Palaeogeography, Palaeoclimatology, Palaeoecology 532 (2019) 109243

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Growth pattern and oxygen isotopic systematics of modern freshwater mollusks along an elevation transect: Implications for paleoclimate reconstruction

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ARTICLE INFO

Keywords:
Sclerochronology
Seasonality
Asian Monsoon
Gastropods
Temperature archives
Modern lakes

ABSTRACT

Fossil mollusk shells are widely distributed in the geologic records and their oxygen isotopic compositions have been used to reconstruct seasonality, local climatic and elevation conditions. However, interpretation of isotope data from fossil shells to estimate paleoclimate and elevation is often ambiguous. This study examines the oxygen isotopic systematics of modern freshwater gastropods (*Bellamya* and *Radix*) shells along an elevation/climate transect in the Asian monsoon region of China to improve the accuracy of paleoclimate and paleoelevation reconstruction using stable isotopes in fossil shells. The results from sclerochronological analyses of the shells show that the intra-shell oxygen isotopic pattern is determined by seasonal variations in lake water temperature and water isotopic composition as well as the life cycle of the organism. Both *Bellamya* and *Radix* appear to grow throughout the year in lakes where water temperature does not fall below 13 °C. *Radix* in the high elevation cold habitat, although prefers to grow in the warmer months, can survive through the freezing temperature. The $\delta^{18}O$ patterns in the shells are similar across the elevation/climate transect, showing high $\delta^{18}O$ values in the winter months and low $\delta^{18}O$ values in the summer months, consistent with the expected pattern in Asian monsoon region. The average growth rates of the shells were highest at the lowest elevation site (warm and humid climate) but were similar at the mid to high elevation sites. For large shells (> 2.2 cm for *Bellamya* and > 1.4 cm for *Radix*), average growth temperatures, calculated using the aragonite oxygen isotope thermometer, closely approximate the annual mean water temperature while their intra-shell variability is a good proxy for the amplitude of seasonal variations in monthly air temperature. This suggests that large shells of both *Bellamya* and *Radix* are excellent archives of lake environmental conditions and most suitable for paleoenvironmental studies.

1. Introduction

Oxygen isotope analyses of biogenic carbonates have long been established as valuable tools to reconstruct the past climatic and environmental conditions (e.g., Urey et al., 1951; Lowenstam and Epstein, 1954; Woodruff et al., 1981; Shackleton, 1986; Miller et al., 1987). Previous studies on marine and freshwater mollusk shells (both bivalves and gastropods) have shown that seasonal variations in water temperature and water chemistry control the oxygen isotopic signatures of the shells (e.g. Arthur et al., 1983; Wefer and Berger, 1991; Andreasson and Schmitz, 1996; Purton and Brasier, 1997; Dettman et al., 1999; Leng and Lewis, 2014; Parker et al., 2017). Many mollusk shells are composed of the carbonate mineral aragonite, and the equilibrium fractionation factor and temperature relationship for oxygen isotopes in aragonite has been calibrated through studies of both biogenic aragonite (Grossman and Ku, 1986; Thorrold et al., 1997; Dettman et al., 1999) and synthetic aragonite (Romanek et al., 1992; Kim and O'Neil, 1997; Kim et al., 2007). Using this relationship, if any two of the three parameters - water temperature, water $\delta^{18}O$ and shell $\delta^{18}O$ are known, the third can be calculated for any mollusk shells consisting of

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https://doi.org/10.1016/j.palaeo.2019.109243
Received 22 January 2019; Received in revised form 16 June 2019; Accepted 21 June 2019
Available online 29 June 2019
0031-0182/

aragonite. Marine mollusk carbonate often precipitates in oxygen isotopic equilibrium with the ambient water (e.g., Wefer and Berger, 1991; Lécuyer et al., 2004), but "vital effect" (i.e., isotopic disequilibrium) has been observed in some marine mollusk shells (Fenger et al., 2007 and the reference therein). Similarly, freshwater mollusk shells often appear to be formed in equilibrium with environmental water (e.g., Dettman et al., 1999, 2004; Kelemen et al., 2017). For example, Dettman et al. (1999, 2004), through detailed isotope analysis of growth layers in mollusk shells (unionid bivalves) and monitoring of both the temperature and the oxygen isotopic composition of river water over a course of nearly 2 years, have demonstrated that in river systems, the measured $\delta^{18}O$ values of river water are consistent with the predicted values from the $\delta^{18}O$ values of the growth layers in the shells of unionid bivalves and the measured water temperatures using the equilibrium fractionation factor and temperature relationship for aragonite. They have also shown that unionid bivalves in temperate region do not produce new shell materials when temperature falls below 12 °C and thus their bulk shell $\delta^{18}O$ values are biased towards warm growing season. Other studies have reported similar bias towards warmer temperature in other freshwater bivalves such as *Corbicula* and *Dreissena* (Joy, 1985; Neumann et al., 1993). Fossil freshwater mollusk shells are widespread in the geologic records and their oxygen and clumped isotopic compositions have been used to reconstruct paleoclimates and paleoelevations (e.g., Dettman et al., 2001; Murphy et al., 2009; Saylor et al., 2009; Wang et al., 2008, 2013; Huntington et al., 2015). Possible bias in shell growth could affect the accuracy of paleoclimate and paleoelevation reconstruction from fossil shells.

This study examines oxygen isotopic systematics in modern *Radix* sp. and *Bellamya* sp. from lakes along an elevation/climate transect spanning an elevation range from near sea level to > 4 km above sea level. The genera were chosen for two main reasons: (1) modern *Radix* and *Bellamya* snails occur worldwide and thus have great potential for isotope study of ancient continental climates; and (2) they are abundant in Late Cenozoic sedimentary deposits and are potential archives of paleotemperature and paleoelevation. The primary objective of this study is to assess if modern freshwater mollusk shells can faithfully record the present-day climate and elevation condition and to address the following questions:

- How does seasonal variation in lake water temperature influence the growth pattern and life span of these freshwater snails?
- How do life cycle and seasonal growth pattern affect the temperatures calculated from the oxygen isotope compositions of bulk shell and lake water using the carbonate oxygen isotope thermometer?
- Does the growth pattern within the same species of gastropods vary with elevation/climate?

The results have important implications for paleoclimate reconstructions using stable isotope data from fossil freshwater shells.

2. Study sites

We collected and analyzed the stable isotope compositions of modern freshwater snail shells and water samples from three lakes (i.e., Fuxian Lake, Liuxihe Reservoir and Lake Manasarovar) located at different elevations in the Asian summer monsoon region in south and southwest China. These lakes form an elevation/climate transect stretching from ~170 m above sea level (a.s.l.) to ~4600 m a.s.l. (Fig. 1).

2.1. Fuxian Lake

Fuxian Lake (24°17′–24°37′ N, 102°49′–102°57′ E, 1721 m a.s.l.), the third largest lake in China, is located in Yunnan Province in Southwest China, about 60 km southeast of the capital city Kunming (Fig. 1). It is an oligotrophic lake with a mean depth of 89.6 m, a maximum depth of 155 m and a water surface area of 212 km^2. The climate in this region is characterized by mild winters and cool summers (IAEA/WMO, 2018). The long-term average annual temperature of lake water varied from 13 °C in January to 23 °C in August, with an average annual water temperature of 17.6 ± 3.8 °C for the period of 1967–2007 (Gu, 2008). The annual mean temperatures in the surface and bottom water layers are 19.1 ± 1.2 °C (SE) and 14.2 ± 0.1 °C, respectively (De Cui et al., 2008). The mean annual air temperature (MAAT) is 15.6 °C and the average annual precipitation (AP) is 942 mm (900–1200 mm) in the lake area (De Cui et al., 2008). Most of the precipitation in the area falls in the months of May to October, which is controlled by both the Indian Summer Monsoon (ISM) and the East Asian Summer Monsoon (EASM), although ISM is more dominant in this region (Araguas-Araguas et al., 1998). Fuxian Lake receives water from multiple sources (e.g. surrounding streams, rivers, underground springs, direct precipitation on the lake) but has only one discharge channel through Haiku River in the east (Hai-Ao and Jing-Lu, 2009). Therefore, it behaves more like a closed lake system with a long water residence time (Liu et al., 2014).

2.2. Liuxihe Reservoir

Liuxihe Reservoir (23°34′ N, 113°46′ E; 168 m a.s.l.) is located just north of the Tropic of Cancer, ~80 km north of Guangzhou - the capital city of Guangdong province in south China (Fig. 1). The reservoir was established in 1958 with the completion of the Liuxihe Dam on the Liuxi river. It covers 539 km^2 and has a mean depth of 22 m, a maximum depth of 73 m and a water surface area of 14.9 km^2. According to the lake classification by Lewis (1983), Liuxihe reservoir is a warm monomictic lake that is stratified nearly 10 months of the year (Wang et al., 2011). Diatom assemblages in the sediment record from Liuxihe reservoir indicate that environment close to the dam changed from riverine to lacustrine condition within 5 years of the dam construction (Liu et al., 2012). The area has a tropical and subtropical climate. Almost 80% of the annual precipitation occurs during the months of April to September controlled by the EASM while the winter months (October to March) are relatively dry (Xiao et al., 2011). The average water residence time of the reservoir is relatively short and estimated to be around 120 days, varying from ~30 days in wet season up to 340 days in the dry season (Liu et al., 2012). The residence time is particularly short in the wet season due to large inflow volume of water. The watershed of the reservoir contains hills covered with forests and is less affected by human activity (Wang et al., 2011). Long-term average (1958–2012) temperature and precipitation data from Conghua Meteorological Station (Guangzhou) near the reservoir show that the MAAT in the area is 21.5 ± 5.8 °C and the average monthly air temperature varies from 12.5 ± 1.5 °C for January to 28.5 ± 0.6 °C for July. The minimum monthly air temperature recorded for the same period is 9 °C (January 2011) and the maximum is 31 °C (July 2003). The annual average precipitation for the same period is 156.8 ± 32 mm. Surface water temperature, on the other hand, varies from 14 °C in January to as high as 32 °C in August with an average of 23 ± 3 °C during the period of 2000–2007 (Peng et al., 2012).

2.3. Lake Manasarovar

Lake Manasarovar (30°34′–30°47′ N, 81°22′–81°37′ E, 4590 m a.s.l.), also known as Mapam Yumco, is located in southwest Tibet on the Qinghai–Tibetan Plateau (Fig. 1). The lake is one of the highest freshwater lakes in the world. Lake Manasarovar has a mean depth of 46 m, a maximum depth of 72.6 m, and a water surface area of 412 km^2. The lake is fed by both precipitation and melt-water runoff and has only one transient outlet to neighboring lake La'nga Co (Yao et al., 2015). The climate in the lake area is cold and arid, with precipitation controlled primarily by the ISM (Yao et al., 2009). The MAAT in this region is 3.6 °C (between 0.3 and 6 °C) as recorded at the Pulan County and

Fig. 1. Location map.
(Google maps: Imagery © 2016 Landsat, Data SIO, NOAA, U.S. Navy, NGA, GEBCO, Map data © 2016 Google, ZENRIN) showing the lakes from where the samples were collected.

Burang County weather stations at slightly lower elevations (Yao et al., 2009; Yao et al., 2015). The estimated MAAT and AP for the lake area based on satellite data are 3 °C and 154 mm/yr, respectively (Niu et al., 2007). Winter usually experiences subzero temperatures, and frozen ground and water bodies. Summer, on the other hand, is significantly warmer, with water temperature reaching up to 15 °C (Yao et al., 2009). The lake and surrounding area receive most of the annual precipitation during the summer monsoon season (June to August). There is no long-term surface water temperature record for Lake Manasarovar. Hourly surface water temperatures recorded continuously throughout a year at lake Ngangla Ring Cuo (a large closed-basin lake located about 160 km northeast of Lake Manasarovar on the plateau) show that the surface water temperatures varied from 0 °C in the winter to a maximum of 17 °C on the warmest day in the summer. The mean annual water temperature (MAWT) was 7 °C and an average summer water temperature was 12.8 °C (Huntington et al., 2015).

3. Ecology and habitats of *Bellamya* and *Radix*

3.1. Bellamya

Bellamya is a freshwater mollusk with a wide geographic distribution and is found in parts of North America, Africa, and Asia. The genus *Bellamya* belongs to the family Viviparidae. It is a large freshwater snail that may reach a shell length of up to 70 mm (Solomon et al., 2010). They are found in shallow littoral zones, ranging in water depth from 0.3 to 3 m, of calm freshwater water bodies with rooted aquatic vegetation, such as lakes or ponds with sandy and muddy substrates, slow flowing streams, irrigation channels, rice fields, and roadside moats (Schmeck, 1942; Jokinen, 1982). *Bellamya* is a filter feeder and detritivore that feeds on periphyton, decaying plant tissues, and occasionally on carrion (Browne, 1978).

Male *Bellamya* typically can live up to 3 years, and females tends to live up to 5 years. Female gives birth to live, fully-developed offspring (Jokinen, 1982). *Bellamya* may survive within a wide range of temperatures (0°–30 °C), although their reproductive ability reduces in the winter (Jokinen, 1982; Karatayev et al., 2009). In cold winters, *Bellamya chinensis* either move into deeper water (Jokinen, 1982) or burrow into sediments for hibernation (Ribi et al., 1986). *Bellamya* shells tend to display short intervals with thicker or darker growth layers in ornamentation reflecting a decrease in rate of growth. Schmitz and Andreasson (2001) have observed that $\delta^{18}O$ values of *Bellamya* shells from temperate regions show a noticeable positive shift during the winter and these peaks are correlated to the winter growth bands.

3.2. Radix

Radix has a wide geographic distribution because of its ability to survive in extreme boreal climate (Økland, 1990; White et al., 2008; Von Oheimb et al., 2011; Taft et al., 2012). The genus *Radix* is a member of the family Lymnaeidae and subclass Pulmonata. Although the shell of a fully-grown adult *Radix* could reach up to ~30 mm in height (Jokinen, 1982) and 25 mm in width (Clarke, 1981), most of the individuals only grow nearly half of their maximum size in a population. They are found in both freshwater and brackish water, in quiet environments such as in shallow littoral zones of lakes, slow flowing rivers, irrigation channels, and bays (Økland, 1990; Mischke et al., 2010; Taft et al., 2012). The genus can also sustain in water bodies that are covered in ice for more than half a year in extreme environments of Siberia, Norway, Tibetan Plateau, and eastern Pamirs (Økland, 1990; Mischke et al., 2010; Taft et al., 2012). *Radix* usually has a life span of about one year and can survive in the freezing winter by migrating from littoral zones into the deeper water and staying active under the ice cover in frozen lakes (e.g., Taft et al., 2012). Thus, it appears that there is no "shut-down" temperature at which the organism ceases to grow. Supply of nutrients is a more growth-limiting factor for the organisms than the freezing temperature condition.

Radix is a herbi-detritivore confined to the upper part of benthic zone, usually at a depth of < 5 m, and feeds on cyanobacteria, diatoms, protozoa and phytoplankton (Stift et al., 2004; Taft et al., 2012). These snails move regularly in search of nutrients and therefore the sampling location of an individual might be different from the location where it had originated.

4. Materials and methods

4.1. Materials

Modern mollusk specimens were collected from Fuxian Lake in the summer of 2013 and 2016, from Liuxihe Reservoir in early July of 2013, and from Lake Manasarovar in August of 2007 and 2013. Both *Bellamya* sp. and *Radix* sp. were found in Fuxian Lake and Liuxihe Reservoir, but only *Radix* sp. was found in Lake Manasarovar. This is likely because *Bellamya* cannot withstand an extended period of freezing temperatures (Jokinen, 1982; Karatayev et al., 2009). All the *Radix* specimens from Liuxihe Reservoir were collected from live snails due to the absence of well-preserved shells along the lakeshore. Live snails were picked from shallow water areas near the lakeshore. *Bellamya* from Liuxihe Reservoir and all the other shells used for sclerochronological analyses from Fuxian Lake and Lake Manasarovar were collected from the shell accumulation zone along the lakeshore. Shells analyzed in this work were well preserved and displayed no signs of damage. Water samples were collected on a monthly basis from the low elevation and mid elevation lakes (Fuxian Lake and Liuxihe Reservoir) for more than a year during the period of 2013–2016 for stable isotope analyses. For the high elevation lake on the Tibetan Plateau, only two lake water samples were collected in 2007 from the east side of the lake due to difficulty in access as the lake is in a remote area with extreme climatic and topographic conditions and only accessible during a limited time period of the year. We also collected a rain sample at Holy Land Hotel near Lake Manasarovar in August 2010.

4.2. Subsampling and isotopic analysis of mollusk shells

The shells were cleaned with 30% H_2O_2 in an ultrasonic bath for at least 15 min to remove organic matter and inorganic particles from the surfaces followed by rinsing with DI water and drying at room temperature. The shells were then subsampled along the ontogenetic spiral of growth (i.e., parallel to the growth lines) using a slow speed drill with a diamond-tipped drill bit (tungsten carbide bit coated with diamonds) of 0.1 mm diameter. Sampling began from the youngest part of the shell at the aperture moving sequentially towards the older part up to the apex (the oldest part of a shell). To procure a minimum of 150 μg sample powder (typically 150–320 μg), the diameter of the drilled hole varied up to 1 mm depending on its position along the shell. The holes were drilled adjacent to each other in order to capture the highest possible resolution in seasonal variations recorded by the shell during its lifespan (Fig. 2). Samples are thus numbered according to serial sample number and not in absolute scale units. The numbering start at the aperture with serial number 0 for each shell.

Drilled fractions were collected in 10 mm borosilicate vials and dried overnight at 70 °C. The vials were then sealed with rubber septa and flushed with helium for 10 min. 100% phosphoric acid was injected into individual flushed vial. The vials were left at 25 °C for at least 6 h for phosphoric acid to react with the aragonite. CO_2 released from the reaction was analyzed for oxygen isotope ratios using a GasBench II connected to a Thermo Finnigan MAT DELTA^{plus} XP stable isotope ratio mass spectrometer (IRMS) at the Florida State University. The results are reported in standard δ notation as $\delta^{18}O_{Ar}$ in per mil (‰) relative to the international carbonate standard VPDB. Analytical precision based on repeated analyses of lab standards over the project period is ± 0.1‰ (1σ) or better for $\delta^{18}O_{Ar}$. Carbonate standards that were used to calibrate the $\delta^{18}O$ values of the mollusk samples are NBS-19 ($\delta^{18}O_{VPDB}$: −2.2‰), PDA ($\delta^{18}O_{VPDB}$: −5.34‰), Roy-cc ($\delta^{18}O_{VPDB}$: −12.02‰) and MERK ($\delta^{18}O_{VPDB}$: −16.2‰), and YW-CC-st-1 ($\delta^{18}O_{VPDB}$: −23.5‰).

4.3. $\delta^{18}O$ and δ^2H analyses of water samples

Oxygen and hydrogen isotopic compositions of the lake water samples were analyzed using traditional CO_2 and H_2 equilibration methods (Epstein and Mayeda, 1953; Thermo Finnigan Operating Manual). 500 μl of water samples were pipetted into 10 mm borosilicate vials each containing a platinum catalyst. Special care was taken to minimize evaporation during the transfer process. The vials were then flushed with 2% H_2 in He and were allowed to equilibrate isotopically at 23 °C for 2 h. The H_2 in the headspace of each vial was then introduced via a Finnigan Gas Bench II interface into the mass spectrometer for hydrogen isotope measurements. The sample vials were then flushed with 0.3% CO_2 in He and were equilibrated at 23 °C temperature for at least 20 h before headspace CO_2 was introduced into the IRMS for oxygen isotope measurements. The oxygen and hydrogen isotope data are reported in the standard δ notation as $\delta^{18}O_w$ and δ^2H_w values relative to the international standard VSMOW. Analytical precision on repeated analyses of water isotope standards over the period of analysis is ± 0.1‰ (1σ) for $\delta^{18}O_w$ and ± 2‰ for δ^2H_w. Water standards that were used to calibrate the isotope values of lake water are QD (δ^2H_{VSMOW}: −35.8‰; $\delta^{18}O_{VSMOW}$: −10.6‰), TB-TAP (δ^2H_{VSMOW}: −135.0‰; $\delta^{18}O_{VSMOW}$: -18.35‰), SLC-TAP (δ^2H_{VSMOW}: −121.7‰; $\delta^{18}O_{VSMOW}$: -16.2‰), YW-ST-1 (δ^2H_{VSMOW}: −11.6‰; $\delta^{18}O_{VSMOW}$: −2.18‰), and DI-evp (δ^2H_{VSMOW}: −6.1‰; $\delta^{18}O_{VSMOW}$: +0.1‰).

4.4. Estimating shell growth temperature

Studies have shown that the oxygen isotopic composition of mollusk carbonates, if precipitated in equilibrium with the ambient water, is a function of ambient temperature and the isotopic composition of environmental water during the shell accretion process (e.g., Epstein and Mayeda, 1953; Kim et al., 2007; Kelemen et al., 2017). We use the following aragonite-water isotope fractionation relationship of Kim et al. (2007) to calculate the growth temperatures from the $\delta^{18}O$ values of shells and lake water:

$$1000\ln\alpha_{aragonite-water} = 17.88 \pm 0.13(103/T) - 31.14 \pm 0.46 \quad (1)$$

where, $\alpha_{aragonite\text{-}water}$ is the equilibrium oxygen isotope fractionation factor between aragonite and water, T is the temperature of water in Kelvin. The calculated temperatures are compared with measured lake water temperatures in order to investigate the growth patterns of selected freshwater mollusks and the influence of seasonal temperature change on shell growth.

5. Results and interpretation

5.1. Isotopic compositions of water samples

Hydrogen and oxygen isotopic compositions of water samples (i.e., δ^2H_w and $\delta^{18}O_w$ values), along with their respective sampling locations and times, are summarized in Supplementary Table 1. As shown in Fig. 3, water samples from Lake Fuxian, Lake Manasarovar, and other freshwater lakes from Tibetan Plateau (TP) plot below the global meteoric water line (GMWL) indicating the effect of evaporation on lake water (Gonfiantini, 1986). Water samples from Liuxihe Reservoir, on the other hand, plot on or close to the GMWL, suggesting that evaporation did not significantly alter the reservoir water composition.

$\delta^{18}O_w$ of a lake is determined by several factors including $\delta^{18}O_w$ of precipitation, amount of precipitation over the watershed, evaporation, and lake water residence time (Wei and Gasse, 1999). $\delta^{18}O_w$ values of

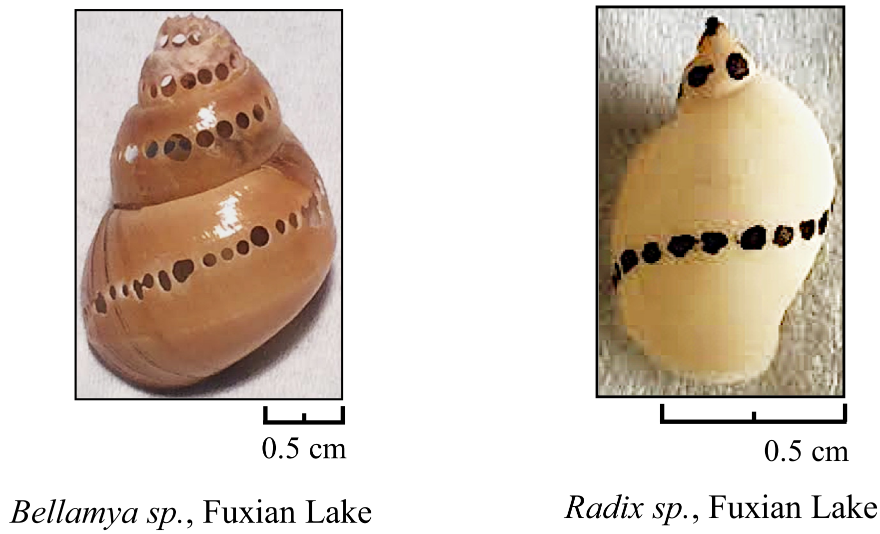

Fig. 2. Photos showing examples of serial sampled shells of *Bellamya* sp. and *Radix* sp.

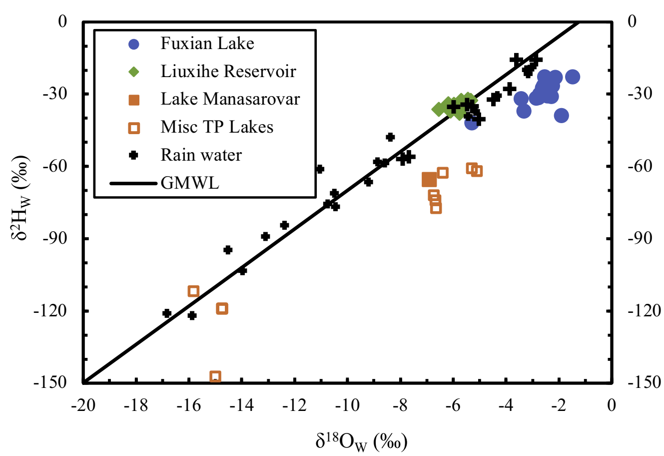

Fig. 3. Plot of δ^2H_W vs. $\delta^{18}O_W$ for lake and rain water samples. GMWL stands for the global meteoric water line.

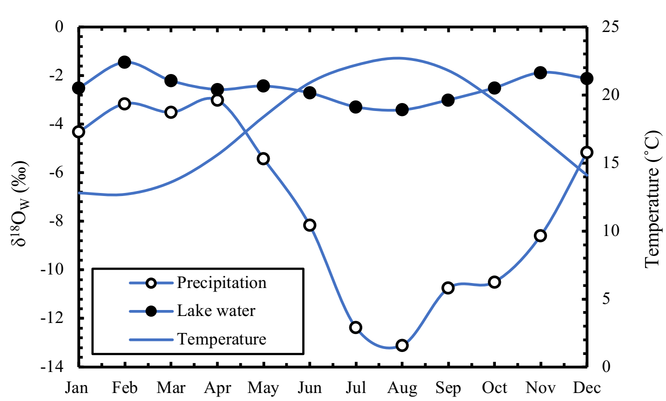

Fig. 4. Seasonal variations in the water temperature, and in the $\delta^{18}O_W$ of Fuxian Lake and $\delta^{18}O_W$ of precipitation in the area.

Fuxian Lake water display a small seasonal variability (< 2‰) from −3.4‰ in August to −1.5‰ in February during the three-year study period (2013–2016), with a mean of −2.5 ± 0.5‰ (n = 14) (Fig. 4). The relatively small variation in $\delta^{18}O_w$ of lake water can be attributed to a large well-mixed lake with a long water residence time (Liu et al., 2014). Fuxian Lake is located in the Asian summer monsoon region where summer precipitation has lower $\delta^{18}O_w$ values than winter precipitation, a pattern characterized by a progressively depleted $\delta^{18}O_w$ values towards the peak of rainfall season in August due to the "amount effect"- a strong negative correlation between the monthly average $\delta^{18}O_w$ values of precipitation and the precipitation amounts (Hodell et al., 1999; Wang et al., 2012). $\delta^{18}O_w$ values of Fuxian Lake water display a similar seasonal pattern (i.e., lower $\delta^{18}O_w$ in the summer and higher $\delta^{18}O_w$ in the winter) as seen in precipitation but in a much more subdued manner (Fig. 4). The annual weighted mean $\delta^{18}O_w$ of modern rainfall in this region recorded at the IAEA-GNIP (International Atomic Energy Agency Global Network of Isotopes in Precipitation) station in Kunming (25°02′ N, 102°68′ E, 1892 m a.s.l.) is −10.2 ± 1.1‰, with the weighed monthly average $\delta^{18}O_w$ of precipitation varying from −13.1‰ in August to −3.0‰ in April for the period of 1986–2003 (IAEA/WMO, 2018). Lake water, on the other hand, is considerably enriched in heavier isotope ^{18}O relative to precipitation, indicating significant effect of evaporation on lake water isotope composition as evaporation preferentially removes light water molecules, leaving the remaining water enriched in the heavy oxygen and hydrogen isotopes (Gonfiantini, 1986).

The $\delta^{18}O_w$ values of monthly water samples collected from the Liuxihe Reservoir during 2013–2016 varied from −6.5% in August to −4.1‰ in March, with an average of −5.7 ± 0.6‰ (n = 15), reflecting seasonal variations in the $\delta^{18}O_w$ of precipitation in the region (Fig. 5). The weighted monthly mean $\delta^{18}O_w$ of precipitation

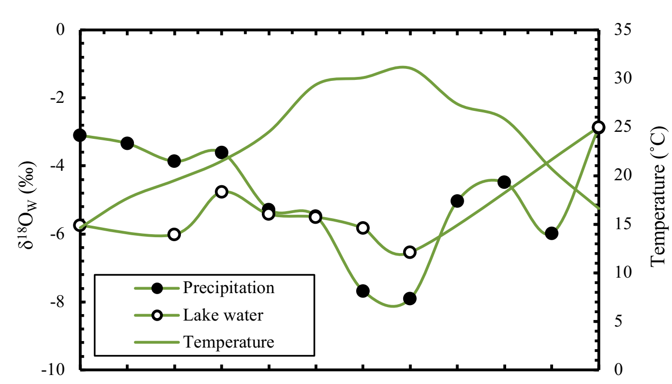

Fig. 5. $\delta^{18}O_{Ar}$ values of serial samples from individual shells and the calculated temperature (black smooth line) variation along the direction of shell growth during the life span of each snail analyzed from Fuxian Lake (A–F).

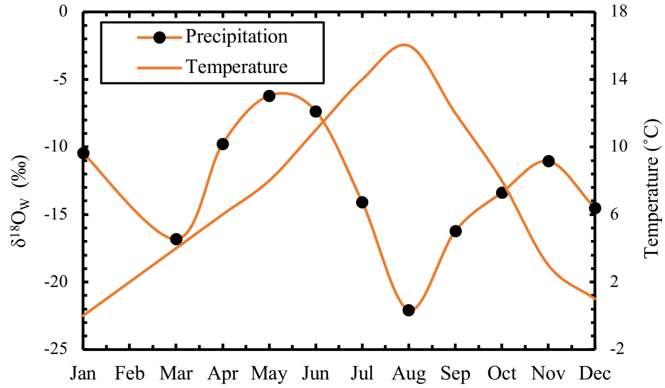

Fig. 6. Seasonal variations in the water temperature and $\delta^{18}O_w$ of Liuxihe Reservoir and precipitation in the area.

(1986–1989) in the region recorded in Guangzhou (23.13° N 113.32° E, 7 m a.s.l.) range from −7.6‰ in July to −3.7‰ in April (IAEA/WMO, 2018). The weighted annual mean $\delta^{18}O_w$ of precipitation in Guangzhou for the same period is −5.8 ± 1.1‰ (IAEA/WMO, 2018), which is similar to the measured average lake water $\delta^{18}O_w$ of −5.7 ± 0.6‰.

There are limited water isotope data available from the Lake Manasarovar area due to limited accessibility to the lake. The rain sample that we collected near the lake in August 2010 has a $\delta^{18}O_w$ of −26.7‰ (Supplementary Table 1). The two lake water samples that we collected in August 2007 yielded $\delta^{18}O_w$ values of −6.9 ± 0.1‰. Yao et al. (2009) collected water samples in August of 2005 from seven different locations in the lake, which yielded an average $\delta^{18}O_w$ value of −5.5 ± 3.0‰ for lake water. These measured water $\delta^{18}O_w$ values are considerably higher than the $\delta^{18}O_w$ value of the rain sample (−26.7‰) from the lake area and also higher than the annual weighted average $\delta^{18}O_w$ value of precipitation (−16.5 ± 1.7‰ for the period of 1986–1992) recorded at the IAEA-GNIP station in Lhasa (29.67° N, 91.10° E, 3658 m a.s.l.) (IAEA/WMO, 2018) (Fig. 6). The large difference in the $\delta^{18}O_w$ values between lake water and precipitation in the region is the result of intense evaporation that preferentially removes light isotopes from lake water (Gonfiantini, 1986).

5.2. Oxygen isotopic compositions of mollusk samples

Shells of *Bellamya* sp. and *Radix* sp. snails were serial-sampled for oxygen isotope analysis of aragonite, the mineral component of the shells (Table 1; Supplementary Tables 2–4). The oxygen isotope compositions of the serial aragonite samples (i.e., $\delta^{18}O_{Ar}$ values) from individual shells reveal significant isotopic variations along the growth direction of the shell (Supplementary Figs. 1–3), reflecting seasonal variations in lake environmental conditions during the growth of the shells.

5.2.1. Fuxian Lake

One specimen of *Bellamya* sp. and five specimens of *Radix* sp. from Fuxian Lake were serial-sampled, yielding a total of 215 samples, for isotope measurements (Supplementary Fig. 1). The size of the *Bellamya* shell as measured from apex to the basal inflection of the aperture was 2.3 cm with 4.2 whorls while most of the *Radix* shells were of ~1 cm or smaller with two exceptions (i.e., CJ-13s-6 and CJ-13s-19) with around 2.4 whorls (Table 1). The $\delta^{18}O_{Ar}$ values of the shells range from −4.5‰ to −1.1‰, with larger shells displaying larger intra-shell $\delta^{18}O_{Ar}$ variations than smaller shells (Supplementary Fig. 1; Supplementary Table 2). Shell CJ-13s-19 is the largest *Radix* shell analyzed from Fuxian Lake. This specimen is about 1.5 cm in size (at least 4 mm larger than the other *Radix* shells serial-sampled from Fuxian Lake). It also displays the largest variation in $\delta^{18}O_{Ar}$, indicating that it has captured a larger range of seasonal variation than the other serial sampled *Radix* shells.

Table 1
Summary table of all the analyzed mollusk shells from three locations.

Shell ID	Mollusk species	Location	Height (mm)	No. of whorls	No. of serial samples	Lifespan (Months)	Seasons captured	Estimated average growth rate (mm/month)	Distance between subsamples (mm)
FLS-2	Bellamya	Lake Fuxian	23	4.2	85	30	May–Dec1–Dec2–Dec3–July	0.8	0.3
CJ13s-6	Radix	Lake Fuxian	11	2.5	27	6	March–August	1.8	0.4
CJ13s-14	Radix	Lake Fuxian	10	2.5	26	6	May–Oct.	1.7	0.4
CJ13s-15	Radix	Lake Fuxian	9	2.3	23	5	May–Sept.	1.8	0.4
CJ13s-16	Radix	Lake Fuxian	10	2.4	24	6	Nov.–April	1.7	0.4
CJ13s-19	Radix	Lake Fuxian	15	2.4	30	12	August–June/July	1.3	0.5
LXH-B1	Bellamya	Liuxihe Reservoir	21	4.2	73	9	Mar–Dec1–Jan	2.3	0.3
LXH13s-8	Radix	Liuxihe Reservoir	10	2.3	19	4	Mar–July 6th	2.5	0.5
LXH13s-9	Radix	Liuxihe Reservoir	9	2.3	11	4	Mar/Apr–July 6th	2.2	0.8
LXH13s-10	Radix	Liuxihe Reservoir	10	2.4	18	4.5	Feb/Mar–July 6th	2.3	0.6
TB07s-2	Radix	Lake Manasarovar	10	2.5	26	6	May–Nov	1.7	0.4
TB07s-3	Radix	Lake Manasarovar	22	3.5	45	12	May1–May2	1.8	0.5

The intra-shell $\delta^{18}O_{Ar}$ variation observed in this shell is 2.8‰, consistent with that observed in the *Bellamya* shell from the same lake (Supplementary fig. 1 A and B). Shell CJ-13 s-16, like most of other *Radix* analyzed in this study, displays relatively small intra-shell $\delta^{18}O_{Ar}$ variability ($\Delta^{18}O = 0.8$). However, the $\delta^{18}O_{Ar}$ values of serial samples from this shell are higher than those from the other *Radix* specimens from the same lake (Supplementary Table 2).

5.2.2. Liuxihe Reservoir

One shell of *Bellamya* sp. and three shells of *Radix* sp. yielded a total of 121 serial samples from Liuxihe Reservoir for isotopic measurements (Supplementary Fig. 2). *Bellamya* shell displays a larger range of $\delta^{18}O_{Ar}$ variation than the *Radix* shells. The *Bellamya* specimen (LXH-B1) analyzed from Liuxihe Reservoir is 2.1 cm in height with about 4.2 whorls, similar to its counterpart from Fuxian Lake. The size of *Radix* shells varies from 0.9 cm to 1.0 cm with around 2.3 whorls (Table 1). $\delta^{18}O_{Ar}$ values recorded by the *Bellamya* shell range from −8.5‰ to −5.7‰ (Supplementary Fig. 2A). $\delta^{18}O_{Ar}$ values of the *Radix* shells vary from −8.2‰ to −6.6‰ and fall within the $\delta^{18}O_{Ar}$ range observed in the *Bellamya* shell (Supplementary Fig. 2). There are dark growth lines in the *Bellamya* shell; frequency of the growth lines increases towards the late ontogeny of the shell.

5.2.3. Lake Manasarovar

Two *Radix* shells TBS07s-2 and TBS07s-3 from Lake Manasarovar were serial-sampled, which yielded 72 samples for isotope analysis to examine seasonal growth patterns (Supplementary Fig. 3). Shell TBS07s-2 is 1 cm in length and has 2.5 whorls. The size of TBS07s-2 is 2.2 cm; it has 3.5 whorls (Table 1). The bigger shell size of TB07s-3, along with the higher number of whorls, indicates a longer lifespan compared to TB07-02. The $\delta^{18}O_{Ar}$ values of serial samples from shell TB07s-3 vary from −4.9‰ to −2.8‰, very similar to the $\delta^{18}O_{Ar}$ range of −5.0‰ to −2.9‰ observed in shell TB07–02 (Supplementary Table 4). Both *Radix* shells display relatively small intra-shell $\delta^{18}O_{Ar}$ variability ($\Delta^{18}O = \sim 2‰$) (Supplementary Fig. 3).

5.3. Reconstruction of shell growth patterns and temperatures

Using Eq. (1) and the annual average $\delta^{18}O_w$ (±1σ) of lake water (except for Lake Manasarovar), we calculated the temperatures from the $\delta^{18}O_{Ar}$ values of serial samples from each shell from our study sites (Figs. 7–9; Supplementary Tables 5–7).

5.3.1. Fuxian Lake

For the *Bellamya* shell (FLS-2), the calculated temperatures range from 14 ± 2 °C to 27 ± 2 °C (Fig. 7A) and are within the observed variation range of lake water temperature (Gu, 2008; our own measurements). The average of all calculated temperatures from this shell is 21 ± 4 °C, which is very close to the annual mean surface water temperature of 19.1 ± 1.2 °C (De Cui et al., 2008). Comparison of the calculated temperatures with the measured monthly average lake water temperature indicates that this individual lived for > 2 years and was likely born in May (or June) and died in June (or July) two years later (Fig. 7A). The growth patterns differ between juvenile and mature stages where the shell growth rate is reduced and the seasonal cycle is more distinct (Fig. 7A).

For the *Radix* shells, intra-shell isotopic and temperature patterns vary depending on the shell size (Fig. 7B–F). *Radix* usually has a lifespan of about one year and fully-grown adults can reach up to 2.5 cm in height (Økland, 1990; Taft et al., 2012). Most of our *Radix* shells analyzed from Fuxian Lake are about ~1 cm or smaller, with two exceptions (i.e., CJ-13s-6 and CJ-13s-19), and lived through only part of the year (Table 1), which explains the small intra-shell $\delta^{18}O_{Ar}$ and temperature variations in these smaller shells (Fig. 7B–D).

Comparison of the calculated temperatures (Fig. 7B–D) with measured water temperatures (Fig. 4) suggests that these smaller *Radix* shells were born and lived during the warm season between the months of May and November as they did not record any winter temperatures (< 15 °C), except shell CJ3s-16. The calculated growth temperatures for shell CJ3s-16 suggest that this individual was born probably in November, lived through the cold season and died in April/May (Figs. 7E and 4). The highest $\delta^{18}O_{Ar}$ value recorded by this shell likely represents growth in the coldest month (January). This suggests that *Radix* can reproduce and grow during the cool season in a mid-latitude lake like Fuxian Lake where the coldest water temperature (~13 °C) is substantially above the freezing temperature. The growth rate of this individual is similar to the average growth rates of other *Radix* shells analyzed from Fuxian Lake (Table 1).

The largest *Radix* shell analyzed from Fuxian Lake is specimen CJ-13s-19, which is about 1.5 cm in size, at least 4 mm larger than the other *Radix* shells serial-sampled from this lake (Table 1). The magnitude of its intra-shell $\delta^{18}O_{Ar}$ variations is the same as that observed in the *Bellamya* shell from Fuxian Lake (Supplementary Fig. 1). Temperatures calculated from the serial $\delta^{18}O_{Ar}$ values of this shell vary from 15 ± 2 °C to 29 ± 2 °C, very similar to the temperature range calculated for the *Bellamya* shell from the same lake (Fig. 7A and F). The average growth temperature calculated for this large *Radix* shell is 21 ± 4 °C (Fig. 7F), which is the same as that derived from the *Bellamya* shell (Fig. 7A) and also close to the annual mean surface water temperature (De Cui et al., 2008). Highest temperature recorded by this shell (28 ± 2 °C), although higher than the highest measured long-term monthly average lake water temperature of 23 °C in August (Fig. 4; Gu, 2008), is very similar to the water temperature of 27.5 °C that we measured at 7 cm depth on June 22, 2013. Comparison of the calculated temperature pattern with the long-term water temperature record suggests that this individual was born in the warm summer (possibly in July or August) and died in July or August a year later (Figs. 4 and 7F). It appears that approximately 2/3rd of the shell materials in this shell were added in the first 6 months, suggesting that the growth rate of *Radix* decreases towards the late ontogeny (Fig. 7F).

Other *Radix* specimens in this study (i.e., CJ13s-6, CJ13s-14, and CJ13s-16) lived for about half a year and had lengths of ~1 cm, whereas CJ13s-19 lived for almost an entire year and only grew 0.5 cm more than the other individuals and had a slower average growth rate than the others. The consistently higher growth rate of smaller *Radix* specimens (~1.7 mm/month) also supports this observation of slower shell growth as the snail matures (Table 1).

Among all the shells analyzed in this study, the *Bellamya* (FLS-2) lived the longest (~2.5 years), and captured the entire range of annual seasonal variations in water temperature, similar to the nearly full-sized (~1.5 cm) *Radix* shell (CJ13s-19). $\delta^{18}O_{Ar}$ values of the rest of the *Radix* shells fall within the range displayed by *Bellamya* and have recorded the environmental conditions for only a part of a year. The intra-shell isotopic variation patterns and estimated growth rates suggest slower growth rates towards the late ontogeny in both *Bellamya* and *Radix*.

5.3.2. Liuxihe Reservoir

The *Bellamya* specimen (LXH-B1) analyzed from Liuxihe Reservoir is slightly smaller than its counterpart from Fuxian Lake (Table 1). Growth temperatures calculated for this shell range from 17 ± 3 °C to 31 ± 3 °C (Fig. 8A), which fall within the observed variation range of lake water temperatures (Fig. 5). The average temperature recorded by this shell is 26 ± 4 °C, which is slightly higher than the annual mean water temperature (23 ± 3 °C) measured by Peng et al. (2012) between 2000 and 2007. Comparison of the calculated temperatures with the water temperature record (Fig. 5) suggests that this individual was likely born in early spring, between March and April, and lived for less than a year. Areas with dark growth lines yielded the highest $\delta^{18}O_{Ar}$ values and the lowest calculated temperatures, indicating that these dark areas were formed in the winter months. A larger portion of the shell grew in the warm months (Fig. 8A). Therefore, reconstructed temperature from the bulk shell should be biased towards the warmer

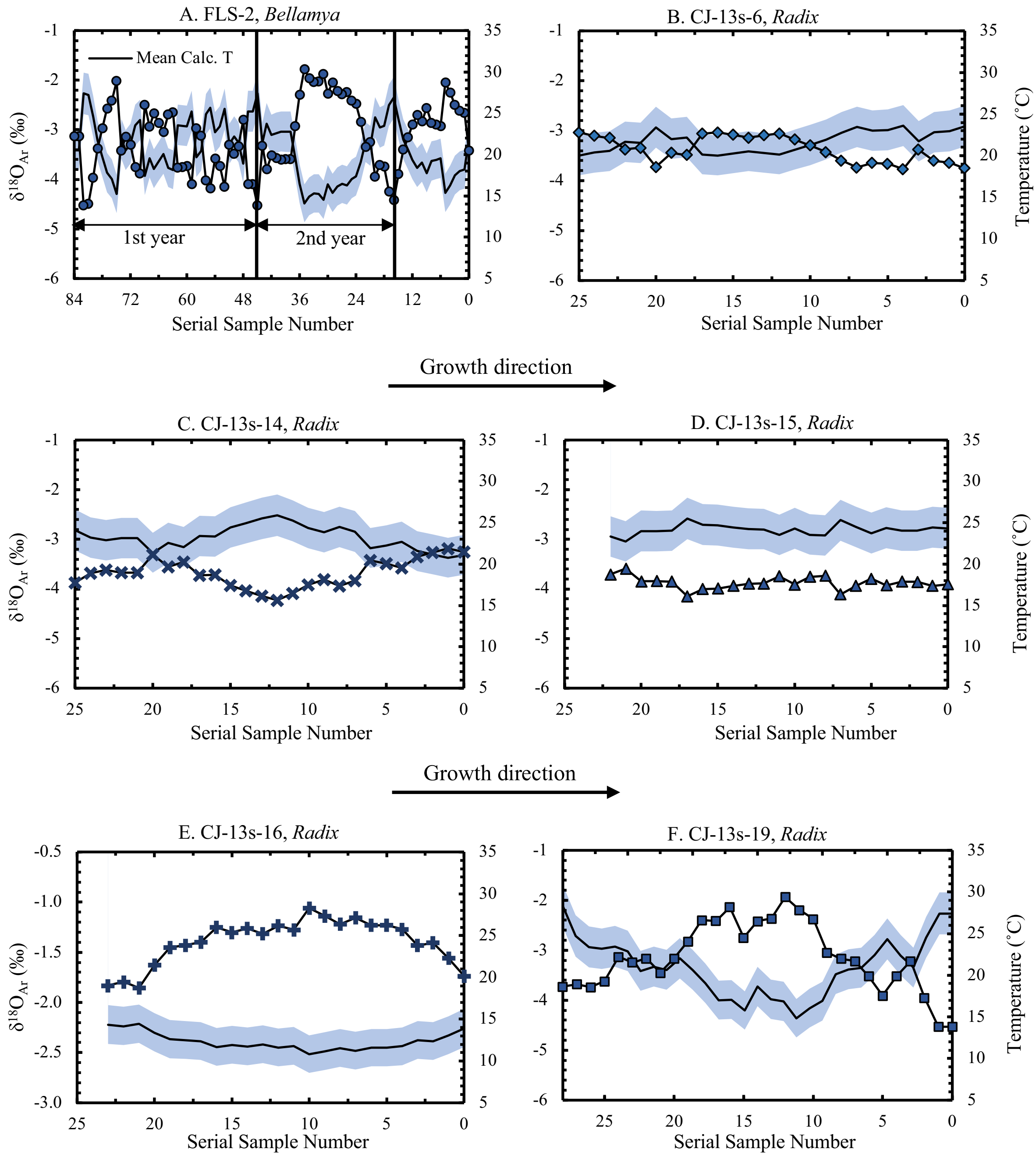

Fig. 7. $\delta^{18}O_{Ar}$ values of serial samples from individual shells and the calculated temperature (black smooth line) variation along the direction of shell growth during the life span of each snail analyzed from Liuxihe Reservoir (A–D).

season. This explains why the average temperature recorded by the shell is higher than the annual average water temperature. From the size of the shell and its intra-shell $\delta^{18}O_{Ar}$ variation pattern, it appears that this snail lived only part of its usual lifespan (about 3–5 years). Early death of the organism could be a result of water drainage to contain the water level in the reservoir. The dramatic fluctuation in water level in the reservoir can disturb the nearshore shallow water habitat of the mollusks and also the sources of nutrients for the mollusks.

For the *Radix* shells, the calculated temperatures range from 21 ± 2 °C to 29 ± 3 °C, suggesting that these shells were born in early spring, likely between March and April, and lived through the spring and early summer until they were collected live in early July (Figs. 6 and 8B–D). The larger shells (LXH13s-8, LXH13s-10) lived longer than the smaller one (LXH13s-9) and therefore have captured a slightly more isotopic variation during their lifespan compared to their smaller counterpart (Fig. 8B–D). The lowest temperature recorded by these *Radix* shells is higher than the winter water temperature (15 °C) of the lake. The highest temperature recorded by the shells, within error, is consistent with the June–July lake water temperatures (Fig. 5). Despite the incomplete record captured by the *Radix* shells, these shells appear to have recorded the temperature variations effectively as they grew.

The data suggest that the *Bellamya* and *Radix* specimens studied here were likely born between March and April. Therefore, it appears that early spring is the favorable time for the new organisms to be born in the reservoir area.

5.3.3. Lake Manasarovar

Because of the limited water isotope data available for Lake Manasarovar, we calculated temperatures for our shell samples using

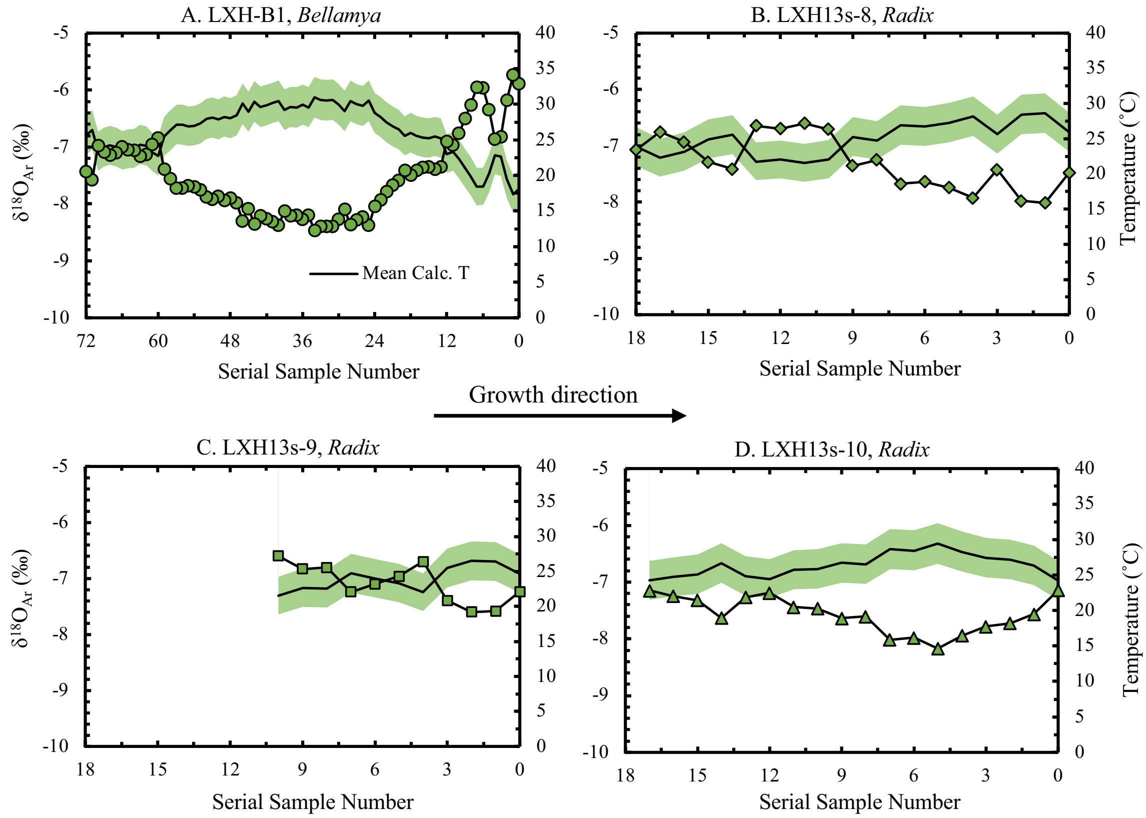

Fig. 8. Seasonal variations in the water temperature in the region recorded at lake Ngangla Ring Cuo (~160 km northeast of Lake Manasarovar; Huntington et al., 2015) and the monthly average $\delta^{18}O_w$ of precipitation (1986–1992) in Lhasa (located ~940 km SE of the lake) (IAEA/WMO, 2018).

Eq. (1) and the $\delta^{18}O_w$ value of our water samples (−6.9‰), the average water $\delta^{18}O_w$ value (−5.5‰) from Yao et al. (2009), and the average (−6.2‰) of the former two water $\delta^{18}O_w$ values (Fig. 9). Calculations were also performed using lake water $\delta^{18}O_w$ value ranging from −3.0‰ to −10.0‰ at 1‰ interval along with the measured $\delta^{18}O_{Ar}$ values of our *Radix* specimens, and only water $\delta^{18}O_w$ values between −5.0 to −7.0‰ yielded realistic temperatures for the lake area. This suggests that seasonal variation in lake water $\delta^{18}O_w$ in a given area is small, much smaller than seasonal variation in precipitation $\delta^{18}O_w$ in the region (Fig. 6). The relatively small isotopic variations in lake water may be expected given the large size and semi-closed nature of the lake. Thus, our calculated temperatures should still provide a reasonable approximation for the seasonal trend in growth temperature.

Temperatures calculated from the $\delta^{18}O_{Ar}$ values of serial samples from TBS07s-2 fall between −1 °C to +15 °C, with an average of 9.0 ± 4 °C (Fig. 9A; Supplementary Table 7), which is close to the annual mean surface water temperature (~7 °C) of Ngangla Ring Tso (Huntington et al., 2015). Comparing the calculated temperature (Fig. 9A) with the surface water temperature record from Ngangla Ring Tso (Fig. 6), it appears that this individual lived for about half a year (Fig. 9A). It was born in late May and died around end of November of the same year. Small fluctuations in $\delta^{18}O_{Ar}$ (< 2‰) in the shell could be a result of mixing with ^{18}O-depeleted summer precipitation and/or meltwater that entered the lake through surface runoff from the glaciers in the area during the summer. Rivers that discharge into the lake have an average $\delta^{18}O_w$ value of −15.0‰ (Yao et al., 2009). Therefore, mixing with surface runoff will lower the $\delta^{18}O_w$ of lake water. Sharp increase in $\delta^{18}O_{Ar}$ towards the terminal shell marks the end of summer monsoon season and the onset of dry season. Since the majority of the shell grew in the summer, the $\delta^{18}O_{Ar}$ value of the bulk shell will be

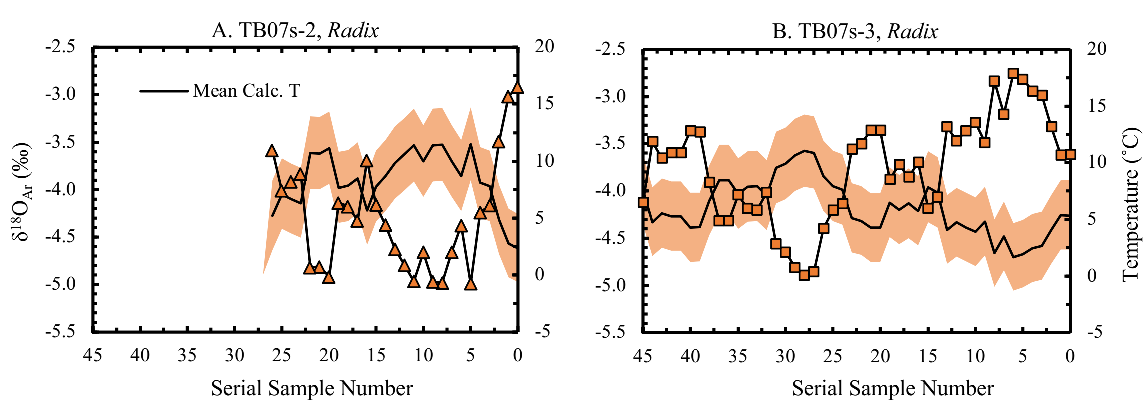

Fig. 9. $\delta^{18}O_{Ar}$ values of serial samples from individual *Radix* shells and the calculated temperature variation (black smooth line) along the direction of shell growth during the life span of each snail analyzed from Lake Manasarovar.

biased towards warmer months. The average growth rate of this shell (~1.7 mm/month) is similar to that of *Radix* in the Fuxian Lake (Table 1).

The calculated temperatures along the growth direction for TBS07s-3 fall between −1 °C to +14 °C, with an average of 6 ± 3 °C, similar to the annual mean water temperature (~7 °C) of Ngangla Ring Tso (Huntington et al., 2015). The temperature profile of the shell suggests that this snail lived for about one year and was born mostly likely in May and died around May a year after (Figs. 9B and 6). There are some fluctuations in calculated temperature during summer months mostly likely due to mixing of melt water from the glaciers and fluctuations in air temperature. The calculated growth temperatures suggest that the shell section between serial samples [20] and [4] likely accreted between October to February because during this period the $\delta^{18}O_{Ar}$ of shell increased from −4.2 to −2.8‰ and temperature decreased by ~5 °C (Fig. 9B). This section is smaller compared to the summer section [45–20], suggesting that rate of shell growth decreased in the winter. The growth pattern and life cycle revealed by serial isotopic data from this individual is consistent with previous observation (Taft et al., 2012), confirming that *Radix* sp. can live through the freezing winter by moving to deeper water or by hibernating under the ice cover until the ice cover disappears.

We performed the same temperature calculation using the $\delta^{18}O_{Ar}$ values of serial sampled *Radix* specimens and the $\delta^{18}O_w$ value of water samples collected and analyzed by Taft et al. (2013) from Lake Manasarovar in 2009. The $\delta^{18}O_w$ value reported in their table is −3.39‰ whereas the value stated in their text is +3.39‰. We used both $\delta^{18}O_w$ values to calculate temperature using the thermometry Eq. (1). Only a $\delta^{18}O_w$ value of −3.39‰ provides reasonable temperatures expected for the lake area. Both the $\delta^{18}O_w$ and $\delta^{18}O_{Ar}$ values reported in Taft et al. (2013) are significantly higher than the values found in this study. Since Lake Manasarovar is a large lake, this difference could be due to the different sampling locations. Water samples in their study were collected from the western end of the lake close to the ephemeral outlet to Lan'ga Co whereas samples in this study were collected close to the eastern edge of the lake. Yao et al. (2009) analyzed water samples from the seven locations along the lake periphery and found a large range of $\delta^{18}O_w$ values (−11.35 to −3.35‰). This suggests that $\delta^{18}O$ of lake water can vary greatly with location in the lake. The more negative $\delta^{18}O_w$ values are found near the inlet channels where ^{18}O-depleted melt water or streams flow into the lake and the $\delta^{18}O_w$ values become progressively higher away from the inlets and towards the outlet. This happens because with increasing distance from the inflow channels, evaporation becomes a more dominant control on the lake water composition than the mixing with surface runoff.

The calculated temperature range for the *Radix* specimens analyzed by Taft et al. (2013) falls between −1 to +11 °C, with an average of ~5 °C, which is also close to the annual mean water temperature (~7 °C) of Ngangla Ring Tso (Huntington et al., 2015). These values are very similar to the temperature values obtained in this study. This confirms that *Radix* sp. shells effectively record the ambient water conditions and are a good recorder of seasonal variations in lake environment. This study also supports that there is no "shutdown" temperature for *Radix* sp. and they continue to live under the ice cover in the winter when the lake is frozen. However, the Tibetan *Radix* sp. appears to prefer warmer water and have slower growth rates in the winter. Therefore, temperature recorded by the bulk shell may be slightly biased towards warmer months.

6. Discussion

6.1. Influence of seasonal variation in water temperature on growth pattern and $\delta^{18}O$ of shells

The studied lakes are all located in the Asian summer monsoon region where summer precipitation has lower $\delta^{18}O_w$ values than winter precipitation, which is primarily controlled by the "amount effect"- a strong negative correlation between the monthly average $\delta^{18}O_w$ values of precipitation and the precipitation amounts (Hodell et al., 1999; Wang et al., 2012). $\delta^{18}O_w$ values of Fuxian Lake water display a similar seasonal pattern (i.e., lower $\delta^{18}O_w$ in the summer and higher $\delta^{18}O_w$ in the winter) as seen in precipitation but in a much more subdued fashion (Fig. 4). This would result in lower $\delta^{18}O_{Ar}$ values of carbonate formed in equilibrium with lake water in the summer assuming no change in temperature. Higher temperatures also lead to lower $\delta^{18}O_{Ar}$ values of carbonate when formed in equilibrium with the same water (i.e., $\delta^{18}O_w$ remains the same). Therefore, one would expect seasonal variations in temperature and $\delta^{18}O_w$ values of these lakes to result in lower $\delta^{18}O_{Ar}$ values in shell carbonates produced in the summer than those formed in the winter if the shell carbonate is precipitated in equilibrium with the lake water. The intra-shell $\delta^{18}O_{Ar}$ patterns in all the *Bellamya* and *Radix* shells analyzed in this study are consistent with this expected seasonal pattern (Figs. 7–9), suggesting that these mollusks produce their carbonate shells in equilibrium with the ambient water.

The $\delta^{18}O_{Ar}$ variations and the reconstructed growth temperature patterns within the shells suggest that both *Radix* sp. and *Bellamya* can grow in the winter in lakes where the lowest average temperature does not fall below 13 °C. Comparing the average growth rates of the shells, it appears that growth rate of *Radix* is independent of the time of the year when the organism is born. The intra-shell isotopic variation patterns and estimated growth rates, however, suggest slower growth rates towards the late ontogeny in both *Bellamya* and *Radix* (Figs. 7A and 9B).

A previous study on *Radix* ontogeny observed that most of the individuals in *Radix* genus only grow about half of their maximum size (~25–30 mm) in a population (Clarke, 1981). This implies that most of the *Radix* found in a population would be < 15 mm, which is reflected in our samples. Our data also support the observation made by Taft et al. (2013) that *Radix* has no "shutdown" temperature and can survive through freezing temperatures in high elevation lakes by moving into deeper water below the ice cover, although their growth rate is slower in the winter (Fig. 9B).

6.2. Influence of life cycle and seasonal growth on temperatures recorded in shells

Our data show that intra-shell $\delta^{18}O_{Ar}$ variations and reconstructed growth temperatures can vary depending on the life spans and growth rates of the snail (Figs. 7–9). Among all the shells analyzed in this study, the *Bellamya* from Fuxian Lake lived the longest (Fig. 7A) and captured the entire range of annual seasonal variations in water temperature. Its counterpart from Liuxihe Reservoir, which is slightly smaller and lived a shorter life, also appears to have recorded almost the entire seasonal range of water temperature variation (Figs. 8A). The intra-shell temperature variation ranges recorded in the *Bellamya* shells (> 2.1 cm in size) are very similar to the magnitude of seasonal variations in monthly average air temperatures at each site (Fig. 10B. Among all the *Radix* shells analyzed in this study, shells larger than 1.4 cm in size appears to have captured the seasonal variations in the lake environment throughout a year (Figs. 7F and 9B) and their intra-shell temperature range is very close to the annual variation range of monthly average air temperatures (Fig. 10B). The rest of the *Radix* shells, which were all ~1 cm or smaller in size, have only recorded lake environmental conditions for part of the year and thus underestimate the magnitude of seasonality at each study site (Fig. 10B).

Comparison of the average growth temperatures calculated for our shells with environmental temperatures shows that the life span of a snail significantly affects the average growth temperature recorded in its shell (Fig. 10C). The average temperatures recorded in the full-size or nearly full-size *Radix* shells (> 1.4 mm) and the 2.3 mm *Bellamya* shell closely approximate the MAWT whereas the average temperatures of the smaller shells can be either higher or lower than the MAWT

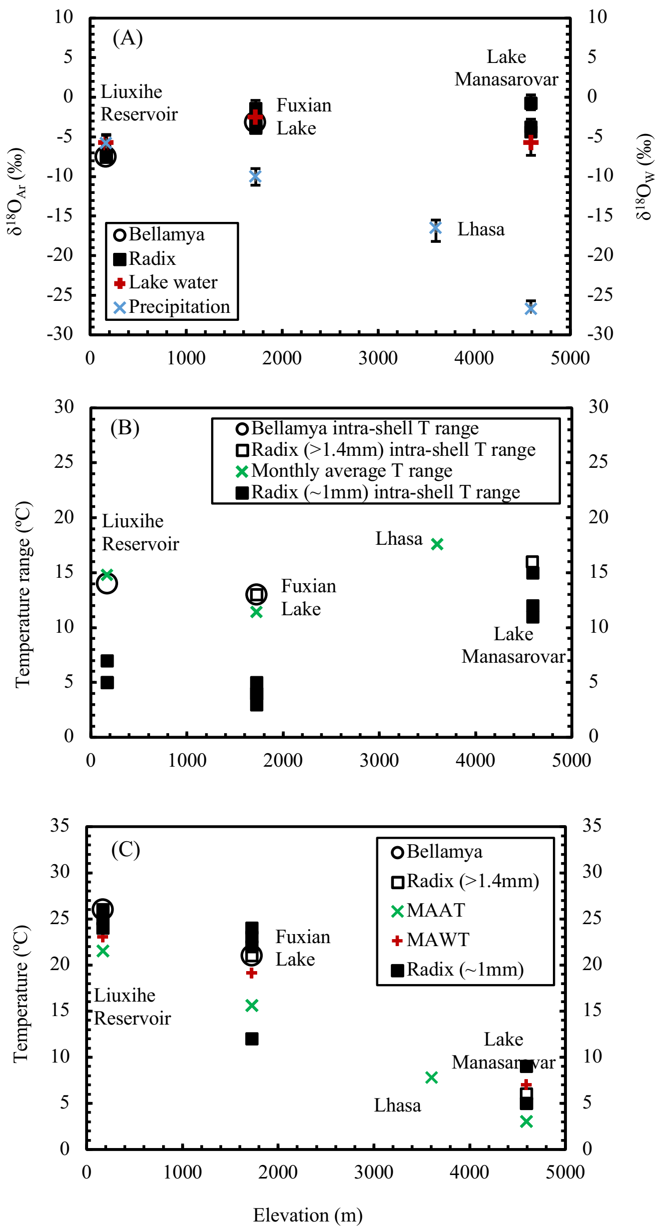

Fig. 10. Comparisons of average $\delta^{18}O_{Ar}$ values of individual shells, and average δ^{18}Ow values of lake water and precipitation (A); annual range of average monthly average air temperatures and magnitude of intra-shell temperature variation (B); and average growth temperatures of individual shells, MAWT, and MAAT (C) among study sites.

depending on their growth periods (Fig. 10C). This suggests that the larger shells (> 2.2 cm for *Bellamya* and > 1.4 cm for *Radix*) are excellent recorders of not only seasonality but also the MAAT at a site (Fig. 10B–C). Previous studies have shown that MAWT can be reliably related to MAAT, regardless of lake size, using a simple transfer function (Hren and Sheldon, 2012). Reliable reconstruction of MAAT and seasonality would provide valuable insights into paleoclimate. Because temperature generally decreases with increasing elevation, paleotemperatures derived from fossil shells have been used to reconstruct paleoelevations (e.g., Wang et al., 2013; Huntington et al., 2015). Similarly, the $\delta^{18}O_{Ar}$ values of fossil shells have been used to reconstruct the $\delta^{18}O_w$ values of ancient meteoric waters, which were then used to reconstruct paleoelevations by using the modern meteoric water isotopic lapse rate in the area (e.g., Saylor et al., 2009; Murphy et al., 2009). Such reconstructions require assumptions about seasonality of shell growth. Our data suggest that selection of shells of certain sizes (> 2.2 cm for *Bellamya* and > 1.4 cm for *Radix*) will allow more reliable paleoclimate and paleoelevation reconstruction.

6.3. *Variation of $\delta^{18}O$, growth pattern, and temperature with elevation*

The three lakes examined in this study span an elevation transect from near sea level to > 4500 m a.s.l. (Fig. 1). Among the three lakes, Liuxihe Reservoir (168 m a.s.l.), which is located in a warm and humid climate, is the least influenced by evaporation (Fig. 3). Both the $\delta^{18}O_w$ and $\delta^{18}O_{Ar}$ values display the smallest deviation from the weighed annual average $\delta^{18}O_w$ value of precipitation in the area (Fig. 10A). This is due to its short water residence time and relatively high precipitation/evaporation ratio. Lake Manasarovar (4590 m a.s.l.) on the arid high Tibetan Plateau, on the other hand, is the most influenced by evaporation and its $\delta^{18}O_w$ and $\delta^{18}O_{Ar}$ values display the largest difference (> 10‰) from the $\delta^{18}O_w$ of local precipitation (Fig. 10A).

As discussed above, both *Bellamya* and *Radix* can be excellent archives of lake environmental conditions only if they are larger than certain size: 1.5 cm or larger for *Radix*, and > 2.2 cm for *Bellamya*. The average temperatures derived from these larger shells decrease with elevation and are an excellent proxy for MAWT (Fig. 10C). These larger shells also allow more accurate reconstruction of seasonality (Fig. 10B). However, smaller *Bellamya* (< 2.2 cm) and *Radix* (< 1.5 cm) shells are not ideal for paleoenvironmental studies as they do not capture the full range of seasonal variations in lake environment and may yield biased information about local climate and elevation.

Bellamya unlike *Radix* is not found in the high elevation lake. This is because *Radix* is ecologically more flexible than *Bellamya* and can survive over a wider temperature range than *Bellamya*. Comparison of estimated growth rates of *Radix* at different elevations (Table 1) suggests that the average growth rate of *Radix* is higher at the lowest elevation site characterized by warm and humid climatic conditions than at the other two sites at higher elevations. However, the growth rates at the mid and high elevation sites appear to be similar (1.3–1.8 mm/month). An earlier study (Gaten, 1986) suggests that winter growth rate for *Radix* is considerably reduced and can be as low as 0.35 mm/month. This implies that the amount of shell material accreted over the freezing winter months could be very low and our sampling technique (at ~0.5 mm sampling interval) may not be able to capture the full range of temperature variations in lake water. However, the serial isotope data from our Tibetan shell TB07s-3 appear to have captured the full range of seasonal variations in water temperature of a high elevation lake (Figs. 9B and 10B). The lowest temperatures recorded by serial samples from this shell (between [4] and [9] in Fig. 9B) represent approximately 3 mm (6 samples × 0.5 mm/sample) of shell growth. If winter is considered to be 4 months (Nov-Feb), the serial data from this shell would suggest a winter growth rate of ~0.8 mm/month (i.e., 6 samples × 0.5 mm/sample/4 months = 0.8 mm/month), much lower than the average growth rate of 1.8 mm/month estimated from this shell (Table 1). Assuming a uniform rate of growth in the remaining 8 months, the rate of shell growth during the warmer months becomes 2.4 mm/month [= (22 mm − 3 mm) / 8 month], comparable to that observed at our lowest elevation site (Table 1).

Similar to *Radix* snails, *Bellamya* from Liuxihe Reservoir (the lowest elevation site) had a much higher growth rate than its counterpart from Fuxian Lake although they have same number of whorls (Table 1). It is important to note that *Bellamya* from Liuxihe reservoir spent most its life in warm water at temperatures of 25°–30 °C (Fig. 8A) whereas the one from Fuxian Lake grew in a cooler environment with a temperature range of 15°–25 °C and spent significant time at temperatures of 15°–17 °C in the second year of its life (Fig. 7A). This suggests that although *Bellamya* can grow throughout the year in mid to low elevation lakes, its optimal growth temperature is probably in range of 25°–30 °C.

Seasonal growth patterns of the shells analyzed in this study show that *Radix* can be born at various times during a year in the low to mid elevation lakes whereas in the high elevation lake, they tend to be born only in the warm season. This suggests that *Radix* is able to reproduce throughout the year in places where seasonal water temperature does not fall below 10 °C. Under extreme climatic conditions on the present-day Tibetan Plateau, *Radix* appears to reproduce only in the summer or late spring. Although *Bellamya* can grow throughout the year(s) in low to mid elevation/latitude climates, *Bellamya* shells analyzed in this study were both born in the spring, earlier than the time observed by Jokinen (1982). This suggests that *Bellamya*, like *Radix*, can reproduce any time from spring to fall in lakes where water temperature does not fall below 13 °C.

7. Conclusions

The intra-shell $\delta^{18}O_{Ar}$ patterns in freshwater snails *Radix* and *Bellamya* from three large freshwater bodies along an elevation transect in the Asian summer monsoon region were examined to improve the interpretation of isotope data from fossil shells as paleoclimate proxy. The results show that seasonal variations in lake water temperature and $\delta^{18}O_w$, along with the life history (time of birth and life span) of an organism, collectively determine the intra-shell $\delta^{18}O_{Ar}$ patterns of these snails. Both *Bellamya* and *Radix* are able to reproduce at any time from early spring to the fall and grow all year in lakes where water temperature does not fall below 13 °C. While *Bellamya* is not found in high altitude Tibetan lakes, *Radix* in the high elevation cold habitat prefers to grow in the summer months but can survive through the freezing winter. Comparison of the calculated temperatures from the oxygen isotope compositions of shells and water with the measured lake water temperatures suggests that both *Bellamya* and *Radix* faithfully record seasonal variations in water temperature. The $\delta^{18}O_{Ar}$ patterns in the gastropod shells are similar across the elevation/climate transect, showing high $\delta^{18}O_{Ar}$ values in shell carbonate formed in the winter months and low $\delta^{18}O_{Ar}$ values in shell carbonate produced during the summer months, which is consistent with the expected pattern in the Asian summer monsoon region. The average growth rates of the snails analyzed in this study were highest at the lowest elevation site characterized by warm and humid climatic conditions but were similar at the mid to high elevation sites. The growth rates of both *Radix* and *Bellamya* appear to decrease towards the late ontogeny. Our data also show that *Bellamya* and *Radix* shells, if they are larger than 2.2 cm and 1.4 cm, respectively, are excellent archives of lake environmental conditions and most suitable for paleoenvironmental studies. The average temperatures recorded in such shells appear to closely approximate the annual mean water temperature while their intra-shell $\delta^{18}O_{Ar}$ variability provides a good proxy for the amplitude of seasonal variations in the monthly average air temperature. However, smaller sized shells do not capture the full range of seasonal variations in lake environment because they represent < 1 year of growth and their intra-shell isotopic variability underestimates the amplitude of seasonality. Thus, smaller sized shells (< 1.5 cm for *Radix* and < 2.3 cm for *Bellamya*) are less suitable for paleoenvironmental reconstruction as they would yield biased information about paleoenvironment.

Acknowledgments

We thank Huai Wang and Qing Zhao for collecting monthly water samples from Fuxian Lake, and Drs. Tao Deng and Hongqu Tang for collecting some of the mollusk samples analyzed in this study. We also thank Editor Dr. Correge and two anonymous reviewers for valuable comments and suggestions that helped to significantly improve the manuscript. This work was partially supported by National Natural Science Foundation of China (Grant Nos. 41672004 & 41888101). Sample preparation and analyses were performed in the Stable Isotope Lab within the Geochemistry Program at the National High Magnetic Field Laboratory, which is supported by National Science Foundation Cooperative Agreement No. DMR-1644779 and the State of Florida.

Data availability

https://data.mendeley.com/datasets/hn7hkbjdps/draft?a=09889b6d-5460-4420-a84e-e57a9f68267d.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2019.109243.

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