$) values of land snail shell aragonite have been used to reconstruct paleo-precipitation $\delta^{18}O$ of times when snails are actively growing their shells (Lécolle, 1985). Because land snails are mainly active during and after rain events (Ward and Slotow, 1992), the majority of the water imbibed by snails is considered to be from rainwater (Riddle, 1983). Hence, much of the oxygen isotopes present in the snail body fluid and the shell primarily derives from oxygen isotopes of local precipitation. While other sources of oxygen isotopes, like from the snail diet, may also contribute to the snail body fluid and shell oxygen isotope content, these sources are likely minimal compared to that obtained from precipitation (Riddle, 1983). Land snail body fluid and their shells are typically enriched in ^{18}O by several per mil relative to that of the precipitation $\delta^{18}O$ (Lécolle, 1985; Goodfriend, 1992), most likely caused by water loss from the snail body fluid through evaporation during snail activity (Balakrishnan and Yapp, 2004). Because precipitation $\delta^{18}O$ primarily varies as a function of air temperature (Dansgaard, 1964; Rozanski et al., 1993), snail shell $\delta^{18}O$ should reflect precipitation $\delta^{18}O$ values as well as air temperature.

A theoretical mathematical model validated with empirical data suggests that atmospheric variables such as relative humidity (RH) and $\delta^{18}O$ of ambient water vapor may also contribute to the snail oxygen isotope budget, in addition to precipitation $\delta^{18}O$ and air temperature (Balakrishnan and Yapp, 2004). Moreover, species ecology and behavior can also affect the snail shell $\delta^{18}O$ values (Yanes et al., 2017). For example, Yanes et al. (2017) documented that among small size land snail taxa (<10 mm in maximum shell dimension) from North America, larger size species exhibited consistently higher $\delta^{18}O$ values than coexisting minute taxa. This isotopic offset has also been documented in the fossil record (Rech et al., 2021).

When interpreting isotopic values derived from land snails living in polar regions it is imperative to understand what part(s) of the year is represented in the shell material. Previous research has suggested land snails are active and grow their shells above 10 °C (Cowie, 1984; Thompson and Cheney, 1996). However, no studies on land snail active periods in cold climates have been conducted and some studies have suggested that snails exhibit a supercooling ability that allows them to survive and be somewhat active during freezing temperatures (Ansart et al., 2001). Due to the uncertainty in the exact number of months when snails are active in the Arctic, we compared snail shell $\delta^{18}O$ values to climate parameters from three hypothetical snail active periods: (1) annual (all 12 months), (2) summer (June to August), and (3) an extended growing season (April to October). By comparing land snail shell $\delta^{18}O$ values to these three potential active periods (even though temperatures are below 10 °C in some scenarios), we expect to gain a better sense of how land snail shells in the arctic track climate.

3. Geographical and environmental setting

3.1. Alaska

Modern land snail samples were collected from 54 locations along a ~1000 km north-to-south transect through Alaska, ranging from Anchorage in the south to near Prudhoe Bay in the north (Fig. 1A). The transect encompasses four major climate zones including maritime, transitional, continental boreal, and arctic zones (Ager, 2007). Matrix vegetation varies from coastal rainforest in the south through taiga and tundra in the north. Along this transect, mean annual temperatures range from −11 to 4 °C, with values of 0–10 °C during the extended growing season, and 11–15 °C during the summer (www.usclimatedata.org; accessed August 2020). Average annual precipitation ranges from 11 to 38 mm, with 15–45 mm during the extended growing season, and 20–63 mm during the summer (www.usclimatedata.org; accessed August 2020). Average RH values range from 63 to 69% annually, 59–67% during the extended growing season, and 59–68% during the summer (www.ncdc.noaa.gov; accessed August 2020). Finally, average precipitation $\delta^{18}O$ values range from −22.6 to −18.0‰ annually, −18.9 to −14.9‰ during the extended growing season, and −16.0 to −12.6‰ during the summer (Bowen, 2020). Precipitation $\delta^{18}O$ values are modeled results from (IAE/WMO, 2015) by (Bowen et al., 2005).

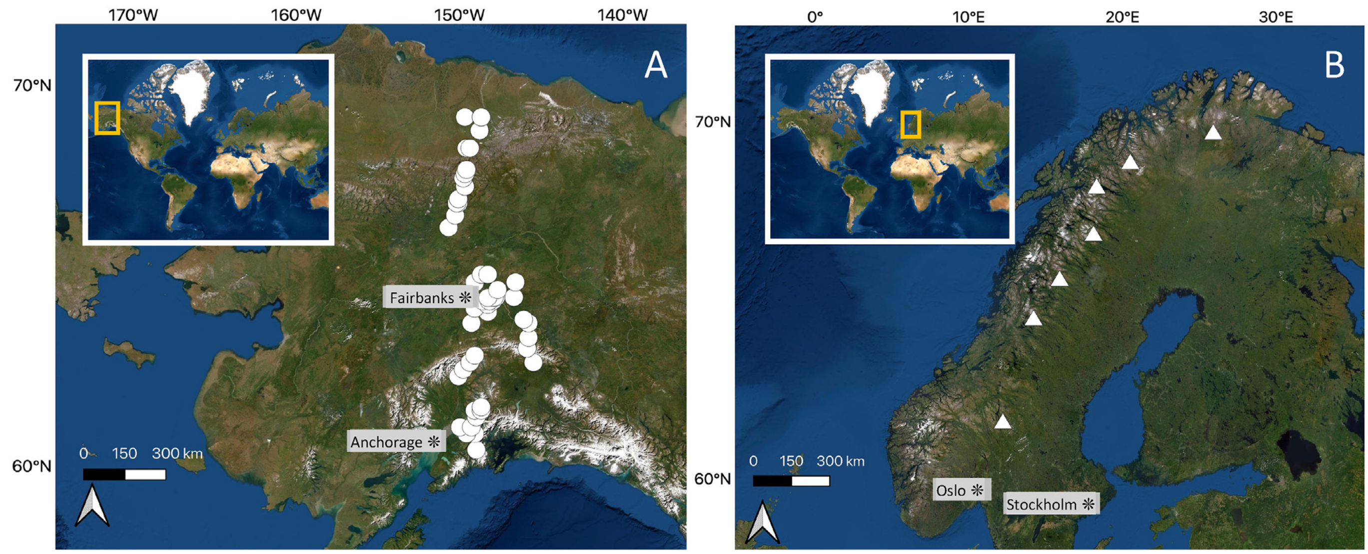

Fig. 1. (A) Locations of modern (2007 & 2018) land snails from Alaska. A total of 81 samples were analyzed from 54 locations (white dots) along a north to south transect. (B) Locations of modern (1983–2014) land snails from Scandinavia (Norway and Sweden). A total of 39 samples were analyzed from 7 locations (white triangles) along a north to south transect. Map base sources: Esri, DigitalGlobe, GeoEYE, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

3.2. Scandinavia

Samples were collected from seven locations along a ~1100 km north-to-south transect of Scandinavia, ranging from Storgjotkölen, Sweden in the south to Váljohka, Norway in the north (Fig. 1B). Northern oceanic and intermediate climates were present across this extent with matrix vegetation being taiga (Weibull et al., 2021). Along this transect, mean annual temperatures range from −2 to 7 °C, with values of 5–13 °C during the extended growing season, and 10–18 °C during the summer (www.climate-data.org; accessed August 2020). Precipitation ranges from 32 to 65 mm annually, 32–36 mm during the extended growing season, and 56–74 mm during the summer (www.climate-data.org; accessed August 2020). RH values range from 74 to 75% annually, 69–75% during the extended growing season, and 66–77% during the summer (www.weather-and-climate.com; accessed August 2020). Finally, average precipitation $\delta^{18}O$ values range from −15.6 to −13.2‰ annually, −13 to −11‰ during the extended growing season, and −11.2 to −9.5‰ during the summer (Bowen, 2020). Precipitation $\delta^{18}O$ values are modeled results from IAE/WMO (2015) by (Bowen et al., 2005).

4. Methods

4.1. Species and sample selection protocol

4.1.1. Alaska

To control species-specific $\delta^{18}O$ differences (Yanes et al., 2017), analyses were limited to two taxa (*Euconulus fulvus* and *Succinea strigata)* which are abundant across the entire coastal maritime to arctic transect. The family Succineidae is present in almost every continent on Earth and has a vast fossil record particularly in Quaternary loess deposits in North America (Pigati et al., 2013) and Europe (Moine et al., 2005). Örstan (2010) found that Succineidae species often live 1–2 years and prefer wet or flooded areas. The family Euconulidae also displays a large geographical distribution, especially throughout North America. *Euconulus fulvus* has a biovolume ~7.3 mm^3 and a maximum shell dimension ~3.5 mm whereas *S. strigata* has a biovolume of ~470 mm^3 and a maximum shell dimension ~14 mm (Nekola, 2014). These species are also routinely preserved in Quaternary loess deposits, paleosols, and modern wetlands.

Individuals were collected from ~100 m^2 areas through field sieving of leaf litter (see Nekola, 2010a,b for details). The geographic location of each station was recorded in digital degrees to the fourth decimal place using a handheld GPS. Samples were collected either in August 2007 or August 2018.

4.1.2. Scandinavia

Seven taxa (*Punctum pygmaeum*, *Vertigo ronnebyensis, Vertigo arctica*, *Euconulus fulvus*, *Columella edentula, Nesovitrea petronella,* and *Discus ruderatus*) were selected for analysis from holdings in the Gothenburg Natural History Museum collection. These taxa were chosen due to their frequency in the museum collection and their characteristic occurrence in Scandinavian taiga. Whereas *Discus ruderatus* and *Nesovitrea petronella* have maximum shell dimensions exceeding 4 mm and biovolumes exceeding 21 mm^3, the remaining taxa have maximum shell dimensions ranging from 1.5 to 3.5 mm and biovolumes from 0.5 to 7.5 mm^3. *Punctum pygmaeum* is one of the smallest and most abundant European land snails living in a wide variety of moist habitats (Kerney and Cameron, 1979; Baur, 1989). *Punctum pygmaeum* was collected from all sites; however, not enough shell material was available to get accurate results from the southernmost location. Hence, *Punctum pygmaeum* data are only available for the six northernmost sites. The genus *Vertigo* has a high diversity of species in the northern latitudes of Scandinavia (Proschwitz, 2003). *Vertigo ronnebyensis* prefers shady coniferous woodlands, and *Vertigo arctica* is usually found on the Scandinavian mountain ridge (Proschwitz, 2003). *Vertigo* species do not extend across the entire Scandinavian transect. *Vertigo arctica* is limited to the north and was only collected from the six northernmost sites, and *Vertigo ronnebyensis* is limited to the south and was only collected from the southernmost site. *Columella edentula* is known to occur in North America and Europe (Luedey et al., 1996). *Nesovitrea petronella* is common in Swedish woodlands, including the mountain-birch forest and above the tree limit in shrubs (von Proschwitz, 1985). Finally, *Discus ruderatus* is often found within the leaf litter of coniferous forests through Europe (Kuzink-Kowalska, 2006) however, in the Scandinavian mountain ridge it is typically found in the mountain birch forest (von Proschwitz, 1985). *Columella edentula, Nesovitrea petronella*, and *Discus ruderatus* were the only species analyzed from all seven locations along the Scandinavian transect; therefore, site average values used for analysis are made from averaging these three species.

The Scandinavian snails were live collected from 1983 to 2014 during the summer months of June–August. About 20 L of ground litter (dead leaves and top soil layer) were sieved in the field. The extracted ground litter volume (1–2 L) was brought to the laboratory and dried, and the snails were sorted by hand. In addition, specimens were also searched and collected directly in the habitats through visual search.

Scandinavian sites exhibit higher precipitation $\delta^{18}O$ values than Alaska: 6.1‰ higher annually, 5.2‰ higher during the extended growing season, and 4.1‰ higher during the summer (Bowen, 2020). Because of these differences, as well as the more limited variability of climate parameters and a longer sampling, the Scandinavian sample set should not be seen as a replicate of the Alaskan sample material. Rather it provides $\delta^{18}O$ values for a larger group of species across a single extensive boreal habitat type in a different part of the Holarctic.

4.2. Stable isotope analyses

Measured shells were strategically selected for isotope analysis by choosing the cleanest-looking shells. Shells were mechanically cleaned with deionized water to remove any remaining debris and air dried before laboratory analysis. Land snail shells were analyzed at the University of Florida using a Finnigan-MAT 252 Isotope Ratio Mass Spectrometer coupled with a Kiel III automated carbonate preparation device. About 40–50 μg of aragonite powder was acidified in 100% H_3PO_4 (Specific Gravity = 1.92) at 70 °C for 10 min resulting in CO_2 measured for carbon and oxygen isotope values. Isotopic values are presented in standard delta notation ($\delta^{18}O$) relative to Vienna Pee Dee Belemnite (VPDB). The standards NBS-19 ($\delta^{18}O$ = −2.20‰ VPDB) and NBS-18 ($\delta^{18}O$ = −23.01‰) were analyzed repeatedly to calibrate and calculate analytical and experimental precision. Analytical precision was better than ±0.1‰ as shown by repeated measurements of samples and standards.

Each isotopic data point represents an average value of two to three snail shells of the same species and from the same microhabitat homogenized together (Table 1). The snail shell $\delta^{18}O$ values generated here were compared to and calibrated with modeled and instrument climate data, including mean annual, extended growing season, and mean summer precipitation $\delta^{18}O$, amount of precipitation, temperature, and relative humidity. Snail shell $\delta^{18}O$ values are reported relative to the VPDB whereas precipitation $\delta^{18}O$ values are reported relative to VSMOW. Finally, data were analyzed using the snail evaporative, steady-state flux balance mixing model by Balakrishnan and Yapp (2004), which accounts for oxygen isotope fractionation and several critical environmental variables impacting the snail oxygen isotope budget.

4.3. Statistical analysis

All statistical analyses were done using R 1.2.5001 (R Core Team, 2020). All data were treated as non-normally distributed. The Kruskal-Wallis test was used to determine whether the multiple samples compared exhibited statistically equivalent median values. The Kruskal-Wallis is an extension of the Mann-Whitney test, which is used in this study when comparing the median value between two samples only. Pearson correlation was conducted to assess the significance of monotonic relationships between two variables. Regression equations were computed to determine the slope and, therefore, the lapse rate of change of the dependent variable (shell $\delta^{18}O$) with respect to changes in relevant independent variables (i.e., latitude, temperature, precipitation $\delta^{18}O$, precipitation amount, and RH). Statistical significance was determined when the p-value was smaller than 0.05.

5. Results

5.1. Alaska

A total of 81 $\delta^{18}O$ analyses were performed on shell aliquots collected along the north-to-south transect in Alaska, with 53 isotope values from *Euconulus fulvus* and 28 from *Succinea strigata* (Table 1). On average, $\delta^{18}O$ values of *S. strigata* are ~0.7‰ higher than $\delta^{18}O$ values for *Euconulus fulvus* (Mann-Whitney test, $p < 0.05$; Fig. 2B). Because snail species differ in oxygen isotope values, we chose to plot *Euconulus fulvus* data only, the most abundant species collected in Alaska, to reduce noise from combining species (Figs. 2 and 3).

Overall, shell $\delta^{18}O$ values ranged from −14.0 to −9.1‰ (Fig. 2A), with an average value of −11.3 ± 1‰. On average, shell $\delta^{18}O$ values were ~8.9 ± 1.1‰ enriched in ^{18}O with respect to average annual precipitation $\delta^{18}O$ (−20.2‰); ~5.7 ± 1.1‰ enriched in ^{18}O with respect to extended growing season precipitation $\delta^{18}O$ (−17‰); and ~3.0 ± 1‰ enriched in ^{18}O with respect to summer precipitation $\delta^{18}O$ values (−14.3‰ vs. VSMOW; Fig. 3D–F).

Along the Alaskan transect, *Euconulus fulvus* shell $\delta^{18}O$ values decrease with increasing latitude (R^2 = 0.28; $p < 0.01$; Fig. 2A). When comparing *Euconulus fulvus* shell $\delta^{18}O$ values to relevant environmental variables, shell $\delta^{18}O$ values increase with increasing annual average temperatures (R^2 = 0.36; $p < 0.01$; Fig. 3A); increasing extended growing season temperatures (R^2 = 0.15; $p < 0.01$; Fig. 3B); increasing annual precipitation $\delta^{18}O$ (R^2 = 0.21; $p < 0.01$; Fig. 3D); increasing extended growing season precipitation $\delta^{18}O$ (R^2 = 0.25; $p < 0.01$; Fig. 3E); and increasing summer precipitation $\delta^{18}O$ (R^2 = 0.19; $p < 0.01$; Fig. 3F). *Euconulus fulvus* shell $\delta^{18}O$ values did not exhibit a statistically significant relationship with increasing summer temperatures (R^2 = 0.10; $p = 0.05$; Fig. 3C) or other environmental variables such as precipitation amount (Fig. 3G–I) or average relative humidity (Fig. 3J-L).

5.2. Scandinavia

A total of 39 oxygen isotope analyses were performed on shell samples collected along the Scandinavia transect (Table 1). Land snail shell species measured include *Punctum pygmaeum* (n = 6), *Vertigo ronnebyensis* (n = 1), *Vertigo arctica* (n = 5), *Euconulus fulvus* (n = 6), *Columella edentula* (n = 7), *Nesovitrea petronella* (n = 7), and *Discus ruderatus* (n = 7).

When all species are considered jointly, shell $\delta^{18}O$ values ranged from −8.9 to −4.1‰ (Fig. 4A), with an average value of −6.2 ± 1.1‰. On average, shell $\delta^{18}O$ values were 8.0 ± 1.3‰ enriched in ^{18}O with respect to average annual precipitation $\delta^{18}O$ values (−14.2‰ vs. VSMOW); 5.6 ± 1.3‰ enriched in ^{18}O with respect to extended growing season precipitation $\delta^{18}O$ values (−11.8‰ vs. VSMOW); and 4.0 ± 1.2‰ enriched in ^{18}O with respect to summer precipitation $\delta^{18}O$ values (−10.2‰ vs. VSMOW; Fig. 5D–F).

Sympatric species at both the microhabitat and regional scale showed significant differences (Kruskal Wallis test, $p < 0.05$) in the $\delta^{18}O$ values of the shell (Fig. 4B and C). Species with larger body sizes (i.e., *Nesovitrea petronella* and *Discus ruderatus*) consistently yielded higher $\delta^{18}O$ values (Fig. 4B and C). Isotopic values for the smallest species *Punctum pygmaeum* were ~2.7‰ more negative than the largest species *Discus ruderatus* (Fig. 4C).

Finally, we compared the oxygen isotope values of snail species that were present at all sampling sites (*Columella edentula*,

Table 1
Oxygen isotope values of modern land snail shells from Alaska (collected in 2007/2018) and Scandinavia (collected 1983–2014) along with relevant instrument climate data. Climate data are presented for three potential snail active periods: average annual values, extended growing season values (months April–October), and summer values (June–August). Acronyms: m asl, meters above sea level, VPDB, Vienna Pee Dee belemnite; RH, relative humidity; SMOW, standard mean ocean water. Alaska temperature and amount of precipitation data were gathered from usclimatedata.org (accessed August 2020). Alaska relative humidity data were gathered from the National Oceanic and Atmospheric Administration (NOAA) available at www.ncdc.noaa.gov (accessed August 2020). Scandinavia temperature and amount of precipitation data were gathered from www.climate-data.org (accessed August 2020). Scandinavia relative humidity data were gathered from www.weather-and-climate.com (accessed August 2020). Alaska and Scandinavia precipitation $\delta^{18}O$ values are modeled results from Bowen (2020), available at www.waterisotopes.org (accessed August 2020).

Locality	Species	Latitude (°N)	Longitude (°W)	Altitude (m asl)	Snail shell $\delta^{18}O$‰ (VPDB)	Mean annual values				Extended growing season values				Summer values			
						T (°C)	Precipitation $\delta^{18}O$‰ (SMOW)	P (mm)	RH (%)	T (°C)	Precipitation $\delta^{18}O$‰ (SMOW)	P (mm)	RH (%)	T (°C)	Precipitation $\delta^{18}O$‰ (SMOW)	P (mm)	RH (%)
Alaska	*Succinea strigata*	60.5	149.0	980	−9.1	3	−19.7	35	69	9	−16.4	44	67	14	−14.1	51	68
Alaska	*Euconulus fulvus*	61.0	149.1	80	−10.2	3	−18.3	35	69	9	−15.2	44	67	14	−12.9	51	68
Alaska	*Euconulus fulvus*	61.0	149.6	30	−9.8	3	−18.1	35	69	9	−15.0	44	67	14	−12.7	51	68
Alaska	*Euconulus fulvus*	61.0	149.6	30	−10.3	3	−18.1	35	69	9	−15.0	44	67	14	−12.8	51	68
Alaska	*Succinea strigata*	61.0	149.6	30	−9.5	3	−18.1	35	69	9	−15.0	44	67	14	−12.8	51	68
Alaska	*Euconulus fulvus*	61.2	150.0	30	−9.8	3	−18.0	35	69	9	−14.9	44	67	14	−12.6	51	68
Alaska	*Euconulus fulvus*	61.2	149.3	125	−9.9	3	−18.6	35	69	9	−15.6	44	67	14	−13.1	51	68
Alaska	*Euconulus fulvus*	61.5	149.0	15	−10.3	4	−18.3	34	69	10	−15.2	40	67	15	−12.8	50	68
Alaska	*Euconulus fulvus*	61.7	149.1	160	−10.5	2	−18.6	38	69	8	−15.6	45	67	13	−13.1	54	68
Alaska	*Succinea strigata*	61.7	149.1	160	−11.4	2	−18.6	38	69	8	−15.6	45	67	13	−13.1	54	68
Alaska	*Euconulus fulvus*	61.7	148.7	190	−11.0	2	−18.8	38	69	8	−15.7	45	67	13	−13.2	54	68
Alaska	*Succinea strigata*	61.8	148.7	990	−12.0	2	−20.3	38	69	8	−17.1	45	67	13	−14.5	54	68
Alaska	*Euconulus fulvus*	62.7	150.1	145	−12.2	−3	−18.8	34	66	5	−15.8	44	60	11	−13.2	63	59
Alaska	*Succinea strigata*	62.7	150.1	245	−11.5	−3	−18.8	34	66	5	−15.8	44	60	11	−13.2	63	59
Alaska	*Euconulus fulvus*	62.9	149.8	420	−11.7	−3	−19.3	34	66	5	−16.1	44	60	11	−13.5	63	59
Alaska	*Euconulus fulvus*	63.1	145.5	1000	−11.7	−3	−21.0	24	66	7	−17.9	31	60	13	−15.2	42	59
Alaska	*Succinea strigata*	63.1	145.5	980	−12.8	−3	−21.0	24	66	7	−17.9	31	60	13	−15.2	42	59
Alaska	*Euconulus fulvus*	63.1	149.4	550	−11.6	−3	−19.6	34	66	5	−16.5	44	60	11	−13.8	63	59
Alaska	*Succinea strigata*	63.1	149.4	580	−11.3	−3	−19.6	34	66	5	−16.5	44	60	11	−13.8	63	59
Alaska	*Euconulus fulvus*	63.3	149.1	730	−12.1	−3	−20.2	34	66	5	−17.1	44	60	11	−14.3	63	59
Alaska	*Euconulus fulvus*	63.5	145.9	700	−10.5	−3	−21.1	24	66	7	−17.9	31	60	13	−15.1	42	59
Alaska	*Succinea strigata*	63.5	145.9	700	−10.2	−3	−21.1	24	66	7	−17.9	31	60	13	−15.1	42	59
Alaska	*Euconulus fulvus*	63.8	145.8	690	−11.7	−3	−21.0	24	66	7	−18.0	31	60	13	−15.1	42	59
Alaska	*Euconulus fulvus*	64.2	145.8	300	−11.8	−3	−20.4	28	63	7	−18.0	31	60	15	−14.6	61	59
Alaska	*Succinea strigata*	64.2	145.8	300	−10.9	−3	−20.4	28	63	7	−17.4	38	59	15	−14.6	61	59
Alaska	*Euconulus fulvus*	64.2	149.3	220	−9.2	−3	−19.8	27	63	7	−16.7	36	59	15	−14.0	58	59
Alaska	*Succinea strigata*	64.2	149.3	220	−10.0	−3	−19.8	27	63	7	−16.7	36	59	15	−14.0	58	59
Alaska	*Euconulus fulvus*	64.3	146.1	280	−11.5	−3	−20.4	28	63	7	−17.3	38	59	15	−14.5	61	59
Alaska	*Euconulus fulvus*	64.5	148.3	150	−9.6	−3	−19.9	27	65	7	−16.8	26	60	15	−14.1	58	63
Alaska	*Euconulus fulvus*	64.6	149.1	120	−11.2	−3	−19.9	27	65	7	−16.8	26	60	15	−14.0	58	63
Alaska	*Succinea strigata*	64.6	149.1	110	−10.8	−3	−19.9	27	65	7	−16.8	26	60	15	−14.1	58	63
Alaska	*Euconulus fulvus*	64.6	149.1	150	−11.7	−3	−19.9	27	65	7	−16.8	26	60	15	−14.1	58	63
Alaska	*Succinea strigata*	64.6	149.1	110	−9.6	−3	−19.9	27	65	7	−16.7	26	60	15	−14.1	58	63
Alaska	*Euconulus fulvus*	64.6	149.1	110	−10.8	−3	−19.9	27	65	7	−16.7	26	60	15	−14.0	58	63
Alaska	*Euconulus fulvus*	64.7	148.3	130	−11.4	−3	−20.0	23	65	8	−16.8	30	60	15	−14.1	46	63
Alaska	*Euconulus fulvus*	64.7	148.3	180	−10.4	−3	−20.0	23	65	8	−16.8	30	60	15	−14.2	46	63
Alaska	*Euconulus fulvus*	64.8	148.0	120	−12.1	−3	−20.0	23	65	8	−16.9	30	60	15	−14.2	46	63
Alaska	*Succinea strigata*	64.8	148.0	130	−10.8	−3	−20.0	23	65	8	−16.9	30	60	15	−14.2	46	63
Alaska	*Euconulus fulvus*	64.8	148.6	260	−11.8	−3	−20.3	23	65	8	−17.2	30	60	15	−14.4	46	63
Alaska	*Euconulus fulvus*	64.8	148.2	400	−10.9	−3	−22.6	23	65	8	−17.1	30	60	15	−14.4	46	63
Alaska	*Succinea strigata*	64.8	148.2	400	−11.8	−3	−22.6	23	65	8	−17.1	30	60	15	−14.4	46	63

(*continued on next page*)

Table 1 (*continued*)

Locality	Species	Latitude (°N)	Longitude (°W)	Altitude (m asl)	Snail shell $\delta^{18}O$‰ (VPDB)	Mean annual values				Extended growing season values				Summer values			
						T (°C)	Precipitation $\delta^{18}O$‰ (SMOW)	P (mm)	RH (%)	T (°C)	Precipitation $\delta^{18}O$‰ (SMOW)	P (mm)	RH (%)	T (°C)	Precipitation $\delta^{18}O$‰ (SMOW)	P (mm)	RH (%)
Alaska	*Euconulus fulvus*	64.9	147.9	190	−11.7	−3	−20.1	23	65	8	−17.0	30	60	15	−14.3	46	63
Alaska	*Succinea strigata*	64.9	147.9	190	−11.0	−3	−20.1	23	65	8	−17.0	30	60	15	−14.3	46	63
Alaska	*Euconulus fulvus*	64.9	147.8	200	−12.5	−3	−20.1	23	65	8	−17.0	30	60	15	−14.3	46	63
Alaska	*Euconulus fulvus*	64.9	147.9	155	−11.1	−3	−20.2	23	65	8	−17.1	30	60	15	−14.4	46	63
Alaska	*Euconulus fulvus*	64.9	146.7	190	−11.5	−3	−20.3	23	65	8	−17.2	30	60	15	−14.5	46	63
Alaska	*Succinea strigata*	64.9	146.7	190	−10.4	−3	−20.3	23	65	8	−17.2	30	60	15	−14.5	46	63
Alaska	*Euconulus fulvus*	64.9	148.3	410	−12.9	−3	−20.6	23	65	8	−17.4	30	60	15	−14.7	46	63
Alaska	*Succinea strigata*	64.9	148.3	410	−11.1	−3	−20.6	23	65	8	−17.4	30	60	15	−14.7	46	63
Alaska	*Euconulus fulvus*	65.1	147.7	200	−10.6	−3	−20.2	23	65	8	−17.1	30	60	15	−14.4	46	63
Alaska	*Euconulus fulvus*	65.3	146.6	360	−13.7	−6	−20.8	23	65	8	−17.6	32	60	15	−14.9	48	63
Alaska	*Succinea strigata*	65.3	146.6	370	−10.0	−6	−20.8	23	65	8	−17.6	32	60	15	−14.9	48	63
Alaska	*Euconulus fulvus*	65.3	149.1	570	−12.3	−6	−21.1	23	65	8	−17.8	32	60	15	−15.1	48	63
Alaska	*Euconulus fulvus*	65.5	148.3	275	−11.7	−6	−20.3	23	65	8	−17.2	32	60	15	−14.5	48	63
Alaska	*Succinea strigata*	65.5	148.3	160	−11.5	−6	−20.3	23	65	8	−17.2	32	60	15	−14.5	48	63
Alaska	*Euconulus fulvus*	65.5	148.7	136	−11.7	−6	−20.4	23	65	8	−17.2	32	60	15	−14.6	48	63
Alaska	*Euconulus fulvus*	65.5	148.3	280	−13.3	−6	−20.5	23	65	8	−17.3	32	60	15	−14.6	48	63
Alaska	*Euconulus fulvus*	66.7	150.7	260	−11.8	−5	−20.8	31	67	6	−17.6	39	65	14	−15.1	54	63
Alaska	*Succinea strigata*	66.7	150.7	260	−10.6	−5	−20.8	31	67	6	−17.6	39	65	14	−15.1	54	63
Alaska	*Euconulus fulvus*	67.0	150.3	380	−11.9	−5	−21.1	31	67	6	−17.9	39	65	14	−15.3	54	63
Alaska	*Euconulus fulvus*	67.3	150.1	370	−12.3	−5	−21.2	31	67	6	−17.9	39	65	14	−15.3	54	63
Alaska	*Euconulus fulvus*	67.3	150.2	330	−11.9	−5	−21.1	31	67	6	−17.8	39	65	14	−15.2	54	63
Alaska	*Succinea strigata*	67.3	150.2	330	−12.0	−5	−21.1	31	67	6	−17.8	39	65	14	−15.2	54	63
Alaska	*Euconulus fulvus*	67.4	150.1	400	−11.4	−5	−21.2	31	67	6	−18.0	39	65	14	−15.3	54	63
Alaska	*Succinea strigata*	67.4	150.1	400	−11.1	−5	−21.2	31	67	6	−18.0	39	65	14	−15.3	54	63
Alaska	*Euconulus fulvus*	67.7	149.7	460	−9.5	−8	−21.4	38	67	3	−18.1	26	65	11	−15.4	20	63
Alaska	*Succinea strigata*	67.7	149.7	460	−11.8	−8	−21.4	38	67	3	−18.1	26	65	11	−15.4	20	63
Alaska	*Euconulus fulvus*	67.9	149.8	615	−10.6	−8	−21.6	38	67	3	−18.2	26	65	11	−15.4	20	63
Alaska	*Succinea strigata*	67.9	149.8	610	−10.4	−8	−21.6	38	67	3	−18.2	26	65	11	−15.4	20	63
Alaska	*Euconulus fulvus*	68.0	149.7	770	−12.3	−8	−21.9	38	67	3	−18.5	26	65	11	−15.6	20	63
Alaska	*Euconulus fulvus*	68.1	149.6	1002	−12.7	−8	−22.3	38	67	3	−18.9	26	65	11	−16.0	20	63
Alaska	*Euconulus fulvus*	68.6	149.6	720	−12.5	−8	−21.4	38	67	3	−18.0	26	65	11	−15.0	20	63
Alaska	*Euconulus fulvus*	68.6	149.4	750	−12.8	−8	−21.5	38	67	3	−18.1	26	65	11	−15.0	20	63
Alaska	*Euconulus fulvus*	69.0	148.8	370	−12.7	−11	−20.7	11	67	0	−17.4	15	65	11	−14.3	21	63
Alaska	*Succinea strigata*	69.0	148.8	370	−11.2	−11	−20.7	11	67	0	−17.4	15	65	11	−14.3	21	63
Alaska	*Euconulus fulvus*	69.3	148.7	240	−14.0	−11	−20.6	11	67	0	−17.2	15	65	11	−14.1	21	63
Alaska	*Succinea strigata*	69.3	148.7	240	−11.5	−11	−20.6	11	67	0	−17.2	15	65	11	−14.1	21	63
Alaska	*Euconulus fulvus*	69.3	149.7	245	−11.1	−11	−20.4	11	67	0	−17.2	15	65	11	−14.0	21	63
Alaska	*Succinea strigata*	69.3	149.7	240	−11.1	−11	−20.4	11	67	0	−17.2	15	65	11	−14.0	21	63
Alaska	*Succinea strigata*	69.3	148.7	250	−10.8	−11	−20.6	11	67	0	−17.3	15	65	11	−14.1	21	63
Alaska	*Euconulus fulvus*	69.3	148.7	240	−12.9	−11	−20.6	11	67	0	−17.3	15	65	11	−14.1	21	63
Scandinavia	*Discus ruderatus*	69.7	25.9	180	−5.8	−2	−15.5	49	75	5	−12.8	60	75	11	−11.0	77	77
Scandinavia	*Vertigo arctica*	69.7	25.9	180	−6.0	−2	−15.5	49	75	5	−12.8	60	75	11	−11.0	77	77
Scandinavia	*Nesovitra petronella*	69.7	25.9	180	−6.0	−2	−15.5	49	75	5	−12.8	60	75	11	−11.0	77	77
Scandinavia	*Columella edentula*	69.7	25.9	180	−5.4	−2	−15.5	49	75	5	−12.8	60	75	11	−11.0	77	77
Scandinavia	*Punctum pygmaeum*	69.7	25.9	180	−5.3	−2	−15.5	49	75	5	−12.8	60	75	11	−11.0	77	77
Scandinavia	*Discus ruderatus*	69.0	20.5	575	−4.9	−2	−15.6	59	75	5	−13.0	73	75	11	−11.2	97	77
Scandinavia	*Vertigo arctica*	69.0	20.5	575	−7.3	−2	−15.6	59	75	5	−13.0	73	75	11	−11.2	97	77

Scandinavia	*Nesovitra petronella*	69.0	20.5	575	−5.6	−2	−15.6	59	75	5	−13.0	73	75	11	−11.2	97	77
Scandinavia	*Columella edentula*	69.0	20.5	575	−8.2	−2	−15.6	59	75	5	−13.0	73	75	11	−11.2	97	77
Scandinavia	*Econulus fulvus*	69.0	20.5	575	−6.8	−2	−15.6	59	75	5	−13.0	73	75	11	−11.2	97	77
Scandinavia	*Punctum pygmaeum*	69.0	20.5	575	−8.9	−2	−15.6	59	75	5	−13.0	73	75	11	−11.2	97	77
Scandinavia	*Discus ruderatus*	68.4	18.3	455	−4.2	−2	−14.2	95	75	5	−11.8	93	75	10	−10.0	104	77
Scandinavia	*Vertigo arctica*	68.4	18.3	455	−6.0	−2	−14.2	95	75	5	−11.8	93	75	10	−10.0	104	77
Scandinavia	*Nesovitra petronella*	68.4	18.3	455	−5.2	−2	−14.2	95	75	5	−11.8	93	75	10	−10.0	104	77
Scandinavia	*Columella edentula*	68.4	18.3	455	−7.2	−2	−14.2	95	75	5	−11.8	93	75	10	−10.0	104	77
Scandinavia	*Econulus fulvus*	68.4	18.3	455	−6.6	−2	−14.2	95	75	5	−11.8	93	75	10	−10.0	104	77
Scandinavia	*Punctum pygmaeum*	68.4	18.3	455	−6.6	−2	−14.2	95	75	5	−11.8	93	75	10	−10.0	104	77
Scandinavia	*Discus ruderatus*	67.2	18.1	535	−6.1	−2	−13.9	95	75	5	−11.6	93	75	10	−10.0	104	77
Scandinavia	*Vertigo arctica*	67.2	18.1	535	−6.7	−2	−13.9	95	75	5	−11.6	93	75	10	−10.0	104	77
Scandinavia	*Nesovitra petronella*	67.2	18.1	535	−5.0	−2	−13.9	95	75	5	−11.6	93	75	10	−10.0	104	77
Scandinavia	*Columella edentula*	67.2	18.1	535	−7.3	−2	−13.9	95	75	5	−11.6	93	75	10	−10.0	104	77
Scandinavia	*Econulus fulvus*	67.2	18.1	535	−5.3	−2	−13.9	95	75	5	−11.6	93	75	10	−10.0	104	77
Scandinavia	*Punctum pygmaeum*	67.2	18.1	535	−7.8	−2	−13.9	95	75	5	−11.6	93	75	10	−10.0	104	77
Scandinavia	*Discus ruderatus*	66.0	15.9	575	−5.6	2	−13.4	95	75	7	−11.2	93	75	11	−9.7	104	77
Scandinavia	*Nesovitra petronella*	66.0	15.9	575	−6.1	2	−13.4	95	75	7	−11.2	93	75	11	−9.7	104	77
Scandinavia	*Columella edentula*	66.0	15.9	575	−7.4	2	−13.4	95	75	7	−11.2	93	75	11	−9.7	104	77
Scandinavia	*Econulus fulvus*	66.0	15.9	575	−7.9	2	−13.4	95	75	7	−11.2	93	75	11	−9.7	104	77
Scandinavia	*Punctum pygmaeum*	66.0	15.9	575	−6.7	2	−13.4	95	75	7	−11.2	93	75	11	−9.7	104	77
Scandinavia	*Discus ruderatus*	64.9	14.2	455	−4.9	7	−13.2	60	74	13	−11.0	72	69	18	−9.5	91	66
Scandinavia	*Vertigo arctica*	64.9	14.2	455	−6.8	7	−13.2	60	74	13	−11.0	72	69	18	−9.5	91	66
Scandinavia	*Nesovitra petronella*	64.9	14.2	455	−5.8	7	−13.2	60	74	13	−11.0	72	69	18	−9.5	91	66
Scandinavia	*Columella edentula*	64.9	14.2	455	−5.0	7	−13.2	60	74	13	−11.0	72	69	18	−9.5	91	66
Scandinavia	*Econulus fulvus*	64.9	14.2	455	−5.3	7	−13.2	60	74	13	−11.0	72	69	18	−9.5	91	66
Scandinavia	*Punctum pygmaeum*	64.9	14.2	455	−5.4	7	−13.2	60	74	13	−11.0	72	69	18	−9.5	91	66
Scandinavia	*Discus ruderatus*	61.8	12.2	730	−4.1	7	−13.7	66	74	11	−11.4	75	69	18	−10.1	94	66
Scandinavia	*Vertigo ronnedyebsis*	61.8	12.2	730	−6.0	5	−13.7	66	74	11	−11.4	75	69	15	−10.1	94	66
Scandinavia	*Nesovitra petronella*	61.8	12.2	730	−5.8	5	−13.7	66	74	11	−11.4	75	69	15	−10.1	94	66
Scandinavia	*Columella edentula*	61.8	12.2	730	−6.3	5	−13.7	66	74	11	−11.4	75	69	15	−10.1	94	66
Scandinavia	*Econulus fulvus*	61.8	12.2	730	−6.8	5	−13.7	66	74	11	−11.4	75	69	15	−10.1	94	66

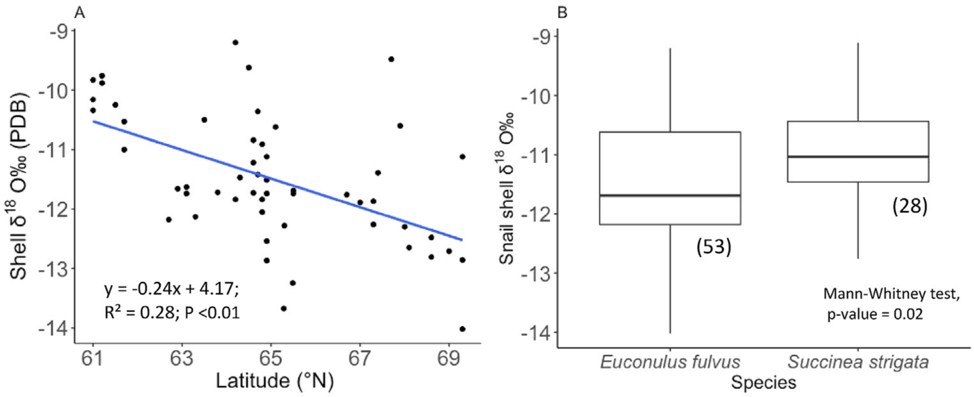

Fig. 2. (A) *Euconulus fulvus* shell $\delta^{18}O$ values versus latitude in Alaska. (B) Boxplots of shell $\delta^{18}O$ values by species, *Euconulus fulvus* and *Succinea strigata*, from all Alaskan locations combined. Data are presented as boxplots. Box extremes represent quartile distribution. Whiskers depict range of values. Solid line inside the plot depicts the median $\delta^{18}O$ value. Numbers in parentheses represent the number of shells analyzed.

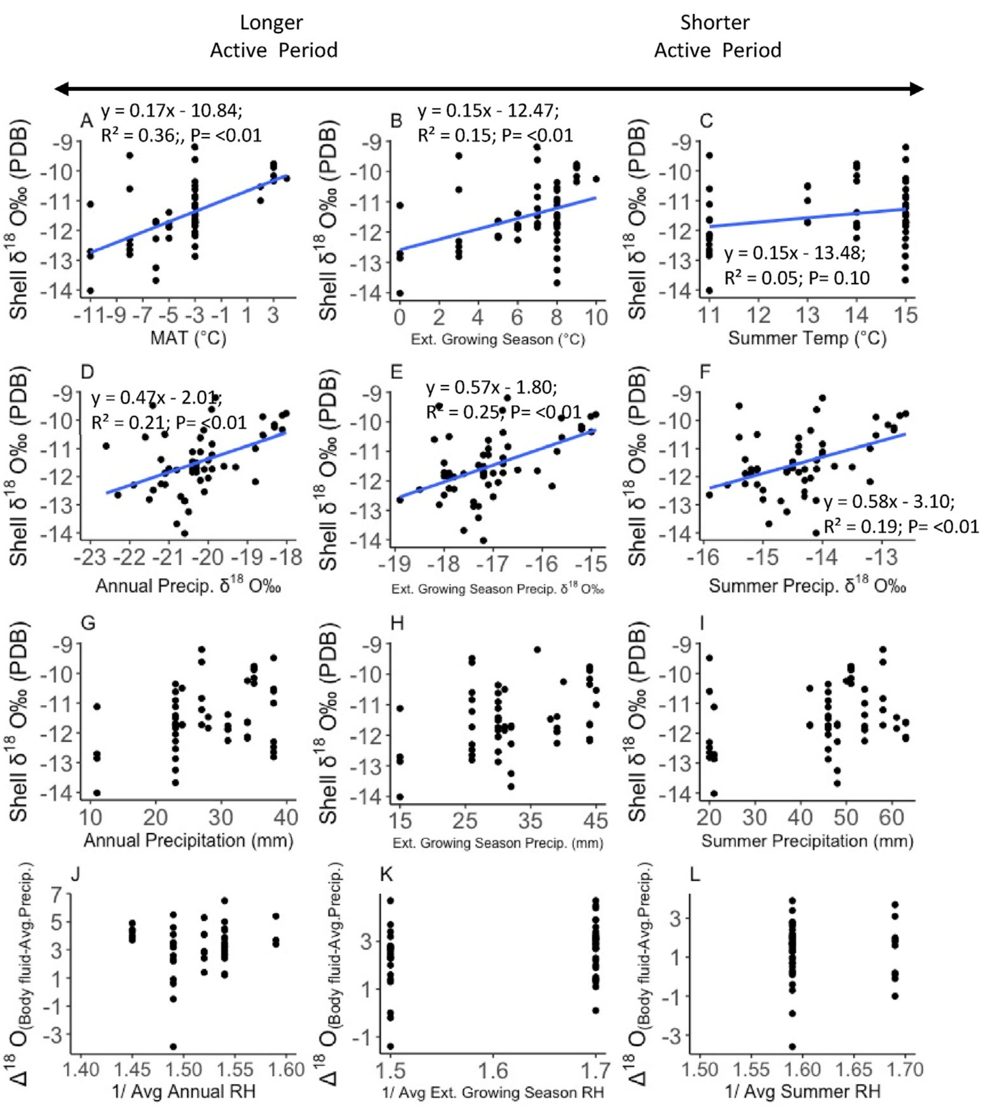

Fig. 3. (A–L) Bivariate relationships between Alaska *Euconulus fulvus* shell $\delta^{18}O$ values and relevant instrument climate parameters. Shell $\delta^{18}O$ values were compared to climate parameters calculated for three hypothetical snail active periods of varying lengths: annual, extended growing season, and summer. Regression lines were added when $P \geq 0.10$. Temperature and amount of precipitation data were gathered from www.usclimatedata.org (accessed August 2020). Precipitation $\delta^{18}O$ values are modeled results from Bowen (2020), available at www.waterisotopes.org (accessed August 2020). Relative humidity data were gathered from the National Oceanic and Atmospheric Administration (NOAA) available at www.ncdc.noaa.gov (accessed August 2020). Acronyms: MAT = mean annual temperature; VPDB= Vienna Pee Dee Belemnite; RH = relative humidity; SMOW = standard mean ocean water; summer months = June–August; extended growing season = April–October.

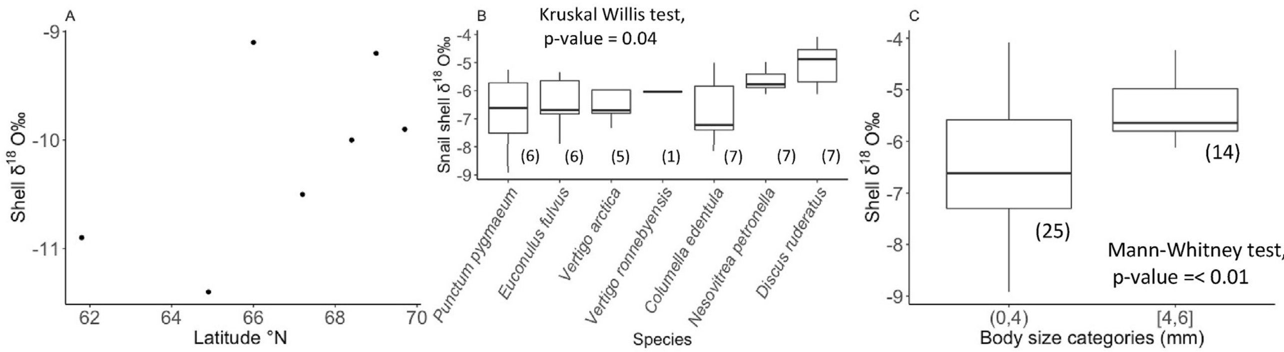

Fig. 4. (A) Site average shell $\delta^{18}O$ of the three snail species, *Columella edentula*, *Nesovitrea petronella*, and *Discus ruderatus*, located at all Scandinavia locations against latitude. (B) Boxplots of shell $\delta^{18}O$ values by species arranged in order of increasing body size — *Punctum pygmaeum*, *Euconulus fulvus*, *Vertigo arctica*, *Vertigo ronnebyensis*, *Columella edentula*, *Nesovitrea petronella*, and *Discus ruderatus* — from all locations in Scandinavia combined. (C) Boxplots of shell $\delta^{18}O$ values by shell size. Body size was grouped into two size categories, 0–4 mm (*Punctum pygmaeum*, *Euconulus fulvus*, *Vertigo arctica*, *Vertigo ronnebyensis*, and *Columella edentula*) and 4–6 mm (*Nesovitrea petronella and Discus ruderatus*). Box extremes represent quartile distribution. Whiskers depict range of values. Solid line inside the plot depicts the median $\delta^{18}O$ value. Numbers in parentheses represent the number of shells analyzed.

Nesovitrea petronella, and *Discus ruderatus*) against environmental parameters. Shell $\delta^{18}O$ values did not show significant relationships with environmental parameters including latitude (Fig. 4A), temperature (Fig. 5A–C), precipitation $\delta^{18}O$ (Fig. 5D–F), amount of precipitation (Fig. 5G–I), or average relative humidity (Fig. 5J-L).

Snail shell $\delta^{18}O$ values from Scandinavia were on average 5.1‰ higher than shells from Alaska. Similarly, Scandinavian average annual, extended growing season, and summer precipitation $\delta^{18}O$ was 6.1‰, 5.2‰ and 4.1‰ higher than average annual, extended growing season, and summer precipitation $\delta^{18}O$ in Alaska, respectively (Table 1).

6. Discussion

6.1. Relationship between snail shell $\delta^{18}O$ values and climate

Land snail shell $\delta^{18}O$ values from the Alaskan transect, between 60 and 70 °N, showed the best-fit linear regression equations against latitude, precipitation $\delta^{18}O$, and temperature (Figs. 2A, 3A-D). Shell $\delta^{18}O$ values increase by ~0.1–0.2‰ for every 1 °C increase in average annual temperature, extended growing season temperature, and summer temperature (Fig. 3A–C). Interestingly, the correlation between snail shell $\delta^{18}O$ and annual temperature (R^2 = 0.36, P = < 0.01) is more pronounced than both summer temperature (R^2 = 0.05, P = 0.10) and extended growing season temperature (R^2 = 0.15, P = < 0.01) suggesting that snails from high latitudes may be active and grow their shell much beyond the summer months.

The oxygen isotope fractionation factor between aragonite and water is temperature dependent, where shell $\delta^{18}O$ increases ~0.23‰ every 1 °C of temperature decrease (Grossman and Ku, 1986). In contrast, precipitation $\delta^{18}O$ during rain events decreases by ~0.58‰ for each 1 °C decrease in temperature (Rozanski et al., 1993). Because the influence of temperature in precipitation (decrease of ~0.58‰/1 °C) is greater than the effects of temperature in aragonite-water fractionation factor (increase of ~0.23‰/1 °C), it is expected that precipitation $\delta^{18}O$ is the main environmental factor influencing the snail oxygen isotope budget (see also discussion in Balakrishnan et al., 2005).

Shell $\delta^{18}O$ values are significantly correlated with annual, extended growing season, and summer precipitation $\delta^{18}O$ (Fig. 3D–F). The following linear regression equation describes Alaskan shell $\delta^{18}O$ values vs. annual precipitation $\delta^{18}O$ (Fig. 3D):

$$\delta^{18}O_{shell} = 0.5(_{FX1}\ 0.05)\ _{FX1}\ \delta^{18}O_{precip.} - 2.0(_{FX1}\ [R^2 = 0.21;\ Eq.\ 1]$$

When comparing Alaskan extended growing season precipitation $\delta^{18}O$ values to snail shell $\delta^{18}O$ values, we observe the linear regression equation (Fig. 3E):

$$\delta^{18}O_{shell} = 0.6(_{FX1}\ 0.05)\ _{FX1}\ \delta^{18}O_{precip.} -1.8(_{FX1}\ [R^2 = 0.25;\ Eq.\ 2]$$

When comparing Alaskan summer precipitation $\delta^{18}O$ values to snail shell $\delta^{18}O$ values, we observe the linear regression equation (Fig. 3F):

$$\delta^{18}O_{shell} = 0.6(_{FX1}\ 0.05)\ _{FX1}\ \delta^{18}O_{precip.} - 3.1(_{FX1}\ [R^2 = 0.19;\ Eq.\ 3]$$

Results from this study are remarkably comparable to a previously published coarse-scale study in North America and the Caribbean (between 18 and 64 °N) by Yanes et al. (2019). When comparing snail shell $\delta^{18}O$ values to annual average precipitation $\delta^{18}O$ values they found the equation:

$$\delta^{18}O_{shell} = 0.5(_{FX1}\ 0.05)\ _{FX1}\ \delta^{18}O_{precip.} - 2.2(_{FX1}) \quad (4)$$

According to these equations, land snail shell $\delta^{18}O$ values appear to increase 0.5‰ for every 1‰ increase in average annual precipitation $\delta^{18}O$ values. However, the rate increases to 0.6‰ for every 1‰ increase in extended growing season and summer precipitation $\delta^{18}O$ values, suggesting a slightly higher influence of precipitation $\delta^{18}O$ from warmer months in polar areas.

These results also show a clear and reasonably consistent relationship between increasing precipitation $\delta^{18}O$ values and increasing temperature. Our research further validates land snail shell $\delta^{18}O$ values as a reliable proxy for precipitation $\delta^{18}O$ in high latitudes. The results presented here, according to the R^2 values, suggest land snail shell $\delta^{18}O$ values track annual temperature best followed by extended growing season precipitation $\delta^{18}O$, annual precipitation $\delta^{18}O$, and extended growing season temperature. Snails are possibly active during much of the fall and spring and not just the summer as initially hypothesized. Future research on snail ecology and behavior in polar regions should be conducted to test this hypothesis further.

When comparing shell $\delta^{18}O$ values to the amount of precipitation and RH, no trends were found for any active period scenario (Fig. 3G-L). Although tropical and subtropical sites, like the Canary Islands, show a negative relationship between shell $\delta^{18}O$ values and

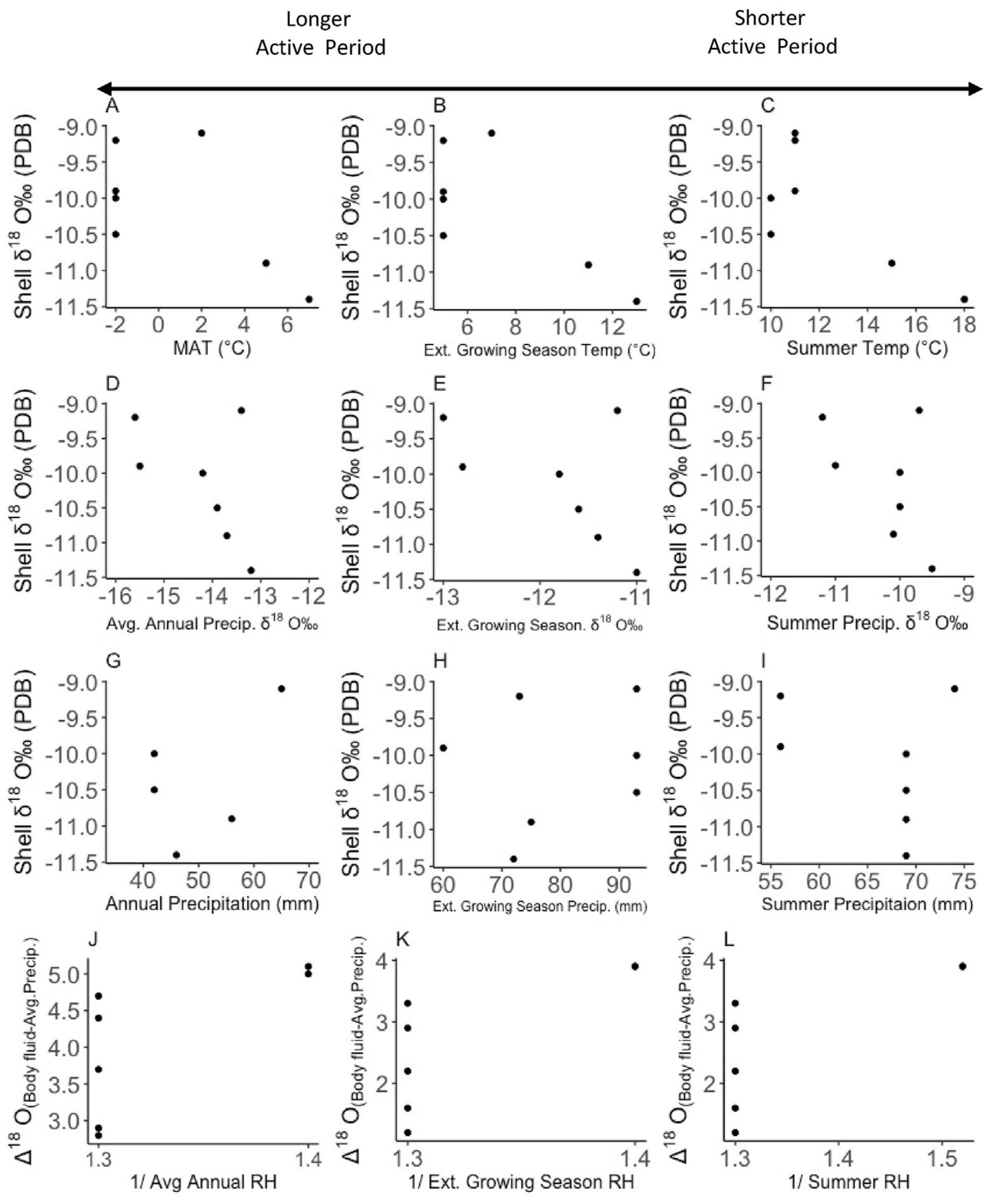

Fig. 5. (A–L) Bivariate relationships of site average shell $\delta^{18}O$ values of the three snail species, *Columella edentula, Nesovitrea petronella,* and *Discus ruderatus,* located at all Scandinavia locations and relevant instrument climate parameters. Shell $\delta^{18}O$ values were compared to climate parameters calculated for three hypothetical snail active periods of varying lengths (annual, extended growing season, summer). Temperature and amount of precipitation data were gathered from www.climate-data.org (accessed August 2020). Precipitation $\delta^{18}O$ values are modeled results from Bowen (2020), available at www.waterisotopes.org (accessed August 2020). Relative humidity data were gathered from www.weather-and-climate.com (accessed August 2020). No regression lines were added because no statistical significance was observed. Acronyms: MAT = mean annual temperature; VPDB= Vienna Pee Dee Belemnite; RH = relative humidity; SMOW = standard mean ocean water; summer months = June–August; extended growing season = April–October.

precipitation amount (Yanes et al., 2009), this relationship is not observed at high latitudes. Furthermore, Yapp (1979) found that the ^{18}O content of the snail body fluid was linearly related to the inverse of relative humidity. Our calculated body fluid $\delta^{18}O$ data from Alaska, using the equation by Grossman and Ku (1986) did not display a clear relationship with the inverse of relative humidity, suggesting that at polar regions, precipitation $\delta^{18}O$ is the main environmental factor impacting the snail oxygen isotope budget (Fig. 3D–F).

Land snail shell $\delta^{18}O$ values from the Scandinavia transect did not show significant relationships with local instrument climate parameters (Fig. 5A-L). This could be explained by the reduced climate gradient across the seven locations studied, which vary much less than the Alaskan climate gradient. In the Scandinavia transect, annual (−2 to 7 °C), extended growing season (0–10 °C), and summer (10–18 °C) temperatures range less than 10 °C. Most importantly, annual (−15.6 to −13.2‰), extended growing season (−13 to −11‰), and summer (−11.2 to −9.5‰) precipitation $\delta^{18}O$ values ranged a mere ~2‰.

Finally, although the Alaskan and Scandinavian transects are located along the same latitudinal gradient (60–70 °N), the snail shells from these locations produced very different $\delta^{18}O$ values in response to different climate regimes between the two regions (Fig. 6A and B). On average Scandinavian shells were 5.1‰ enriched in ^{18}O compared to Alaskan shells, which is essentially the same as the difference in precipitation $\delta^{18}O$ values between the two regions (5.2‰). This further verifies the strong influence of precipitation $\delta^{18}O$ upon snail oxygen isotopes at polar regions. Even though snail

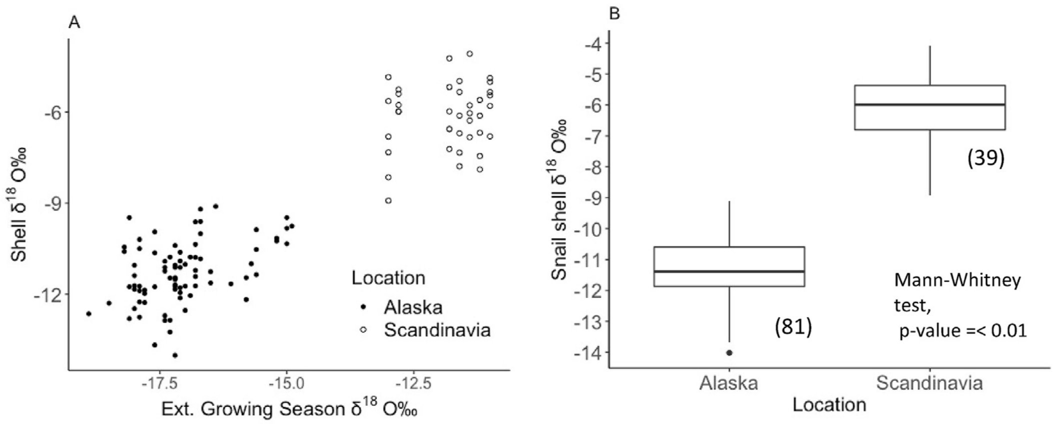

Fig. 6. (A) Scatterplot of all collected snail (all species combined) shell $\delta^{18}O$ values from Alaska (closed circles) and Scandinavia (open circles) vs. extended growing season (April–October) precipitation $\delta^{18}O$ values. (B) Boxplot of snail shell $\delta^{18}O$ values of Alaska and Scandinavia. Box extremes represent quartile distribution. Whiskers depict range of values. Solid line inside the plot depicts the median $\delta^{18}O$ value. Numbers in the parentheses represent the number of shells analyzed. Dot depicts outlier.

samples from both transects were not collected using equal protocols, because they come from various field trips throughout different years and collectors, the comparison of oxygen isotope values of snails between regions is not compromised. Land snail $\delta^{18}O$ values merely reflect the environmental conditions when snails lived and grew their shells, and these values are independent of how snails are collected and curated. Thus, isotopic comparisons are appropriate as long as species identification and geographical context are presented.

6.2. Natural range of modern snail oxygen isotope values

Previously published modern land snail shell $\delta^{18}O$ values, which were collected globally from locations between the latitudes 43 °S and 66 °N, exhibit values that range from −11.9‰ to +4.5‰ (Yapp, 1979; Goodfriend and Magaritz, 1987; Bonadonna et al., 1999; Yanes, 2015; Yanes et al., 2019). These isotopic values are derived from a wide variety of habitats (from deserts to tropical forests) and species of variable sizes (from minute to large) and trophic status (from herbivores to carnivores) (Wilbur, 1983). The new modern land snail shell $\delta^{18}O$ values reported in this study expand this range on the negative side down to −14.0‰ (Fig. 7), which are the most negative $\delta^{18}O$ values ever reported for modern land snail shells.

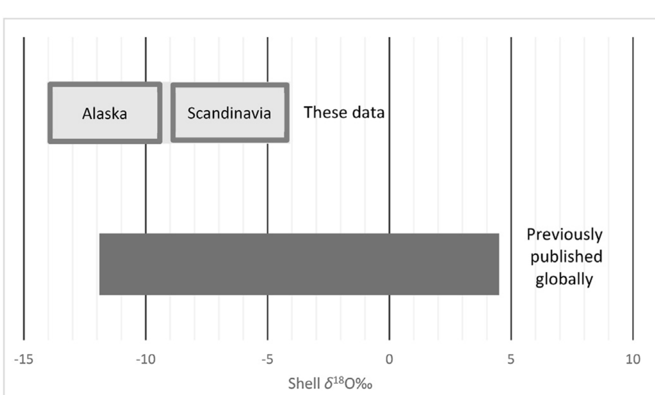

Fig. 7. Ranges of published modern land snail shell $\delta^{18}O$ values globally (Yapp, 1979; Goodfriend and Magaritz, 1987; Bonadonna et al., 1999; Yanes, 2015; Yanes et al., 2019) compared to the range of modern land snail shell $\delta^{18}O$ values produced in this study for Alaskan and Scandinavian snails.

This work illustrates that studying land snails from new regions can expand the known natural range of isotope values in snail shells.

6.3. Relationship between oxygen isotope values of snails and body size

In Alaska and Scandinavia, larger body size species were found to have significantly higher $\delta^{18}O$ values than smaller species. This general pattern has been previously observed at lower latitudes in Europe (Yanes et al., 2012; Yanes and Fernández-Lopez-de-Pablo, 2017; Bullard et al., 2017) and North America (Yanes et al., 2017; Rech et al., 2021). The physiological mechanisms underlying this pattern remain opaque, especially given that larger snails have a greater ability to burrow deeply into soil/talus/woody debris and have a smaller surface-to-volume ratio, which should both lead to lower evaporation rates. Regardless of the cause, clearly, the $\delta^{18}O$ values should be corrected for body size if an analysis pools results spanning taxa of approximately a half order of magnitude or more in biovolume.

6.4. Snail evaporative steady-state flux balance mixing model

Shell $\delta^{18}O$ values from Alaska and Scandinavia were examined using the evaporative steady-state flux balance-mixing model published by Balakrishnan and Yapp (2004). This model assumes that precipitation $\delta^{18}O$, water vapor $\delta^{18}O$, relative humidity, and air temperature are the most important factors that control snail body fluid and shell $\delta^{18}O$ values (Balakrishnan and Yapp, 2004). Model calculations also assume that precipitation and water vapor $\delta^{18}O$ values are in isotopic equilibrium and snail body water is lost primarily through evaporation (Balakrishnan and Yapp, 2004). Although this model incorporates a large number of unknown variables and assumptions, it can provide a semiquantitative estimate of the potential relative humidity preferred by the studied snail species in these cold regions. Three plausible model scenarios were considered.

(1) Annual scenario. Here we assume that snails were able to grow for most of the year supposing that polar snails should exhibit high supercooling abilities and may be able to be active at certain times of the day/night even during freezing conditions (Fig. 8A). If this scenario is credible, then Scandinavian snails, with a shell $\delta^{18}O$ value of −6.2‰, grew at times when the temperature was on average ~1 °C,

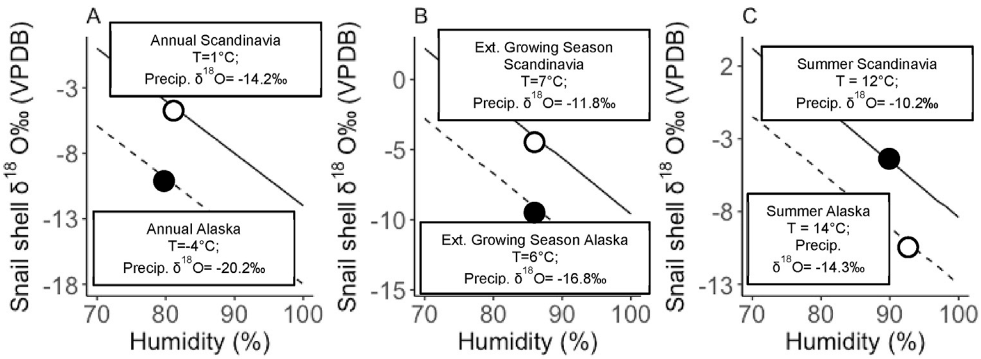

Fig. 8. Calculated relationships of land snail shell $\delta^{18}O$ values as a function of relative humidity (RH) using the evaporative steady-state flux balance-mixing model by Balakrishnan and Yapp (2004). Curves were calculated for three hypothetical snail active periods: (A) annual (B) months April–October (extended growing season), and (C) months June–August (summer). (A) If snails grew during most of the year, the model predicts that a shell with a $\delta^{18}O$ value of −11% for Alaska (dashed line) and −6% for Scandinavia (solid line) should have grown at times when RH was about 78% (black dot) or 80% (white dot), respectively. (B) If snails grew mostly during the extended growing season, April–October, the model predicts that a shell with a $\delta^{18}O$ value of −11% for Alaska (dashed line) and −6% for Scandinavia (solid line) should have grown at times when RH was about 86% (black dot) or 86% (white dot), respectively. (C) If snails grew during the summer season only, the model predicts that a shell with a $\delta^{18}O$ value of −11% for Alaska (dashed line) and −6% for Scandinavia (solid line) should have grown at times when RH was about 92% (black dot) or 90% (white dot), respectively.

precipitation $\delta^{18}O$ was −14.2‰, and RH was ~80%. Furthermore, Alaskan snails, with a shell $\delta^{18}O$ value of −11.3‰ were active at average temperatures of −4 °C, precipitation $\delta^{18}O$ of −20.2‰, and RH values of ~78%. In this situation, snails must have been active at times when RH was around 78–80% in both regions.

(2) Extended growing season scenario. This second situation assumes that organisms were able to be active and grow their shell beyond the summer months, from April to October (Fig. 8B). If this alternative scenario is correct, Scandinavian snails, with an average shell $\delta^{18}O$ value of −6.2‰, grew shell material at times when the temperature was on average ~7 °C, precipitation $\delta^{18}O$ was −11.8‰, and RH was ~86%. Moreover, Alaskan snails, with an average shell $\delta^{18}O$ value of −11.3‰ should have grown at temperatures of ~6 °C, precipitation $\delta^{18}O$ values of −16.8‰, and RH values of ~86%. This scenario predicts that snails were active during consistently high RH values of ~86% in Scandinavia and Alaska.

(3) Summer scenario. This scenario assumes that snails primarily grew their shells during the summer months of June-July-August (Fig. 8C). If correct, then Scandinavian snails, with an average shell $\delta^{18}O$ value of −6.2‰, grew at temperatures of ~12 °C, summer rain $\delta^{18}O$ values of −10.2‰, and RH values of ~90%. Similarly, Alaskan snails, with an average shell $\delta^{18}O$ value of −11.3‰ precipitated shell material when temperatures were ~14 °C, summer rain $\delta^{18}O$ values of −14.3‰, and RH values of ~92%. This summer scenario predicts that snails were mostly active during very high RH conditions of ~90–92% in both study regions.

Although we are not certain which of the three proposed scenarios best replicates snail active periods in polar regions, and scenario 1 (year-round active period) is highly unrealistic, we propose that the second scenario (the extended growing season active period) may be the most plausible based on what we know about general snail physiology and ecology. Interestingly, even though model input parameters (climate) are different for Scandinavia and Alaska, the model predicts similar RH conditions for snails in either region. The model predicts that the investigated small-size snails should have been active at very humid conditions, certainly above 75%, but most likely above 85%. Are these very high RH values reasonable for the study area? While the average RH values for Alaska and Scandinavia are around 70%, snails appear to have grown at significantly higher RH conditions, which can be reached at night, during rainy days, or by buffering with specific microhabitats in which the snails lived.

6.5. Spatial trends in oxygen isotope values of land snails

Bowen and Wilkinson (2002) illustrated that variations in precipitation $\delta^{18}O$ values can be best explained by the nonlinear variation of air temperature along latitude following the Rayleigh fractionation process between liquid water and water vapor. This relationship is described by the following second-order polynomial equation:

$$\delta^{18}O_{global\ precip.} = -0.0051(\text{Latitude})^2 + 0.1805(\text{Latitude}) - 5.247 \quad (5)$$

Yanes et al. (2019) compared the global meteoric precipitation equation Eq. (5) to all published low elevation land snail shell $\delta^{18}O$ values in North America along latitude (Eq. (6)) and found striking similarity with precipitation.

$$\delta^{18}O_{snail\ shell} = -0.0056(\text{Latitude})^2 + 0.2178(\text{Latitude}) - 2.727 \quad (6)$$

Adding our data from Alaska, and expanding to all altitudes, we observed consistent similarities (Eq. (7), Fig. 9A) (see Fig. 10).

$$\delta^{18}O_{snail\ shell} = -0.01(\text{Latitude})^2 + 0.14(\text{Latitude}) - 1.55 \quad (7)$$

The same relationship found between published North America data and precipitation $\delta^{18}O$ held true when comparing the global meteoric precipitation equation (Eq. (5)) to all land snail shell $\delta^{18}O$ values in Europe, including the Scandinavian transect, along latitude (Eq. (7), Fig. 9B).

$$\delta^{18}O_{snail\ shell} = -0.01(\text{Latitude})^2 + 0.23(\text{Latitude}) - 3.43 \quad (8)$$

When gathering all previously published low elevation, <500 m above sea level, global snail shell $\delta^{18}O$ data, including both transects analyzed in this study, the following equation was produced:

$$\delta^{18}O_{snail\ shell} = -0.01(\text{Latitude})^2 + 0.48(\text{Latitude}) - 8.38 \quad (9)$$

Europe, North America, and global snail shell $\delta^{18}O$ values along

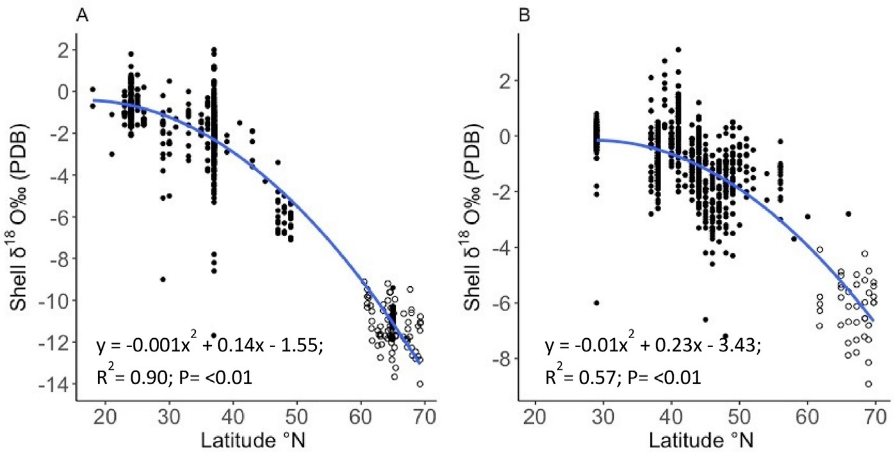

Fig. 9. (A) Alaskan snail shell $\delta^{18}O$ values (open circles) combined with previously published modern snail shell $\delta^{18}O$ values from North America (closed circles). (B) Scandinavian snail shell $\delta^{18}O$ values (open circles) combined with previously published modern snail shell $\delta^{18}O$ values from Europe (closed circles).

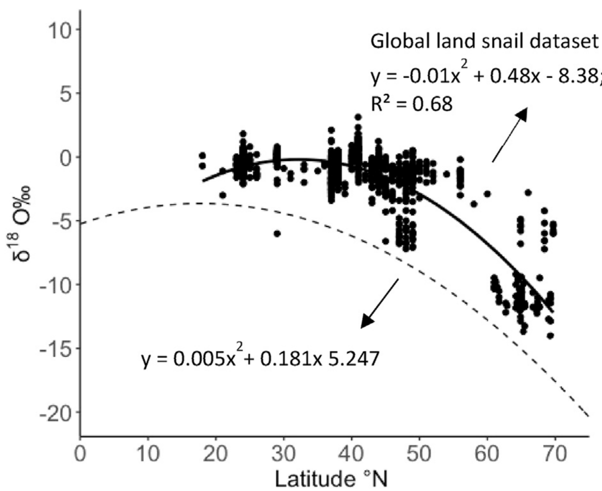

Fig. 10. Comparison between $\delta^{18}O$ values of global meteoric precipitation (dashed line) by Bowen and Wilkinson (2002) in SMOW scale and published global low elevation (<500 m a.s.l) land snail shell $\delta^{18}O$ values in VPDB scale (solid line) along latitude. Acronyms: VPDB= Vienna Pee Dee Belemnite; SMOW = standard mean ocean water; m a.s.l. = meters above sea level.

latitude generated here are comparable to global meteoric precipitation equation by Bowen and Wilkinson (2002), even when combining different snail species. Noise from variations at the microhabitat scale and taxonomy are lost at continental spatial scale making land snails a remarkably good proxy for precipitation $\delta^{18}O$ at coarse scales, similar to the findings of Yanes et al. (2019).

7. Conclusions

$\delta^{18}O$ values of land snail shells collected from a 60–70 °N latitude transect in Alaska primarily responded to changes in air temperature and precipitation $\delta^{18}O$ and not to total precipitation amount or relative humidity. This suggests that shell $\delta^{18}O$ values in Alaska from fossil shells could be applied as a paleo-precipitation $\delta^{18}O$ proxy. In contrast, shell $\delta^{18}O$ values from snails retrieved from a transect in Scandinavia at similar latitudes did not show a statistically significant relationship with local climate parameters, which is likely related to a subdued climatic gradient in Scandinavia compared to a more pronounced climate gradient transect in Alaska. Importantly, average shell $\delta^{18}O$ values from Scandinavia were, on average, ~5.1‰ enriched in ^{18}O compared to snails from Alaska, which is in agreement with the difference in precipitation $\delta^{18}O$ (~5.2‰) between the two regions.

This work presents the highest latitude and most negative shell $\delta^{18}O$ results of modern snails ever reported. In addition, snail $\delta^{18}O$ values from this study are concordant with previously published data from middle and lower latitudes of America and Europe, which further confirms that land snail shell $\delta^{18}O$ values primarily reflect variations in precipitation $\delta^{18}O$. Intriguingly, shell $\delta^{18}O$ values in the current study positively correlated with snail body size, with larger species consistently exhibiting higher $\delta^{18}O$ values, which calls for attention when using multiple species in paleoclimate studies at the local and microhabitat scale. However, on coarse spatial scales with significant variability in climate parameters at the continental to global scale, isotopic differences between snail species, size, microhabitat, and active period preferences may not be as critical.

Author contributions

Catherine B. Nield: Conceptualization, Formal analysis, Investigation, Writing – original draft, Visualization, Funding acquisition. **Yurena Yanes**: Conceptualization, Formal analysis, Investigation, Writing – review & editing, Supervision, Funding acquisition. **Jeffrey S. Pigati**: Conceptualization, Writing – review & editing, Funding acquisition. **Jason A. Rech**: Conceptualization, Writing – review & editing, Funding acquisition. **Ted von Proschwitz**: Writing – review & editing, Resources. **Jeffrey C. Nekola**: Conceptualization, Writing – review & editing, Resources, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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