Freshwater mollusc sclerochronology: Trends, challenges, and future directions

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A B S T R A C T

Freshwater is an essential resource for human life; however, its future availability is of ongoing concern due to the impacts of climate change, industry, and population pressures. Freshwater mollusc sclerochronology regularly contributes to questions of direct relevance to the future sustainability of this resource, as well as the conservation of endangered freshwater mollusc species, and its relationship with humans through time. Despite this, research within mollusc sclerochronology overwhelmingly focuses on the analysis of marine species. To encourage more interest in this vital subdiscipline, this paper reviews publications on freshwater mollusc sclerochronology published between 2000 and 2021 and highlights key themes and essential findings, challenges, and opportunities specific to freshwater mollusc sclerochronology. The present study reviewed 111 publications where researchers studied the incremental growth patterns and/or completed temporally constrained geochemical analysis of the growth patterns of freshwater molluscs, as well as 22 review papers that addressed freshwater mollusc sclerochronology research. The review identified a focus on the analysis of bivalve taxa from river or lake habitats in the Northern Hemisphere and found that research generally could be divided into four key areas of interest: development of methodology, conservation of habitat or species, paleoenvironmental reconstruction, and archaeology. The paper also considers the effectiveness of different methodologies and geochemical proxies within freshwater contexts and aims to identify unique challenges faced by researchers in the hope to aid and direct future investigations. One key challenge facing this field is the variability of freshwater environments and the need for more high-resolution monitoring of habitats in modern calibration studies. Opportunities for future research include the development of low-cost methodologies to aid in the accessibility of this technique to researchers across the world.

1. Introduction

Freshwater is an essential resource for human life and its presence has dictated the location of human settlements for thousands of years (Kummu et al., 2011; Turrero et al., 2013). Considering the effects of climate change, industry, and population pressures, the future availability and management of freshwater is a major sustainability concern, addressed by the United Nation's Sustainable Development Goal 6 (*Transforming our World: The 2030 Agenda for Sustainable Development,* 2015). Furthermore, freshwater molluscs are among the most endangered taxa on earth and several calls have been made for more research to aid conservation of these animals and their habitats (Böhm et al., 2021; Ferreira-Rodríguez et al., 2019; Lopes-Lima et al., 2021). Therefore, sclerochronology, the study of growth patterns and their

corresponding geochemistry and ultrastructures in the accretionary hard parts and skeletons of organisms, when applied to freshwater molluscs can contribute valuable insight into questions that are relevant to species and habitat conservation and climate change, through modern and ancient lenses. Despite this, marine mollusc sclerochronology continues to be the subject of more publications and review papers than freshwater sclerochronology (Nelson, 1967, p. 186; Peharda et al., 2021). While the discipline of sclerochronology grows exponentially, growth in the subdiscipline of freshwater mollusc sclerochronology is less clear (Fig. 1). This paper aims to highlight key findings, challenges, and areas of future research opportunity in the subdiscipline of freshwater mollusc sclerochronology to encourage more interest in this important subdiscipline. This will be done via a review of the historical context of freshwater shell sclerochronology, followed by a

comprehensive review of the scientific literature on freshwater shell sclerochronology since 2000.

Sclerochronology refers to "the study of physical and chemical variations in the accretionary hard tissues of organisms, and the temporal context in which they formed…" (Oschmann, 2009). The application of sclerochronology to freshwater molluscs is not new. Evidence for research into the growth patterns of freshwater mussels stretches back to the 18th century, when Carl Linnaeus noted the annual growth rings and extended age of freshwater pearl mussel, *Margaritifera* sp. (Pulteney, 1781; for a list of early works, see Tevesz and Carter, 1980). By 1859, however, researchers had begun to question whether the growth rings of *Margaritifera margaritifera* consistently represented an annual growth cycle, and variations in growth through ontogeny were well established (von Hessling, 1859). The connection between freshwater mollusc shell growth and temperature was made by the early 1900s (Lefevre and Curtis, 1912), as was an understanding of the formation of growth lines and the presence of 'pseudoannual' growth increments (Coker et al., 1922). From here, differences in the growth of specimens in different habitats (such as lakes vs rivers) were explored (Brown et al., 1938; Grier, 1922), as was the use of growth patterns as a means of dating the shells (Chamberlain, 1931).

The first studies exploring freshwater mollusc shell geochemistry began in the middle of the 20th century. Trueman (1944) investigated the role of strontium in the formation of aragonite and calcite shells of various marine and freshwater bivalve species. Comfort (1949) assessed the distribution of porphyrin fluorescence and its relationship with shell pigmentation among marine, freshwater and land molluscs. Clayton and Degens (1959) analysed freshwater mussels alongside other types of freshwater and marine carbonates to understand if carbon and oxygen stable isotopes could be used to differentiate freshwater and marine environments. Building on previous work on Sr/Ca in freshwater molluscs (Odum, 1957), Nelson (1963) measured strontium stable isotopes, and strontium and calcium composition in freshwater mussels. They found that there was a non-homogeneous distribution of strontium in the shell and thus spent further work investigating the relationship between shell structure and the distribution of strontium and other trace elements (Nelson, 1964, 1967). These papers included some of the earliest evidence of sclerochronology as we know it today applied to freshwater molluscs as Nelson performed geochemical analysis on different growth layers. It is estimated that approximately 40–50 publications on freshwater mollusc sclerochronology were published before 2000 (Dettman et al., 1999; Fritz and Poplawski, 1974; Rosenthal and Katz, 1989).

This paper reviews research published between 2000 and 2021 on the topic of freshwater mollusc sclerochronology to give an overview of current trends, and highlight key findings, challenges, and opportunities for the subdiscipline, and potential areas of future focus. The review includes papers which have studied incremental growth patterns and/or temporally constrained geochemical analysis of these growth patterns or microstructures, as per the definition by Oschmann (2009). Although we recognize the ongoing debate over terminology in the discipline, (see Gröcke and Gillikin, 2008; Helama et al., 2006; Zuykov and Schindler, 2019, for further information), this paper chooses to continue the promotion of the more general term 'sclerochronology', as have others, in the hope that this be used more consistently (Peharda et al., 2021; Trofimova et al., 2020). Studies involving only bulk analysis of whole shells were not included. The publications were primarily found by searching the 'Discovery' and 'Web of Science' databases with keywords such as 'freshwater' 'shell' 'sclerochronology' 'isotopes' 'trace elements', as well as from the bibliography of review articles and other articles published during this time (in particular, Peharda et al., 2021; Pfister et al., 2019). As has been mentioned previously, a complete review of all research on this topic is challenging as the term 'sclerochronology' is not consistently applied in publications on this topic, therefore the publications included in this review are intended to represent a thorough review of recent research, rather than a complete review (Peharda et al., 2021). In total, the database includes 133 publications: 22 review publications which include no/minimal original research, and 111 research papers. A full database of reviewed publications and references are available in Stringer and Prendergast (2023a, 2023b).
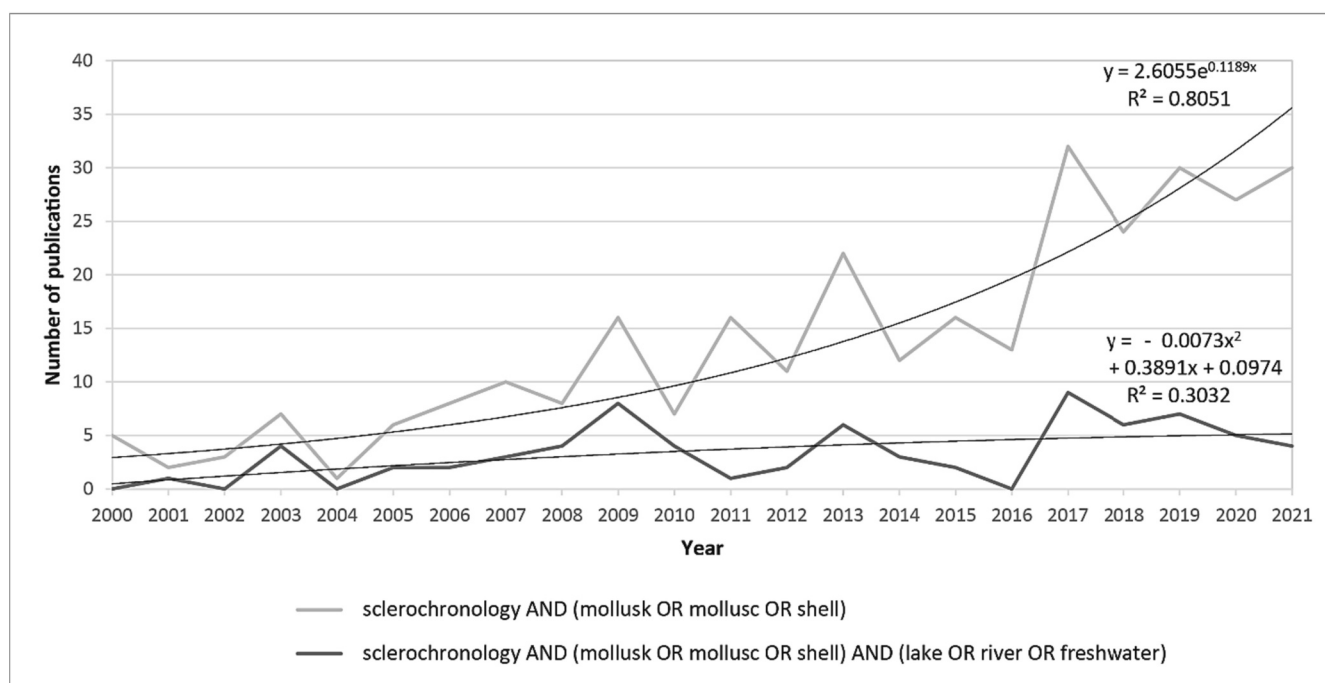

Fig. 1. Number of publications between 2000 and 2021 on the topics of mollusc sclerochronology (light grey) and freshwater mollusc sclerochronology (dark grey) with associated trendlines (exponential and polynomial, respectively). Exact search terms are provided in legend. Trendlines determined through method of best fit. Data retrieved from Web of Science, June 21, 2022.

2. Geography of previous studies

Most of the studies reviewed in this paper are based on sites in Europe (particularly Northern Europe), the USA, and Asia (particularly Nepal and Tibet) (Fig. 2). Similar Northern Hemisphere and continental bias was also apparent in a recent geographical review of sclerochronological research on extant marine bivalves (Peharda et al., 2021). This bias exists despite freshwater molluscs living throughout the world, on almost every continent and in a wide variety of habitats (Graf and Cummings, 2019; Lydeard and Cummings, 2019a; Strong et al., 2008). The bias could be linked to a higher diversity of freshwater molluscan taxa identified in these popular geographic regions, however biologists have questioned whether this diversity reflects actual taxonomic richness or a dearth of systematic studies of freshwater molluscs in other regions (Lydeard and Cummings, 2019b). An alternative source of geographic bias may be the dominance of first authors from these same regions. An analysis of the country of each first author's institution showed a clear bias for researchers from these regions, particularly the USA and Germany (Fig. 3). No research was produced in an African Institution. The dominance of the Global North in academic knowledge production is well known across other scientific and academic disciplines (Collyer, 2018). The expensive, specialized equipment and methodology often necessary in sclerochronology likely acts as a barrier to researchers from the Global South where academic funding is generally less available (Mouton and Waast, 2009). Efforts have been made to explore and report on the effectiveness of lower-cost analysis methods (e.g., Araujo et al., 2014; Hausmann et al., 2019; Shoults-Wilson et al., 2014), and continuing work in this area will further benefit these communities as well as the subdiscipline as a whole.

Over 70% of studies reviewed in this paper investigated river or stream environments, while lacustrine environments were investigated by almost 40% of research. Few studies investigated specimens from freshwater wetlands (Frenzel and Harper, 2011) or springs (Harzhauser et al., 2012; Shanahan et al., 2005), despite these locations being known hotspots for freshwater mollusc diversity (Strong et al., 2008). A small number of studies were concerned with tank experiments or specimens grown in controlled environments (Anadón et al., 2010; Füllenbach et al., 2014; Goodwin et al., 2019; Zhao et al., 2017a). While Pfister et al. (2019) recently reviewed oxygen stable isotope data from stream/river freshwater mollusc sclerochronology studies from 25 basins around the world, representing 9 Köopern-Geiger climatic zones, a similar global review of freshwater mollusc sclerochronology studies from other hydrological environments, particularly lakes, is missing. Such a review may provide vital insights into overall trends in the impact of geography and climate zones on growth and geochemistry records, strengthening interpretations and facilitating further research.
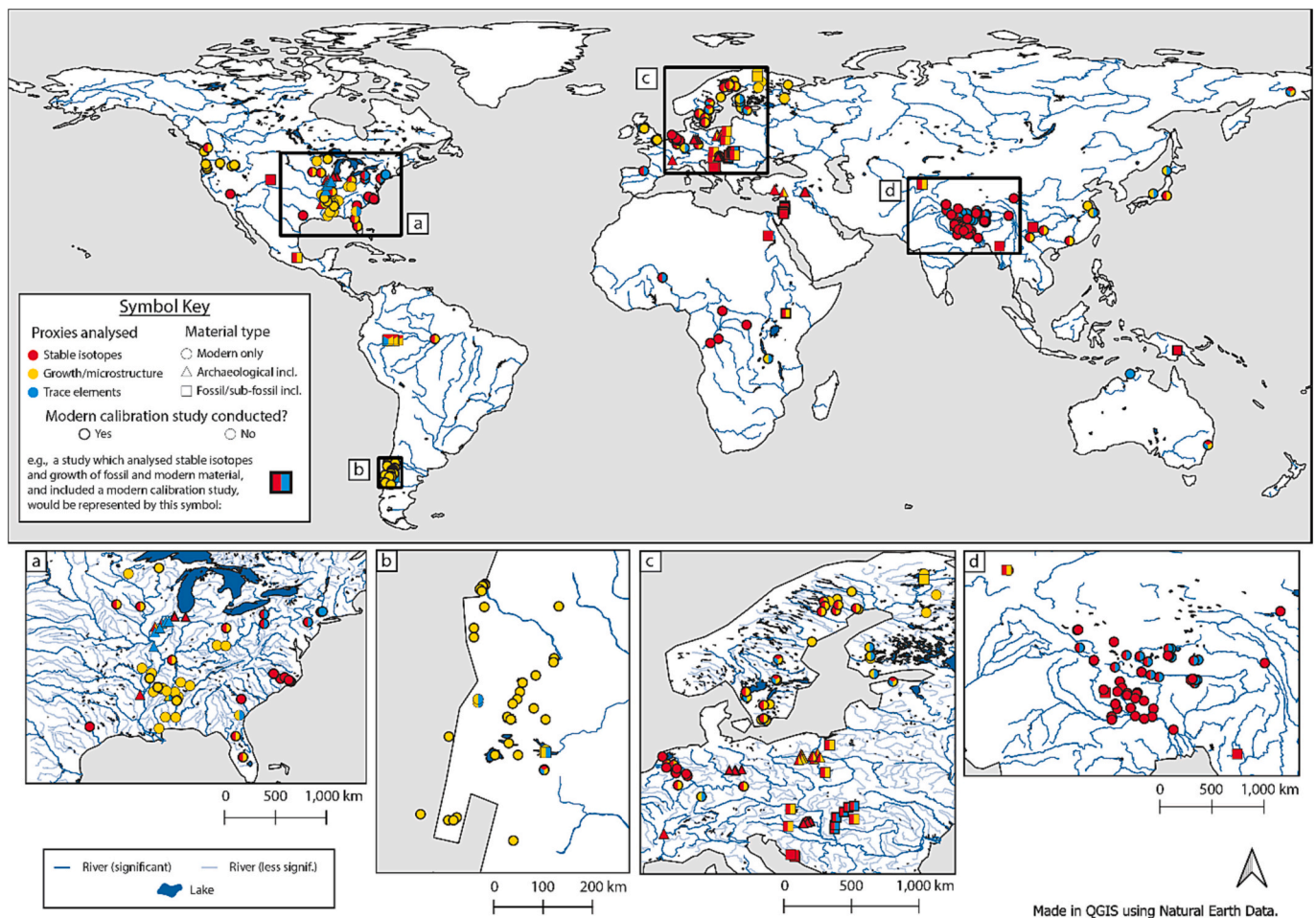

Fig. 2. A map of sites from which freshwater molluscs were investigated as part of sclerochronology research, published between 2000 and 2021. Each site is represented by a symbol which denotes the proxies analysed in the study (stable isotopes, growth/microstructure, trace elements), the age of the material investigated (only modern material; archaeological material included; fossil/sub-fossil material included) and whether a modern calibration study was conducted. Some sites may be used across several studies; therefore, symbols may be overlapping. Close-up depictions of the western USA (a), central Chile (b), Europe (c), and the Tibetan plateau (d) are provided due to the density of sites in these regions. Publications did not always specify GPS coordinates of sites; therefore, some sites are approximate locations based on maps or place names published by the authors. The full geospatial project and data about each site can be accessed in Stringer and Prendergast (2023a, 2023b).
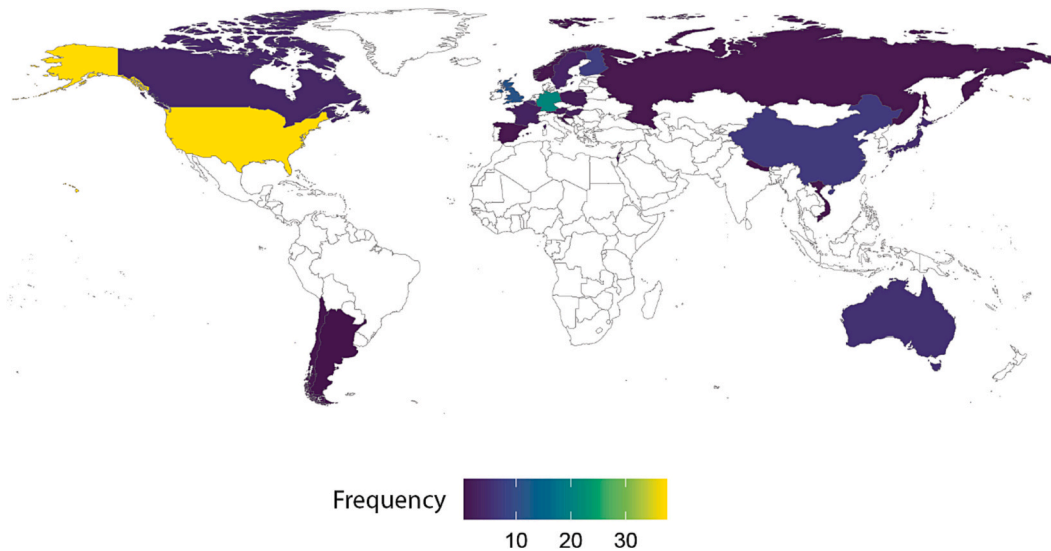
Fig. 3. The frequency of countries listed as the country of the institution of the first author of each publication featured in this review. Each article represents a frequency of 1. If an author belonged to several institutions across multiple countries, then each country was awarded a fraction of 1.

Most studies focused on singular sites/bodies of water or relatively small geographical areas. However, some investigated specimens from more extensive geographical areas, while global analyses were performed by Pfister et al. (2019) and Haag and Rypel (2011). Haag and Rypel (2011) reviewed the growth and longevity data of freshwater molluscs from 146 populations across seven different countries and/or territories, and 16 states of the USA. Gajurel et al. (2006) collected water samples, temperature records, and freshwater molluscs from streams/rivers and closed bodies of water from across the Himalayan Valleys and Ganga plain in Nepal and India. Valdovinos and Pedreros (2007) investigated how shell growth rates of *Diplodon chilensis* were affected by eutrophication across 23 Chilean lakes of varying geographic and hydrological attributes. Black et al. (2015) compared long-term mollusc and tree growth chronologies across the Pacific Northwest, USA to understand how growth is impacted by hydroclimatic variability. Several studies investigated *Radix* sp. collected from hydrological features across broad geographical areas of the Tibetan plateau (Chen et al., 2016, 2021; Taft et al., 2013), while Roy et al. (2019) analysed specimens along an elevation transect in the Asian monsoon region of China. These studies provide useful insights in the influence of large-scale climatic and geographic features on local records. Studies at different geographical scales (global, regional, local) provide a stronger understanding of the limitations of our interpretations, therefore more global and regional investigations for different parts of the world are important.

3. Which taxa have been investigated?

186 different freshwater taxa are represented across the studies reviewed here. Most studies involve the analysis of just one to three taxa. Few studies involve more than ten (Gajurel et al., 2006; Haag and Commens-Carson, 2008; Rypel et al., 2008), and the publications by Haag and Rypel (2011) and Harzhauser et al. (2012) are unusual for the inclusion of over 30 taxa each. Large-scale analyses of different taxa are important as they allow for the sclerochronological potential of many species to be assessed, possibly opening-up these species to future investigations, and simultaneously revealing new habitats and geographical regions for research. The analysis of several taxa from the same region can help determine which taxon is most ideal for sclerochronological research in that area (e.g., smallest influence of vital effects) and therefore can strengthen future investigations (Chen et al., 2021).

While most studies involved taxa identified to species level, some could not. This was generally attributed to a lack of systematic taxonomic study in a particular region, such as in the case of *Radix* sp. in the Tibetan plateau (Chen et al., 2016; Taft et al., 2012), or the fragmentary nature of the fossil record (Demény et al., 2012). Although the taxa used by Kelemen et al. (2021) and Langlet et al. (2007) could be identified to species level, a lack of previous research on these African bivalves limited the interpretations that could be made. As these gaps in research usually unequally effect regions where freshwater mollusc sclerochronology is already struggling, research alongside malacologists to better understand species habitat, life history, and conchology will help the subdiscipline work towards geographical equity.

Freshwater bivalve taxa appeared more frequently in the reviewed publications than gastropods: 81% of studies analysed only bivalve taxa, 14% of studies analysed only gastropod taxa, and just 5% of studies analysed both bivalves and gastropods. This is despite the overwhelming majority of freshwater molluscan species being gastropods rather than bivalves (Lydeard and Cummings, 2019b; MolluscaBase Eds, 2022; Strong et al., 2008). This trend was also apparent in the sclerochronology publications of marine species from 2010 to 2019 (Peharda et al., 2021). Bivalves may be more popular in freshwater mollusc sclerochronology research because they are well attested as effective environmental biomonitors beyond sclerochronology and have been used as such for decades (Schöne and Krause, 2016). Their relatively sedentary lifestyle reduces the number of variables at play when reconstructing the hydrological record, which is particularly important in variable habitats such as rivers (Graf and Cummings, 2019; Schöne and Krause, 2016). Furthermore, bivalve sampling methodologies are generally more transferable across taxa, while gastropod methodologies may vary depending on the size, shape, and microstructure of the taxa in question (although, for a view of more taxonomic diversity among bivalves, see Kelemen et al., 2021). Bivalve sampling methodologies generally involve the cross-sectioning of a valve and drilling/milling of the incremental layers visible in the cross-section (Fig. 4), while gastropods may be analysed through incremental drilling of the outer or inner layers without sectioning (e.g., Gajurel et al., 2006; Harzhauser et al., 2012; Mannino et al., 2003; Prendergast et al., 2016), sampling of a cross-sectioned shell (e.g., Füllenbach et al., 2014; Long et al., 2020), or other analyses, including use of opercula (e.g., Anadón et al., 2010; Galimberti et al., 2017; Loftus et al., 2017; Milano and Szymanek, 2019; Muschitiello et al., 2013). Furthermore, gastropod taxa can often be smaller, limiting the amount of carbonate available for analysis and often leading them to be crushed whole and bulk-analysed (and
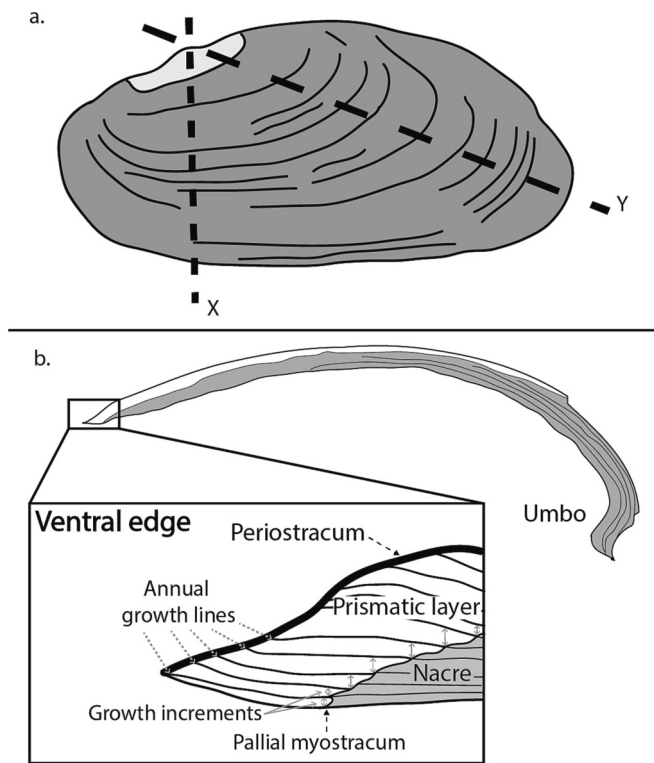
Fig. 4. Conchology and ultrastructure of freshwater bivalve, *Margaritifera margaritifera*. Fig. 4a. demonstrates the cutting axes (dashed lines) most frequently used in the analysis of this species. The axis of minimum growth (X) is often used for *M. margaritifera* and some other species (e.g., *Unio pictorum*, *U. tumidus*, *Alathyria profuga*, Cucumerunio novahollandiae; e.g., Dunca et al., 2005; Herath et al., 2018; Schöne et al., 2004; Versteegh et al., 2009), while the axis of maximum growth (Y) is also commonly used (e.g., Carroll et al., 2006; Gaillard et al., 2019; Izumida et al., 2011; Zhao et al., 2017a). Fig. 4b. provides a close-up of the ultrastructure of *M. margaritifera*, including the growth patterns investigated in sclerochronology (adapted from Schöne et al., 2004, Fig. 2; Dunca et al., 2005, Fig. 2).

therefore, not included in this review) (see Apolinarska et al., 2015; Apolinarska and Pełechaty, 2017; de Francesco and Hassan, 2013). Improvements in the capabilities and accessibility of high-resolution analytical techniques, such as secondary ion mass spectrometry (SIMS) and nanoscale SIMS (NanoSIMS), is likely to increase the analysis of taxa where size currently limits intra-specimen sampling.

Table 1
Taxa analysed in 5 publications or more. 'Frequency' refers to number of publications the taxon has appeared in.

Species	Frequency	Class	Life expectancy
Margaritifera margaritifera	20	Bivalve	>200 years (Mutvei and Westermark, 2001)
Unio pictorum	10	Bivalve	~15 years (Versteegh et al., 2009)
Unio tumidus	8	Bivalve	~15 years (Versteegh et al., 2009)
Amblema plicata	7	Bivalve	~18–54 years (Haag and Rypel, 2011)
Radix sp.	6	Gastropod	~1–1.5 years (Chen et al., 2021)
Corbicula fluminea	5	Bivalve	~1–5 years (Yan et al., 2009)
Diplodon chilensis (patagonicus)	5	Bivalve	>90 years (Soldati et al., 2009)
Quadrula pustulosa	5	Bivalve	~39–48 years (Haag and Rypel, 2011)
Unio crassus	5	Bivalve	~15 years (Versteegh et al., 2009)

While 186 different freshwater taxa are represented in the literature, only nine of these taxa appeared in five studies or more (See Table 1). The popularity of these taxa is likely partially due to geography and availability: six of the eight taxa are today found in Europe and/or North America where research is centred. *Corbicula fluminea* is native to East Asia but has successfully become an invasive species in Europe, North and South America, and Asia, therefore it can provide records for habitats across most of the world (Crespo et al., 2015). Longevity of certain species was probably also an important factor. *Margaritifera margaritifera* and *Diplodon chilensis (patagonicus)* are among the longest-lived freshwater molluscs in the world and can provide valuable long-term climate archives, stretching across decades or centuries depending on the individual or following the construction of master chronologies using cross-dating methods (e.g., Helama et al., 2006; Schöne et al., 2004, 2007, 2020; cross-dating discussed further below (Section 5.1)). Finally, species may be preferentially analysed due to economic or conservation significance. The economic importance of freshwater mussels in the pearl industry was an early motivator for research (Chamberlain, 1931; Isley, 1914; Riedl, 1928; von Hessling, 1859), and their economic importance may still play a role in research direction today (Li et al., 2017; Yoshimura et al., 2010). The Freshwater Pearl Mussel, *Margaritifera margaritifera*, which was overharvested for the pearling industry in the past, is currently classified as 'Critically Endangered' on the IUCN Red List (Moorkens, 2011). At least some of the research on this species appears motivated by the severity of its conservation situation (Dunca et al., 2005, 2011; Helama and Valovirta, 2008; Leppänen et al., 2021).

4. Motivations: what was the overall purpose of the research?

A review of the freshwater mollusc sclerochronology literature published between 2000 and 2021 identified four main overarching themes or motivations for research: 'advancing methodologies', 'conservation', 'paleoenvironmental reconstruction', and 'archaeology'. Each paper was attributed a primary and, where relevant, secondary theme based on the aim of the research or suggested future applications: 'advancing methodologies' papers were focused on improving sclerochronology techniques and methodology; 'conservation' papers used sclerochronology to monitor aspects of ecological health or climate change relevant to conservation efforts; 'paleoenvironmental reconstruction' papers reconstructed past habitats, hydrological systems, or climates; and 'archaeology' papers involved the analysis of materials from archaeological contexts or articles where the implications of the research for archaeology was clear. Overall 'advancing methodologies' appeared most frequently, with 'conservation' and 'paleoenvironmental reconstruction' close behind. Further details of the themes and the relevant studies are given below.

4.1. Advancing methodologies

A contribution to the methodological knowledge of the discipline was an important theme within the reviewed literature. The key contributions are reviewed more thoroughly in the following section of this paper (see Section 5); therefore, this section will discuss general themes within 'advancing methodologies'.

Approximately 61% of research papers analysed isotopes of shell material, while just 28% analysed trace element composition. Growth or microstructural analysis was included in 54% of studies. Just five studies addressed all three proxies. Approximately 62% (69 of 111) of freshwater mollusc sclerochronology research papers written between 2000 and 2021 included a modern calibration study in which freshwater molluscs were collected alongside relevant environmental data and/or water geochemistry. This supplementary information was either collected by the researcher at the site area or was made accessible to the researcher by a past publication or a nearby monitoring programme hosted by an institution, e.g., government or local university. Temperature data was most frequently collected in modern calibration studies

(72%), alongside oxygen stable isotope data (49%). Other investigated parameters included pH (28%), trace element composition (22%), a measure of carbon stable isotopes (19%), stream/river discharge (16%), and electrical conductivity (16%). Additional, situation-dependent parameters were collected in other research, such as chlorophyll-α. 75% of modern calibration studies used data which had been repeatedly collected over an extended period, rather than just spot measurements taken at the time of collection. 55% of studies used data collected by someone other than the researchers.

Several studies analysed freshwater molluscs alongside other proxy records. Comparison of sclerochronological and dendrochronological records allowed for longer and more complete chronologies to be created, and also allowed for researchers to compare the effect of different environmental parameters on each archive-type (Black et al., 2015; Helama et al., 2009, 2010; Rypel et al., 2009; Schöne et al., 2005). Other proxy records included sediment/geological records (Dettman et al., 2001; Kieniewicz and Smith, 2007; Licht et al., 2014), mammalian teeth (Dettman et al., 2001; Licht et al., 2014; Sun et al., 2021), palaeobotanical remains (Harzhauser et al., 2012), and ostracods (Taft et al., 2014). The development of multi-proxy records using various archives helps to validate the results of freshwater mollusc sclerochronology, creates a more robust record, and allows for a broader and more holistic picture of the situation at hand.

4.2. Conservation

Conservation is understandably a popular focus among recent research given ongoing pleas for climate change action and environmental preservation, as well as the pressing conservation crisis facing freshwater molluscs themselves (Böhm et al., 2021; Ferreira-Rodríguez et al., 2019; Lopes-Lima et al., 2021). Several studies spoke specifically to the conservation of freshwater mollusc species via investigating the life history and growth patterns of taxa (e.g., Arnold et al., 2014; Dunca et al., 2011; Haag and Commens-Carson, 2008; Helama and Valovirta, 2008; Li et al., 2017; Valdovinos and Pedreros, 2007; Zotin and Ieshko, 2021). This research has not only shed light on the ideal habitat conditions for taxa, but it has also helped to provide direction for conservation efforts. For example, research by Helama and Valovirta (2008) on the endangered *Margaritifera margaritifera* determined that sclerochronology can be used to create population specific size-at-age models which can inform researchers of the ecological conditions and extinction risk of specific populations. Thus, this can allow for conservation efforts to focus on the most at-risk populations. Furthermore, these models can be created using single mature individuals or already published data, meaning this method does not require more individuals from already threatened populations to be sacrificed.

Other studies focused on the use of molluscs to record the impact of specific pollutants or environmental changes. Programmes such as NOAA's Mussel Watch have been using molluscs as biomonitors of coastal waters for decades, analysing the animals' soft tissues for evidence of bioaccumulated contaminants (Goldberg et al., 1978). Similar applications have been found for molluscs in freshwater habitats as well (Genç et al., 2018; Jamil et al., 1999; Metcalfe and Charlton, 1990; Varol and Sünbül, 2018). A recent push to incorporate sclerochronological methodology in these programmes has allowed for the creation of long-term, high resolution records of environmental change and contamination events (Carilli et al., 2015; Schöne and Krause, 2016; Zuykov et al., 2013). Using shell records can be less time and resource intensive as well as less destructive for populations, as a group of individuals need only be collected once (depending on species longevity) rather than having to return and collect individuals over time, ultimately killing more members of the population (Schöne and Krause, 2016). Sclerochronological analysis of shell records may also be a more simple and cost-effective alternative to other water-monitoring procedures (Gaillard et al., 2019; Kukolich and Dettman, 2021). Therefore, the technique provides many advantages to the monitoring of freshwater environments.

The reviewed studies demonstrated that a wide range of pollutants can be monitored using sclerochronology. These pollutants include those relating to mining and other industrial activities, such as oil and gas production (Geeza et al., 2018; Markich et al., 2002), stream liming (Dunca et al., 2011), the use of road-salt (O'Neil and Gillikin, 2015), and the use of fungicides and pesticides as well as general changes in land-use (Graniero et al., 2021; Kukolich and Dettman, 2021; Risk et al., 2010). Shells record bioavailable contaminants and therefore monitor those pollutants which pose the most risk to humans and their food sources (Schöne and Krause, 2016). This is particularly relevant for the monitoring of freshwater as it supplies drinking water for humans and animals, as well as water for agriculture and food manufacturing. The identification of pollution is also important when designing sclerochronology studies, as research by Dunca et al. (2005) and Carroll and Romanek (2008) found that shells from polluted rivers did not show the same relationship between growth and environmental signals as their counterparts from non-polluted habitats.

The impact of other damaging environmental conditions, not just pollutants, have also been investigated. Eutrophication, as a result of anthropogenic enrichment, impoundment, or other factors, has been monitored in several studies and its negative impact on the local ecology and mussel populations has been noted (Fritts et al., 2017; Mutvei and Westermark, 2001; Valdovinos and Pedreros, 2007; Wilson et al., 2018a, 2018b; Zhao et al., 2017b). Increased erosion as a result of a large earthquake (Risk et al., 2010) and increased evaporation, as a result of impoundment (Van Plantinga and Grossman, 2018), have also been identified using sclerochronology. Flow modification, such as impoundment, is considered to be one of the most negatively impactful factors on freshwater mollusc populations (Lydeard and Cummings, 2019b) and it has also been shown to affect the results of sclerochronology research (Rypel et al., 2009).

Other studies concerned with conservation used freshwater mollusc sclerochronology to help understand the impact of climate change on taxa. For example, Black et al. (2015) found that the amount and timing of precipitation had a larger impact on the growth of freshwater mussel and tree populations in north-west USA than warming temperatures, despite temperature often being a focus of research. As a result of this research, the impact of climate change can be better understood and predicted for this region, and other sclerochronology researchers may be encouraged to investigate the importance of precipitation or other parameters on different populations.

Finally, freshwater mollusc sclerochronology research may have implications for how freshwater habitats contribute to climate change more directly. CO_2 outgassing or evasion from rivers, streams and other freshwater habitats is recognised as a significant part of the global carbon cycle (Raymond et al., 2013). While the effect of the world's largest rivers on global net CO_2 flux has been estimated (Reiman and Xu, 2019; Richey et al., 2002), the influence of smaller rivers is less well understood (Wallin et al., 2013). A novel study by Yoshimura et al. (2015) used carbon stable isotopes of shells and dissolved inorganic carbon (DIC) in water to investigate whether sclerochronology could be used to track inorganic carbon cycling in rivers. This study showed a clear difference in the mean DIC and partial pressure of CO_2 (pCO_2) in the upstream portion of Shintone River, Japan, based on shell records, compared to downstream in Lake Kasumigaura, suggesting that excess CO_2 had been degassed after the water flowed into the lake. The application of this method to other locations could have important implications for understanding the contribution of freshwaters to global carbon cycling and encouraging innovations into ways in which we can minimize the impact of sources of this carbon, such as mineral weathering.

While the studies addressed above were aware of how their research could contribute to conservation efforts, many studies reviewed in this paper verify the use of different species in different regions around the world as effective monitors of past and current hydroclimate, and therefore their findings could have implications for questions of local

climate change and environmental conservation.

4.3. Paleoenvironmental reconstruction

Paleoenvironmental reconstruction was among the most common themes seen in the freshwater sclerochronology research published since 2000. The general term 'paleoenvironmental reconstruction' is used here to refer to any attempts to reconstruct past habitats, hydrological systems, or climates. There is a large cross-over with the theme of archaeology. Those articles which address paleoenvironmental reconstruction specifically related to archaeological contexts are discussed in the following section, however a more studies used fossil or sub-fossil material for this research compared to archaeological (17 studies compared to 9). A wide chronological range of specimens were analysed by those studies investigating fossil or sub-fossil material: from the Holocene epoch(Demény et al., 2012; Long et al., 2020; Neubauer et al., 2014; Taft et al., 2014), to the Pleistocene (Kieniewicz and Smith, 2007; Stevens et al., 2012; Vonhof et al., 2013), Miocene (Błażejowski et al., 2013; Dettman et al., 2001; Harzhauser et al., 2012; Kaandorp et al., 2006; Sun et al., 2021) and Eocene epochs (Buskirk et al., 2016; Licht et al., 2014).

Diagenesis is an essential consideration when analysing the geochemistry of fossil or archaeological material (Collins, 2012; Milano et al., 2016). Diagenesis, which involves the dissolution and recrystallization of carbonate in response to the mollusc's burial environment, heating of the shell, and more, can impact stable isotope and trace element values (Collins, 2012; Milano et al., 2016). Often diagenesis can be investigated through determining if carbonate aragonite has been transformed, partially or fully, into calcite, although this is only relevant to species known to have aragonitic shell layers originally. Collins (2012) provided an effective review of the most common methods used in the identification of diagenesis in freshwater molluscs (thin-section petrography, X-ray diffraction, cathodoluminescence and scanning electron microscopy) and argued for the use of multiple methods, rather than a singular method, for the identification of diagenesis as sometimes one method is insufficient. 52% of studies (17 of 33) analysing the geochemistry of archaeological or fossil material noted which methods they used to determine an absence of diagenesis, and of these only four studies used more than one method to make this determination (Collins, 2012; Kaandorp et al., 2006; Licht et al., 2014; Long et al., 2020). The rate of diagenetic screening was particularly low among studies analysing archaeological material, where only five of seventeen studies noted which methods they used, if any. Thus, the importance of ruling-out diagenesis when working with fossil or archaeological material needs to continue to be emphasised, not only for those people doing the research but also for anyone interpreting the results.

Ten research articles analysed modern and fossil material alongside one another, while nine analysed fossil material alone. Articles where modern and fossil molluscs are analysed alongside one another can be useful as the modern calibration studies are usually performed in the same geographical area to where the fossil material was excavated, therefore increasing the effectiveness and reliability of paleoenvironmental reconstruction conclusions as researchers gain a more in-depth knowledge of the modern geography and relevant climate systems. The modern calibration study, if performed, can also focus on questions of particular interest to the paleoenvironmental reconstruction (e.g., investigating a specific geochemical proxy). Perhaps most importantly, modern calibration studies can investigate the modern ancestors of individuals in the fossil record, and therefore understand how reliable and robust the species is as an archive of environmental conditions. Although only investigating modern specimens, the intensive monitoring study on live aquatic gastropods completed by Shanahan et al. (2005) demonstrated that inter- and intraspecies variations in shell geochemistry can be large even when organisms are living in nearly identical environments, therefore differences in the life history and behaviour of individuals, such as seasonality of shell growth or biology of species, can have a significant effect. Thus, researchers should be cautious when making conclusions about the paleoenvironment based on the analysis of fossil taxa where knowledge of the ancient taxa is limited and/or studies of modern counterparts are unavailable. Nevertheless, understanding the effectiveness of an extant molluscan species as an environmental archive, even when separated from its fossil ancestor by thousands or millions of years, gives freshwater gastropod and bivalve sclerochronology an advantage over other archives, such as diatoms and ostracods, where the impacts of vital effects and the effects of temperature on oxygen isotope fractionation are still debated (Schöne et al., 2020). Another advantage of analysing modern and fossil material concurrently is that comparison of the material can provide insights into the differing issues that affected modern and fossil material, such as issues with preservation or the identification of diagenesis (Demény et al., 2012).

A common aim of the paleoenvironmental reconstruction studies was to use geochemistry to investigate local, regional or global climatic conditions of the distant past (Błażejowski et al., 2013; Demény et al., 2012; Long et al., 2020; Vonhof et al., 2013). Most studies focused on the reconstruction of long-term records of water stable isotopes, which can provide insights into precipitation/evaporation cycles and streamflow patterns through time, both of which are considered "pivotal to improve our understanding and modeling of hydrological, ecological, biogeochemical and atmospheric processes" (Schöne et al., 2020). Kelemen et al. (2017, 2021) verified the use of several bivalve species for the reconstruction of stable oxygen isotope ratio values in the Niger River and three rivers in the Congo River Basin (Congo, Oubangui, and Kasai). These proxy records can now provide insight into past hydroclimate in a region where direct measurements of these parameters are historically scarce, yet the impacts of climate change are predicted to be significant. Gaillard et al. (2019) highlighted the potential for freshwater mollusc sclerochronology to help record hydrological variation in the Amazon Basin. Although a current instrumental monitoring system is in place, the size and complexity of the basin means that the hydrology and geochemistry of the area is not fully understood and the instrumental monitoring system that would be required to reach this resolution would have to be highly complex and expensive. Therefore, sclerochronology can help to support the current instrumental monitoring system. Pfister et al. (2018) also demonstrated that sclerochronology can be used to create long duration stream water isotope data sets to both extend existing records and provide data for nonmonitored streams. Additionally, several studies have shown that freshwater mollusc sclerochronology can be used as a proxy for global-scale atmospheric circulation patterns, including the Intertropical Convergence Zone oscillations/monsoon (Dettman et al., 2001; Gajurel et al., 2006; Licht et al., 2014; Taft et al., 2013; Vonhof et al., 2013; Watanabe et al., 2021), the North Atlantic Oscillation index (Dunca et al., 2005; Schöne et al., 2020), and the El Niño-Southern Oscillation (Herath et al., 2018; Schöne et al., 2007). There is therefore the potential for extending current instrumental records of these patterns and contributing high-resolution, calendar-aligned data to the creation of multi-proxy models of these complex, global scale atmospheric systems. This is particularly significant in regions such as the Tibetan Plateau, which serves as a freshwater source for billions of people and is likely to be extremely sensitive to climate change (Taft et al., 2013).

Another area of interest was the reconstruction of paleoecology and paleohydrology. Kaandorp et al. (2006) used the cyclicity and amplitude of stable isotope profiles to determine that bivalves from two different biotopes were being analysed: a fluvial and a lacustrine group. This helped to establish a more holistic picture of the region's ecosystem as well as providing insight into which specimens could provide the most accurate reconstructions due to the variability of where they lived. Research conducted by Buskirk et al. (2016) concluded that, due to the strong covariance in the stable oxygen and carbon isotope records of fossil shell carbonate, the late Eocene Lake Florissant was likely a closed lake system, thus adding to our understanding of the hydrological

history of the Florissant Formation. While Harzhauser et al. (2012) and Neubauer et al. (2014) investigated paleoclimate and paleohydrology, they were concerned with how these different environments may have impacted the fossil taxa under investigation. In the study by Harzhauser et al. (2012), the disparate geochemical data for related taxa are interpreted as evidence of habitat segregation and the utilisation of different food sources. The study is a good reminder of the influence that different taxa's life history and behaviour may have on the isotope record, and that these aspects need to be considered during interpretation. On the other hand, Neubauer et al. (2014) used stable isotope sclerochronology alongside morphometric analysis to argue that a speciation event that occurred within the Melanopsidae family during the Holocene was the result of a bottleneck effect induced by the eutrophication of a small thermal lake. This study demonstrates the vast variety of questions that freshwater mollusc sclerochronology can help to answer.

On top of the studies above which analyse fossil material, several more analysed modern material but noted the applicability of their results to the future analysis of fossil material (e.g., Chen et al., 2021; Gajurel et al., 2006; Lundquist et al., 2019; Roy et al., 2019; Taft et al., 2012). This demonstrates the potential and perceived value within the field to understand more about the fossil record and paleoenvironment using freshwater mollusc sclerochronology. In some cases, this has translated into paleoenvironmental reconstruction studies (Sun et al., 2021; Taft et al., 2014), while other studies noted the need for additional research before such analysis can be completed (Gajurel et al., 2006). There are, however, a variety of species from varying locations around the world which are waiting to be applied to such contexts and interested scientists should be encouraged to build on these prior modern calibration studies and apply the knowledge to fossil contexts.

4.4. Archaeology

Despite the application of sclerochronology to archaeology being the focus of several review articles or introductions to special issues (e.g., Andrus, 2011; Leng and Lewis, 2016; Prendergast et al., 2018; Prendergast and Stevens, 2014; Thomas, 2015; Twaddle et al., 2016), the sclerochronological analysis of freshwater molluscs with the intent of furthering archaeological research is relatively uncommon in freshwater mollusc sclerochronology articles published between 2000 and 2021. Thus, marine and estuarine mollusc sclerochronology appears to dominate archaeological investigations even though shell middens are found in most aquatic environments on all continents except Antarctica (Andrus, 2011). Yet, the breadth and results of the following articles demonstrated the potential for freshwater mollusc sclerochronology to provide vital insight into the study of past humans.

A variety of archaeological contexts are explored in the reviewed literature, across North America, Europe, southwest Asia, and northern Africa, and throughout the Holocene. Most studies are concerned with the reconstruction of past climates and their impact on human populations (Bar-Yosef Mayer et al., 2012; Çakirlar and Şeşen, 2013; Le Callonnec et al., 2019; Lewis et al., 2017; McLeester and Schurr, 2021; Schöll-Barna et al., 2012). The high-resolution paleoenvironmental records provided by mollusc sclerochronology to archaeological investigations can provide temporally and spatially relevant data directly linked to human settlement and behaviour, therefore allowing for more robust interpretations of human-environment interaction (Prendergast et al., 2018). Schöll-Barna et al. (2012) used sclerochronology applied to modern and archaeological *Unio pictorum* from Lake Balaton, Hungary, to support existing observations of a "5.3 ky BP event" at the site of Balatonkeresztúr-Réti-dűlő. This climatic event is believed to have had impact on the site's settlement and economy. Freshwater mollusc sclerochronology allowed Çakirlar and Şeşen (2013) to explore the importance of local environmental conditions to the survival of urban centres in northern Syria at the end of the 3rd millennium BCE. Their analysis of modern and archaeological shell material suggested that the regular flow of the Jaghjagh River likely contributed to the continued settlement

of Tell Mozan at a time when other urban centres were declining, while the more arid local conditions of Tell Leilan likely made its hydrology and population more vulnerable to climate changes. Sclerochronology provided insight into these microenvironmental conditions when only a regional level assessment of climatic change was otherwise available through other proxy records. Comparatively, McLeester and Schurr (2021) investigated the local impact of a known climatic phase (the Little Ice Age, 15th–19th centuries CE) on settlements in Illinois, USA. While material from 17th and 19th century settlements demonstrated that the climate was indeed much cooler and drier than modern conditions, the authors warned against overinterpreting the significance of these climatic conditions. McLeester and Schurr (2021) also highlighted the issues with projecting chronologically disparate data, such as historical accounts, into the past as local environments may have changed substantially through time. Therefore, freshwater mollusc material from the time and location of interest can provide relevant insight. Archaeological material is also used in multiple studies as a pre-industrial baseline to investigate historical changes in water quality, and can therefore provide insight into human activity of the more recent past and shed light on issues relevant to conservation (Fritts et al., 2017; Wilson et al., 2018a).

While seasonality of collection is recognised as a common goal of sclerochronological analysis of archaeological materials (Andrus, 2011), and has been addressed in several studies of marine mollusc material (e.g., Burchell et al., 2013; Mannino et al., 2003; Prendergast et al., 2016), similar studies on freshwater shells are less common, with only three studies in this review found to explore the question of seasonality in freshwater shells. A pilot study by Bar-Yosef Mayer et al. (2012), later strengthened by a more complete study by Lewis et al. (2017), answered the question of mollusc collection seasonality as part of a larger investigation into the paleoclimate conditions of the Central Turkey archaeological site, Çatalhöyük. The combined data from the two studies suggested that those molluscs found throughout the site's occupation were likely collected in autumn, perhaps due to dwindling resources elsewhere at this time of year, or because it was when the taxa provided the best energetic value. However, Lewis et al. (2017) acknowledged that more detailed analyses of the ventral margins of multiple specimens are needed to verify this result. The one other season of collection study reviewed here, conducted by Collins et al. (2020), completed a high resolution analysis of the final growth margin of archaeological shells collected from a single feature at an archaeological site in southeast Arkansas, USA. The analysis found that the shells from this site were all collected in winter, and the researchers argued that the assemblage represents a single event of mussel collection. As winter is seen as an unfavourable time of year to collect riverine mussels at this site, the researchers suggest that this could be evidence of a response to resource stress, or otherwise uncharacteristic climatic events that caused lower than usual water depth during winter. Together, these three studies demonstrate that season of collection analysis is possible with freshwater molluscs and can provide important insights into wider subsistence networks of past humans, as well as the temporality of archaeological features. The broader research reviewed in the current paper demonstrates that freshwater molluscs can provide a record of seasonal cyclicity (Section 5), therefore it is likely that season of collection research with freshwater archaeomalacological material will increase in popularity as more researchers turn to the archaeological record.

Further studies use sclerochronology to investigate freshwater mollusc remains from archaeological contexts, but do not apply this to paleoenvironmental reconstruction. Two publications investigated the use of freshwater mollusc sclerochronology to determine the origin of shells found in archaeological contexts. Through stable oxygen and carbon isotope analysis, Le Callonnec et al. (2019) determined that molluscs excavated from archaeological sites situated closer to the Rhône in Lyon, France, were likely collected from the Saone instead. They suggested that these shells may have been collected alongside

alluvial deposits in the Saone which were favoured for construction and artisanal uses, thus shedding light on the depositional context of the molluscs. Meanwhile, Apolinarska and Kurzawska (2020) used stable oxygen and carbon isotope analysis of carbonate sampled through incremental and bulk analysis methods to determine whether shells used in bead manufacturing were collected from rivers or lakes. These studies both demonstrate the valuable insights that freshwater mollusc sclerochronology can provide to understandings of manufacturing processes and resource management beyond food.

Helama and colleagues (Helama et al., 2009; Helama and Nielsen, 2008) applied the cross-dating methodology to shells from archaeological contexts. They demonstrated sclerochronological cross-dating of freshwater molluscs from archaeological contexts can be used to understand the chronological relationship between different archaeomalacological assemblages. This may have implications for dating and understanding paleoenvironmental variability across a region. The method has the potential to help make sense of complex stratigraphic features, such as shell middens, especially in cases where the resolution of traditional dating methods, such as AMS radiocarbon dating, is insufficient.

Finally, a study by Maurer et al. (2012) demonstrated that as Unionidae shells can act as recorders of bioavailable strontium ratios ($^{87}Sr/^{86}Sr$) in river water, archaeological shell material can be used alongside other environmental samples to define "local" bioavailable $^{87}Sr/^{86}Sr$ ratios. This may be extremely beneficial to research on past human mobility where defining the "local" bioavailable $^{87}Sr/^{86}Sr$ is required before non-local individuals can be identified.

Thus, freshwater mollusc sclerochronology has the potential to explore a variety of topics relevant to archaeological research, from paleoenvironmental insights to material origins, and can help to build a more holistic understanding of the lives and environments of past humans as well as aid in archaeological research more generally. Research on fragile and precious specimens, such as those found on archaeological sites or in museums, highlights the need for less invasive techniques, such as some forms of traditional sclerochronology drilling (Apolinarska and Kurzawska, 2020), or the use of alternative minimal invasive/non-invasive methods. For example, the low-cost, minimally invasive technique laser induced breakdown spectroscopy (LIBS) has been used with marine archaeological shells as a screening method to determine where further sampling for stable oxygen isotope analysis should be performed, therefore minimising the destruction of precious samples while also maximising results from a limited number of potential samples (Hausmann et al., 2019). This method is yet to be tested with freshwater shells. Furthermore, the preservation of archaeological material may limit the researcher's ability to identify mollusc taxa, making it difficult to conduct simple paleoecological assessments, but also hard to compare the archaeological material to modern sclerochronological studies on the same taxa. Recent advances in paleoproteomics and the matrix-assisted laser desorption/ionization-time of flight mass spectrometry (MALDI-TOF-MS) could assist with these issues, and early research on archaeological freshwater mollusc shell is already showing potential (Sakalauskaite et al., 2020). Sample preparation for this technique could be incorporated alongside standard sclerochronological workflow.

5. Proxies

In the following section we will provide an overview of the broad range of proxies available within freshwater mollusc sclerochronology: physical (growth and microstructure) and geochemical (stable isotopes and trace elements). The effectiveness and applicability of these proxies to different questions is of ongoing interest to the field. This section will provide an overview of some key studies and discoveries, important questions that have arisen, and areas where further research is needed. We focus on factors of particular relevance to freshwater mollusc investigations.

5.1. Growth and microstructure

Mollusc growth is an underpinning feature of sclerochronology and therefore has been well investigated. Generally, growth has been found to be synchronous within a single species' population, demonstrating the important influence of environmental conditions on freshwater mollusc growth (Black et al., 2010; Dunca and Mutvei, 2001; Haag and Rypel, 2011; Li et al., 2017); however, physiology can also play an important role (Rypel et al., 2008; Zotin and Ieshko, 2021). Evidence of biological clocks influencing growth after an individual has been removed from their natural environment demonstrates the influence of vital effects (Rodland et al., 2006; Rypel et al., 2009). Ontogenetic changes in mollusc growth rate are visible among freshwater molluscs, including the typical ontogenetic decrease in growth rate among bivalves (e.g., Herath et al., 2018; Rypel et al., 2008; Schöne, 2008).

Various environmental parameters are said to influence growth rate and therefore can be investigated through the proxy record of shell growth (Fig. 4). Temperature is often recognised as a key influence on growth, with warmer temperatures generally leading to faster growth during certain times of the year or day (e.g., Dunca et al., 2011; Goodwin et al., 2019; Lundquist et al., 2019; Schöne et al., 2004). Primary productivity/availability of food can also result in an increased growth rate, although too many nutrients can also lead to eutrophication which can, conversely, reduce habitat quality leading to lower mollusc growth and survival (Fritts et al., 2017; Valdovinos and Pedreros, 2007). Precipitation and/or river discharge have also been shown to be closely related to growth in some populations (Black et al., 2015; Dunca et al., 2005, 2011; Rypel et al., 2008, 2009; Schöne et al., 2007; Watanabe et al., 2021), while carbon saturation of water has also been identified as a potential influence (Bailey and Lear, 2006; Mutvei and Westermark, 2001). Shell damage, either as the result of mark-recapture experiments or non-anthropogenic causes can also influence an individual's growth (Haag, 2009; Haag and Commens-Carson, 2008; Helama and Valovirta, 2014). Of course, several influences may be at play at any one site. This speaks to the importance of conducting modern calibration studies which consider the influence of a wide range of factors. On top of environmental factors, pollution or anthropogenic environmental manipulation has also shown to influence growth and obscure the impact of natural hydrological parameters in freshwater systems (Carroll and Romanek, 2008; Dunca et al., 2005; Mutvei and Westermark, 2001; Rypel et al., 2009).

The literature has generally shown growth cessation or slower growth to be the result of temperature limits, with Dettman et al. (1999) determining that unionids have a hibernation threshold of approximately 12 °C (Dettman et al., 1999; Goewert et al., 2007), while other thresholds have been calculated for different taxa and/or watersheds (Goodwin et al., 2019; Izumida et al., 2011; Versteegh et al., 2010; Watanabe et al., 2021; Yan et al., 2009; Yoshimura et al., 2010). However, several other causes are also suggested in the literature, including rapid increases in water temperature and/or elevated temperatures (Goodwin et al., 2019; Schöll-Barna et al., 2012), increased precipitation (Gaillard et al., 2019; Yoshimura et al., 2010), brooding (Fritz et al., 2022), high river discharge and turbidity (Kelemen et al., 2017), occurrence of pollution (Dunca et al., 2011), or low water conditions (Kelemen et al., 2017), along with biological rhythms, perhaps impacted by circadian periodicity (Rodland et al., 2006; Rypel et al., 2008; Schöne, 2008; Schöne and Surge, 2012). Some species, such as *Radix* sp. are believed to grow year-round, although they have a limited lifespan and researchers point to amenable water temperature as being the reason why growth can be sustained (Roy et al., 2019). While freshwater environments are generally considered non-tidal and therefore freshwater molluscs are unlikely to show evidence of the tidal cycle as has been seen in intertidal marine species (Schöne and Surge, 2012), more investigations are needed into the impact that regular wetting/drying regimes have on freshwater species, either as the result of tidal systems or long-term climatic systems, such as the El Niño-Southern Oscillation.

These studies may be particularly relevant to individuals located near the bank of rivers or lakes. Already, correlations have been found between *Margaritifera margaritifera* growth patterns and the lunar nodal cycle, which has long-term influences on the ocean tides but which, in this case, may have influenced the food supply of these freshwater bivalves (Helama and Nielsen, 2008; Helama and Valovirta, 2014).

Microstructure may also provide valuable insight into the ambient environment. Füllenbach et al. (2014) demonstrated that first-order lamellae in gastropod *Viviparus viviparus* may be used as a measure of water temperature, although future studies are needed to verify if only water temperature can produce the observed microstructure changes or whether other environmental parameters may cause similar patterns. Environmental impact on mollusc microstructure has also been observed in marine species (e.g., Dodd, 1964; Milano et al., 2017). Further research is needed into the influence of different environmental parameters on freshwater mollusc microstructure.

Growth and geochemistry are tightly related, causing various challenges for interpretation (for further information, see Schöne, 2008). These challenges are reflected in several freshwater mollusc sclerochronology studies which note considerations that should be made when selecting the size/age of molluscs that will be used for sclerochronological analysis. Although arguments for and against the use of younger vs older specimens vary, overall the literature reviewed here highlights that comparing growth between older and younger specimens is difficult due to a variety of differences between the records, including changes in the thickness of microlamellae through ontogeny (Dunca and Mutvei, 2001) and differences in the timing of growth or the range of seasonal variation present in the record (Kukolich and Dettman, 2021; Roy et al., 2019). Research by Błażejowski et al. (2013) demonstrated that three different stages of ontogenetically influenced growth variability has been present in freshwater bivalves since at least the Miocene, and that each of these stages shows differing abilities to record paleoenvironmental information. Therefore, the ontogenetic stage of the individual is of extreme importance when interpreting the results of geochemical analysis. However, while growth influences the geochemical record within molluscs, oxygen stable isotope analysis is also commonly used in freshwater molluscs to create seasonally resolved growth rates and determine the longevity of molluscs by verifying annual growth lines (Goewert et al., 2007; Goodwin et al., 2019; Versteegh et al., 2009, 2010). This method is essential in the case of certain species that do not show evidence of traditional 'annual growth lines' and therefore require additional investigations to understand their growth features (Kelemen et al., 2017). Furthermore, an analysis of the relationship between growth rate and stable oxygen and carbon isotope values throughout the shell can elucidate whether kinetic effects influenced carbon and oxygen isotope fractionation in the faster growing portions of the shell (Yoshimura et al., 2015).

A key method applied to the analysis of freshwater mollusc shell growth, along with other molluscan taxa, is cross-dating, which involves the correlation of growth records across mollusc specimens and other archives to create longer and more detailed records (Peharda et al., 2021). This method has predominantly been performed on the long-lived mollusc species *Margaritifera margaritifera* (Helama et al., 2006, 2009; Helama and Nielsen, 2008; Helama and Valovirta, 2014; Schöne et al., 2004, 2005, 2007, 2020), although some alternative species have been successfully analysed (Black et al., 2015; Rypel et al., 2009). So far, all this research has been conducted with species from riverine environments: an assessment is needed to determine if individuals from lake environments are appropriate for cross-dating studies, given that these individuals usually show less environmental variability (see Section 5.2.1.1).

5.2. Geochemistry

5.2.1. Stable isotope ratios

One of the most frequently used proxies in freshwater molluscs for climate reconstruction are stable isotope ratios. They were discussed or analysed by over half (61%) of the research papers published between 2000 and 2021, with the analysis of stable oxygen isotope ratios ($^{18}O/^{16}O$) appearing most frequently (87%), compared to that of stable carbon isotope ratios ($^{13}C/^{12}C$) (61%), or other isotope systems (15%). In approximately half of these studies (51%), stable oxygen and carbon isotopes are analysed alongside one another.

Most of the reviewed studies analyse stable isotope ratios in shell carbonate by first milling/drilling carbonate powder from the shell and then analysing the carbonate using conventional isotope ratio mass spectrometer (c-IRMS). With this method, the sampling resolution can be limited by the scientist's milling/drilling skill and experience, as well as the mass constraints of the analytical set-up. Alternatively, Pfister et al. (2018) and Long et al. (2020) conducted the first studies applying secondary ion mass spectrometry (SIMS) to freshwater molluscs. This technique allows for small sampling spots (10-40 μm beam-spot diameter) to be analysed at high resolution. Although further research needs to investigate potential offsets between c-IRMS and SIMS in freshwater molluscs, as have been observed in other biogenic carbonates (Aubert et al., 2021; Helser et al., 2018), this technique has great potential for the analysis of samples requiring more detailed analysis (smaller taxa, finer growth patterns).

5.2.1.1. Stable oxygen isotope ratios. Most freshwater molluscs form their shells near oxygen isotopic equilibrium with the surrounding environment, with a recent global assessment of molluscs from 25 river basins across the world determining that the stable oxygen isotope ratio composition of mollusc shells could explain 95% of stable oxygen isotope ratio variation in stream water (Pfister et al., 2019). The stable oxygen isotope ratio composition of freshwater, and by extension the stable oxygen isotope ratio composition of mollusc shell, are controlled by various environmental parameters (e.g., temperature, evaporation/precipitation, etc.), and are known to vary significantly across space and time (Carroll et al., 2006; Fritz and Poplawski, 1974).

The hydrological system type (i.e., lake vs. stream/river) has a major influence on determining the dominant environmental parameters controlling stable oxygen isotope ratio composition of mollusc shell and plays a key role in freshwater mollusc sclerochronological literature (Prendergast and Stevens, 2014). The stable oxygen isotope ratio of water in lake systems is primarily controlled by whether it is a closed or open lake system (aka exorheic or endorheic drainage) and the length of water residence time (Hu et al., 2017; Prendergast and Stevens, 2014). These factors are known to alter through time through factors such as climate change or human activity (Hu et al., 2017; Lu et al., 2021). Closed lake systems often have longer water residence time and therefore the stable oxygen isotope ratio of closed lake water is usually controlled by precipitation-evaporation balance, while open lake systems have shorter water residence times and are impacted more by temperature and the stable oxygen isotope ratio of precipitation . Research conducted on the Tibetan Plateau demonstrated that because lakes in this region are most strongly influenced by evaporation and residence time, the stable oxygen isotope ratio of water from closed lake systems is more positive compared to in open lakes (Fig. 5d; Chen et al., 2021; Hu et al., 2017; Taft et al., 2013). This has therefore allowed for the characterisation of past hydrological systems using fossil material (Chen et al., 2021).

Additionally, lower seasonal oxygen isotope amplitude is characteristic of lake waters compared to river waters (Kaandorp et al., 2006; Vonhof et al., 2013; for an exception, see Gaillard et al., 2019). This is likely due to the longer residence time of lake water obfuscating the seasonal influence of precipitation, temperature, and/or water source on on the stable oxygen isotope ratio of the water. The distinct seasonality of rivers therefore make them a better proxy for reconstructing seasonal variation in precipitation/evaporation and temperature (Błażejowski et al., 2013; Kaandorp et al., 2006; Vonhof et al., 2013). Kaandorp et al.
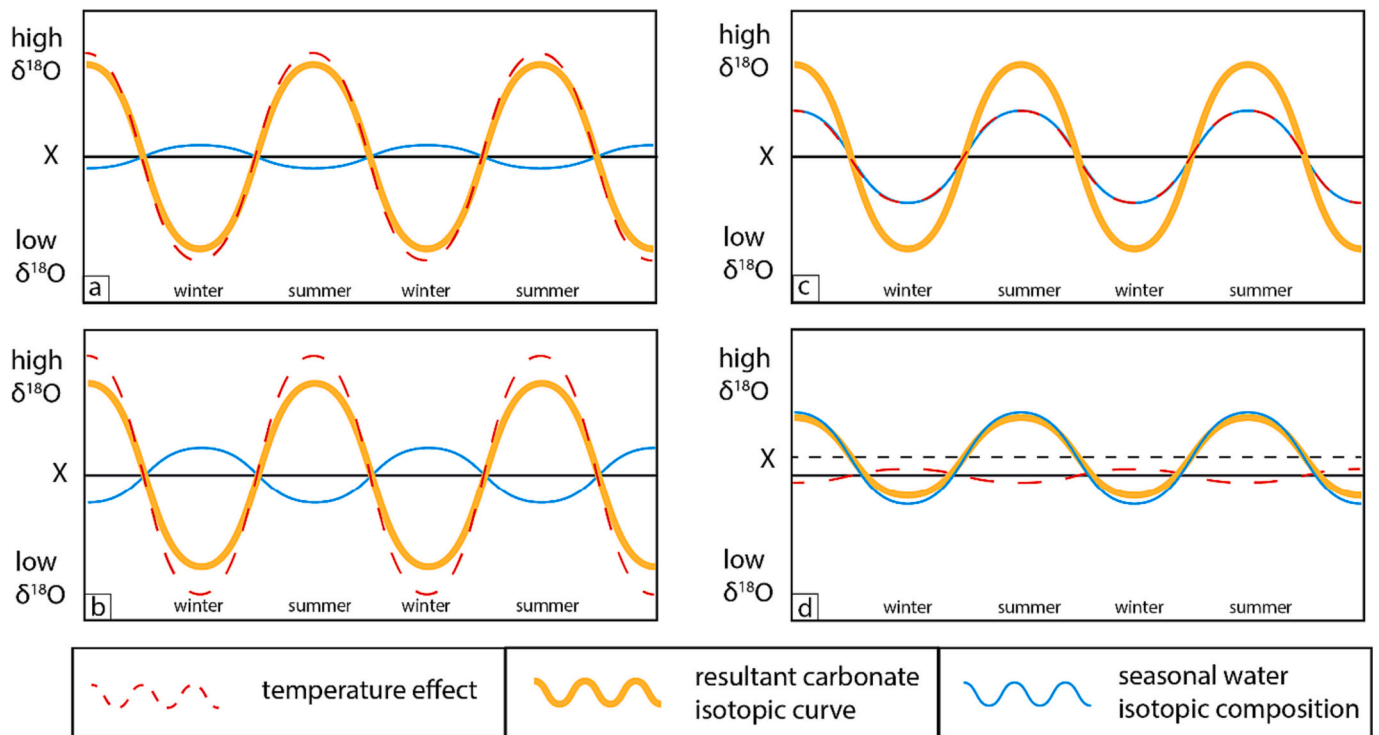
Fig. 5. Simplified models of the interaction between seasonal environmental influences (temperature and seasonal water isotopic composition) and the resultant carbonate isotopic curve. The resultant carbonate isotopic curve is identical in a, b, and c, and therefore demonstrates how different environmental conditions could produce similar isotopic signals in shell carbonate. (a): Temperature is the principal fractionation factor with the water isotopic composition contributing a relatively small amount to the overall carbonate isotopic curve. This reflects conditions such as those described by Schöne et al. (2007) and Yoshimura et al. (2010). (b): Temperature continues to serve as the principal fractionation factor; however, the seasonal water isotopic composition is having more of a countereffect on the resultant carbonate isotopic curve. This reflects meltwater conditions such as those described in the Rhine River by Ricken et al. (2003), and Versteegh et al. (2009, 2010), and in northern Sweden by Schöne et al. (2020). (c): As opposed to the previous examples, here temperature and water isotopic composition are equally effecting fractionation in the same direction. This reflects temperate rivers not impacted by meltwater, such as those conditions described in the Meuse River by Ricken et al. (2003), and Versteegh et al. (2009, 2010). (d): Model of an evaporative closed lake system, such as that described by Chen et al. (2021), where long water residence time and large surface areas lead to evaporation as the principal fractionation factor. This leads to a relative enrichment of stable oxygen isotope ratios in water and an overall more positive signal than in the other examples (dashed line). Seasonal water isotopic composition may also serve as the principal fractionation factor is tropic river systems (Kelemen et al., 2017, 2019, 2021; Vonhof et al., 2013). The amplitude of the carbonate isotopic curve is also shallower in a closed lake system, compared to in a river or open lake system (demonstrated by a, b, and c; Kaandorp et al., 2006, Vonhof et al., 2013). Figure adapted from Prendergast and Stevens (2014), Fig. 3) and Dettman and Lohmann (1993), Fig. 6).

(2006) used the amplitude differences between lake and river specimens to help characterise the preferred habitats of fossilised bivalves from the Pebas Formation of Western Amazonia and therefore gain an understanding of the local ecosystem structure during the Miocene. River type (Gajurel et al., 2006) and even the location of collection sites within the riverine or lacustrine habitat (Taft et al., 2012) may also have an effect on the amplitude of the stable oxygen isotope ratio of water and environmental influences. Therefore, modern calibration studies which include analysis of the stable oxygen isotope ratio of local water are essential. Further work in diverse and complex hydrological environments is needed to better understand how the stable oxygen isotope ratio of shell carbonate and water is influenced by different climatic variables. Just as it is important to understand species behaviour, life history, and physiology, it is essential to have a good understanding of the hydrological background of the site under investigation to effectively interpret the isotopic data.

Another consideration when applying sclerochronology to freshwater mollusc species from lakes is the thermal stratification that can occur seasonally in lake water, usually as a result of local weather and climate, and lake morphology (Kirillin and Shatwell, 2016). Schöll-Barna (2011) demonstrated that measured stable oxygen isotope ratios of freshwater molluscs in Lake Balaton, Hungary, were generally more similar to estimates calculated using the isotope mass balance model rather than measured stable oxygen isotope ratio of surface lake water,

showing the impact of seasonal thermal stratification on the stable oxygen isotope ratio of lake water. Thermal stratification may also impact the amount of temperature variation present at different levels of the lake (Vonhof et al., 2013). Therefore, particularly in lakes, it is essential that any water monitoring occurs near to the mollusc's habitat, rather than at surface level, so that the study can account for changes in thermal stratification and micro-habitats when interpreting the stable oxygen isotope ratio of shell carbonate.

Water source is an important consideration regardless of the freshwater habitat type. Rivers and lakes can be fed via a variety of different sources (e.g., rainfall, groundwater, glacial melt etc.) and the relative contribution of these sources can change through time. This is demonstrated well in research by Versteegh et al. (2009, 2010) where the isotope values of water and shells collected from two different rivers showed different seasonal patterns due to different water sources: in the Meuse River, stable oxygen isotope ratio values are increased in summer due to evaporation and enriched summer precipitation, while they are lower in winter as they reflect groundwater; however in the Rhine river, stable oxygen isotope ratio values are lowest in summer because of the influx of meltwater from the Alps at this time (Fig. 5). The stable oxygen isotope ratio value of these different water sources as well as their seasonal timing are therefore essential to the interpretation of a site.

While most studies determine the stable oxygen isotope ratio of shell carbonate to be an effective proxy for either temperature, precipitation,

evaporation, water source, or a combination of the above, depending on the hydrological and climatic setting, river discharge has also been highlighted as an influence on the stable oxygen isotope ratio of shell carbonate (Herath et al., 2018; Kelemen et al., 2017, 2021; Ricken et al., 2003; Versteegh et al., 2009). Versteegh et al. (2011) determined an empirical, logarithmic, relationship between the stable oxygen isotope ratio of water and discharge in the River Meuse between 1997 and 2007. The nature of the relationship meant that summer droughts (i.e., low-discharge events) could be identified due to a significant shift towards a higher stable oxygen isotope ratio in the water, although high summer discharge events could not be quantified. However, when researchers attempted to apply this relationship to the stable oxygen isotope record of historically collected *Unio* sp. shells, low-discharge events could not be identified consistently. Further work is needed to apply this method to a larger sample size to better understand the controls in place. A similar methodology was applied by Kelemen et al. (2017) to various bivalve species in the Oubangui and Niger Rivers. Logarithmic relationships between the stable oxygen isotope ratio of water and river discharge were calculated for both rivers, which showed strong discharge seasonality. When applied to the stable oxygen isotope record in shell carbonate, low-discharge events could be calculated with some accuracy, however high discharge events were overestimated. This research was then extended to three more sites on two additional African rivers, the Congo and Kasai rivers, in Kelemen et al. (2021). These new sites all showed contrasting discharge regimes. Again, an inverse relationship between discharge and the stable oxygen isotope ratio of water was described by a logarithmic fit in all situations, except on the Kasai River where the relationship was not inversed. The stable oxygen isotope ratio of water and corresponding stable oxygen isotope ratio of shell carbonate were found to have a lower amplitude where seasonal variability is lower, while the inverse was also true. The shell records have the potential to provide a sufficient proxy for discharge throughout the Congo Basin, although a better understanding of species microstructure and appropriate methodologies is needed before this can be shown. Kelemen et al. (2021) ended their study by noting the site-dependent nature of these results, therefore testing the application of this method outside (sub)tropical Africa is needed. This method has important implications for understanding pre-instrumental flow regimes and their connection with local climate and geography, particularly in locations where natural river systems have since been controlled by humans.

Although most freshwater molluscs form their shell at or near oxygen isotopic equilibrium, inter- and intra-species offsets, as well as inter-individual variability, do exist (e.g., Chen et al., 2021; Shanahan et al., 2005). These differences have been attributed to species micro-habitats (Harzhauser et al., 2012; Roy et al., 2019), ontogeny (Arnold et al., 2014; Chen et al., 2021; Kelemen et al., 2017), species physiology and behaviour (Shanahan et al., 2005), or other vital effects. Season or length of growth is also important to take into consideration, as species may grow in equilibrium with the surrounding water for part of the year, but will not record values during other times of year due to growth slowing/cessation, resulting in time-averaging (e.g., Goewert et al., 2007; Yan et al., 2009). The proportion of offset from equilibrium compared to the size of expected variation in the system ultimately influences how effective a taxa may be as a proxy record when applying methods of quantitative environmental reconstruction (Shanahan et al., 2005; van Hardenbroek et al., 2018). Calibration studies are therefore essential to determine the effectiveness of different taxa and the controlling parameters of different environments.

Palaeothermometry equations provide one means of determining the effectiveness of different taxa as environmental archives. Palaeothermometry equations refer to equations which model the carbonate-water fractionation relationship. Corrections need to be made depending on whether the shell under investigation is composed of calcite or aragonite. They contain three variables: stable oxygen isotope ratio of shell carbonate as compared with the Vienna Pee Dee Belemnite

standard ($\delta^{18}O_{VPDB}$), stable oxygen isotope ratio of water as compared with the Vienna Standard Mean Ocean Water standard ($\delta^{18}O_{VSMOW}$) at the time of shell formation, and temperature range at the time of shell formation. These equations allow for the calculation of absolute temperature at the time of shell formation where shell $\delta^{18}O_{VPDB}$ and water $\delta^{18}O_{VSMOW}$ are known or can be estimated (Dettman et al., 1999; Grossman and Ku, 1986). They are also used in modern calibration studies to determine if shell $\delta^{18}O_{VPDB}$ is in equilibrium with water $\delta^{18}O_{VSMOW}$ and quantify this relationship (Goewert et al., 2007; Kaan-dorp et al., 2003; Kelemen et al., 2017; Versteegh et al., 2009); to determine if something other than temperature is the main control over the shell $\delta^{18}O_{VPDB}$ (Schöll-Barna, 2011; Schöne et al., 2007); and/or to help determine growth rate and confirm chronology (Goodwin et al., 2019; Kukolich and Dettman, 2021).

Several palaeothermometry equations exist and are in use among the freshwater shell sclerochronology community. Most studies reviewed in this article use the equation determined by Grossman and Ku (1986) for aragonite-water fractionation (Eq. (1)), or the version of this equation published by Dettman et al. (1999); Eq. (2).

$$T(^{\circ}C) = 19.7 - 4.34\left(\delta^{18}O_{aragonite} - \delta^{18}O_{water}\right) \tag{1}$$

$$10^3 ln\alpha = 2.559 \times \left(10^6 T^{-2}\right) + 0.715 \tag{2}$$

In Eq. (2), $10^3 ln\alpha \approx \delta^{18}O_{aragonite}(\text{‰}) - \delta^{18}O_{water}(\text{‰})$, where $\delta^{18}O$ is on the same scale (VPDB or VSMOW). T is temperature (°C).

In the original study by Grossman and Ku (1986), the aragonite-water fractionation relationship was calculated based on marine gastropods and foraminifera in seawater with a temperature range of 2.6–22 °C. Building on the original study, Dettman and colleagues (Dettman et al., 1999) applied the equation to the shells of freshwater mussels (unionids) collected from rivers/streams and find that their data fits the Grossman and Ku (1986) model well. However, their equation accounts for a systematic error found to apply when water $\delta^{18}O_{VSMOW}$ is below −10‰. They also correct for the fact that the water $\delta^{18}O_{VSMOW}$ and shell $\delta^{18}O_{VPDB}$ are calculated on different scales by subtracting 0.27‰ from the water $\delta^{18}O_{VSMOW}$ value. While these equations are most often applied across the freshwater mollusc sclerochronology literature, other models exist, having been created based on inorganic carbonates (Kim et al., 2007), different biogenic archives(Böhm et al., 2000) aquatic habitats with different temperature ranges (Kim et al., 2007), and shell $\delta^{18}O_{VPDB}$ attained using different methods to account for Instrumental Mass Fractionation (Vihtakari et al., 2016). A study by Shanahan et al. (2005) compared seven equations to their stable oxygen isotope analyses of gastropods from springs in Nevada, USA. They found those equations developed using molluscs in natural habitats were more accurate than those based on carbonate created through inorganic synthesis. Another study by Long et al. (2020) determined that any of the four equations compared in the study could be applied to the analysed material with only a small difference observed among the results (0.03–0.2‰), which was usually less than instrumental errors.

The main limitation of palaeothermometry equations is that they are only as good as the values input into them. Considerations should be made as to how these measured values are collected and input into the equations. Goodwin et al. (2019) proposed that temperature 'envelopes' should be calculated using minimum and maximum temperature for each day, rather than inputting average daily temperature, as this would provide a more accurate estimation as to whether shell growth could have occurred on this day and during what time of day it may have occurred. Furthermore, in many cases, water temperature and the stable oxygen isotope ratio of water are estimated rather than measured due to a lack or limitation on resources, unrealistic monitoring schedules, or the need for non-existent past data. Among the studies reviewed here which investigated the stable oxygen isotope ratios of shell carbonate, 59% collected and/or analysed relevant stable oxygen isotope ratio water data, 53% collected and/or analysed relevant water temperature

data, and only 48% did both. Given the variability of stable oxygen isotope ratios in the water of freshwater systems, this is a concern, and future studies should aim to collect this data wherever possible (Fritz and Poplawski, 1974). In some cases, relative values are sufficient for exploring the questions being asked. For example, studies by Harzhauser et al. (2012) and Neubauer et al. (2014) used estimated intra-shell temperature ranges to better understand fossil molluscs' habitats. However, in the cases where absolute values are preferred but measured data is unavailable, an alternative option is the use of paired proxies.

5.2.1.1.1. Paired proxies: hydrogen isotopes and carbonate clumped isotopes. The stable oxygen isotope ratio of ambient water in freshwater environments can be particularly variable, with the potential to change rapidly due to evaporation or precipitation, and changes in water source (e.g., groundwater input, changes in precipitation source and amount). Furthermore, isolated sections of rivers may be affected by these processes, requiring water monitoring equipment to be placed precisely and in locations relevant to mollusc populations (Fritz and Poplawski, 1974; Prendergast and Stevens, 2014). When looking to reconstruct paleoenvironments, this becomes more challenging as these parameters are even less understood. As such, the use of paired proxies for the stable oxygen isotope ratio of ambient water, particularly hydrogen isotopes and carbonate clumped isotopes, provides an excellent opportunity to reduce uncertainties around estimations of the stable oxygen isotope ratio of ambient water and strengthen paleotemperature reconstructions.

Due to the strong relationship between hydrogen and oxygen in water, hydrogen isotopes provide an independent proxy of the stable oxygen isotope ratio of ambient water. A study by Carroll et al. (2006) investigated composition of stable hydrogen isotopes in the organic matrix of freshwater bivalve *Elliptio* sp. to determine if it could be used as an independent proxy for the stable oxygen isotope ratio of water in freshwater environments. The analysis found that the stable hydrogen and oxygen isotope ratios of the shells were positively correlated and preserved isotopic patterns seen in the water isotopic composition of their different stream habitats, despite concerns about the influence of exchangeable hydrogen on the results. Additionally, the research suggested that stable hydrogen isotope ratios may help to discern whether variation in the stable oxygen isotope ratios of shell is due to meteorological influences, such as precipitation, evaporation, and temperature, or other factors. This study by Carroll et al. (2006) appears to be the only research into the use of hydrogen isotopes in freshwater mollusc sclerochronology, despite the demonstrated potential of the methodology. Further work is needed to better understand fractionation between stable hydrogen isotopes in water and shell and understand the impact of exchangeable hydrogen on the method. Furthermore, future research should investigate the effect of diagenesis on the stable hydrogen isotopes of shell, as well as to test this technique in different species and habitats.

Carbonate clumped isotopes (usually expressed as Δ_{47} or Δ_{48}) are a measurement of the growth temperature of carbonate minerals and therefore can serve as an independent proxy for ambient water temperature when analysing aquatic molluscs (Eiler, 2011; Fiebig et al., 2019). Results can be extended to estimate the stable oxygen isotope ratio of water based on temperature alone, allowing for a more reliable interpretation of the impacts of evaporation, precipitation, and source water on the stable oxygen isotope ratio of water. Three studies in the freshwater mollusc sclerochronology literature demonstrate these different applications. A study by Van Plantinga and Grossman (2018) used carbonate clumped isotopes alongside measurements of stable oxygen and carbon isotope ratios in bivalves from the Brazos River in Texas, USA. A comparison of the stable oxygen isotope ratio and carbonate clumped isotope values in historical and modern shells provided evidence of enhanced evaporation in the modern river, likely due to impoundment and drought, as the stable oxygen isotope ratio was reliably lower in historical shells but the carbonate clumped isotope value remained similar. Another study by Sun et al. (2021) used carbonate

clumped isotopes to investigate whether modern collected shells from Fuxian Lake, China could be compared to Late Miocene fossil shells from an ancient lake at Shuitangba. The carbonate clumped isotope values showed that Late Miocene Shuitangba and modern-day Fuxian Lake experienced similar temperatures, therefore the large amplitude in seasonal stable oxygen isotope ratio variations observed in fossil shells could be interpreted as the result of stronger precipitation seasonality in the Late Miocene compared to today. Finally, Zaarur et al. (2016) analysed carbonate clumped isotopes in Late Glacial and Holocene fossil shells from northern Israel to understand how temperatures compared to today. After using the carbonate clumped isotope results to estimate the stable oxygen isotope ratio value of ambient water during these periods, the researchers identified an unexpected increase in the stable oxygen isotope ratio values from the Late Glacial period to the Holocene which was interpreted as being due to a decrease in the contribution of snowmelt to the hydrology of the area after the Late Glacial Maximum. While these three studies remain the only studies applying carbonate clumped isotopes to freshwater mollusc sclerochronology, this technique is likely to be applied in more research as it continues to grow in popularity in other fields. These studies show the potential of carbonate clumped isotopes with freshwater molluscs, especially in the study of fossil or archaeological materials.

While the results of the above studies are promising and demonstrate the important role that paired proxies can play in freshwater mollusc sclerochronology, both techniques have limitations that may prevent their application. First, the amount of material required for both techniques is large (>2 mg for hydrogen isotopes (Carroll et al., 2006); 3–7 mg for carbonate clumped isotopes (Trofimova et al., 2020)). The size limitation often precludes the analysis of material milled using high resolution incremental methods, and sometimes results in bulk analysis, particularly of small gastropods (e.g., Zaarur et al., 2016). Second, both techniques require a longer period of analysis than standard stable oxygen isotope analysis: it takes approximately 3 h to analyse one carbonate clumped isotope sample (Eiler, 2011), while various lengthy steps mean that it takes longer to get the results of hydrogen isotopes as well (Carroll et al., 2006). This translates into additional monetary cost, on top of the cost of any additional equipment or standards needed for the analysis. Third, there remains several key unknowns when it comes to the interpretation of these methods, such as the impact that diagenesis and the vital effects of molluscs have on these techniques. Further research also needs to investigate whether the thin organic layers often found in species of Unionoida may create similar issues with contamination as has been experienced in other organic-rich materials, such as teeth (Araujo et al., 2014; Eiler, 2011). Finally, analytical precision for carbonate clumped isotopes is much higher than that determined for hydrogen isotopes by Carroll et al. (2006) ($<\pm0.003$‰ vs ±3‰; Carroll et al., 2006; Zaarur et al., 2016), allowing for more nuanced interpretations using this technique. Despite both techniques having potential as paired proxies for freshwater mollusc sclerochronology, the broad applicability of carbonate clumped isotopes translates into research interest. Headway is being made to reduce required sample size (Banerjee and Ghosh, 2022; Müller et al., 2017) and analysis time (Yanay et al., 2022), while the dearth of research into hydrogen isotopes in biogenic carbonates continues. Therefore, carbonate clumped isotopes become more accessible to research each day and are likely to become more central to freshwater mollusc sclerochronology research in future.

5.2.1.2. Stable carbon isotope ratios. Stable carbon isotope ratios in freshwater and mollusc shell exist within a complex system of biological, geological, and meteorological influences. However, the larger potential range of the stable carbon isotope ratio in freshwater compared to marine waters (−35‰ to +5‰, compared to −6.56‰ to +3.10‰, respectively; Campeau et al., 2017; Cheng et al., 2019), makes stable carbon isotope ratios in freshwater mollusc shell potentially a hugely valuable

archive which can help investigate various research topics, such as precipitation regimes (Taft et al., 2012), fossil species habitats (Kaandorp et al., 2006), and global carbon cycling (Yoshimura et al., 2015).

Stable carbon isotope ratios measured in freshwater molluscs derive predominantly from environmental dissolved inorganic carbon (DIC). DIC and its stable carbon isotope value is the product of three components: dissolved CO_2 and carbonic acid (H_2CO_3), the bicarbonate ion (HCO_3^-), and the carbonate ion (CO_3^{2-}) (Cole and Prairie, 2014). The relative proportion of these different components determine the pH of the water, and their relationship is also influenced by salinity and, to a lesser extent, temperature (Fig. 6). HCO_3^- is the component believed to be used by bivalves for shell growth (Kaandorp et al., 2006; Schöne and Krause, 2016). The carbon fractionation factor between bicarbonate and inorganic aragonite is $2.7 \pm 0.6‰$ (Romanek et al., 1992), although studies on freshwater molluscs have provided alternative values of $2.0 \pm 0.7‰$ (Yoshimura et al., 2015) and $-4.0 \pm 0.7‰$ (Kaandorp et al., 2003). Most studies continue to use the inorganic aragonite value devised by Romanek et al. (1992), but future research should focus on understanding the diversity of carbon isotope fractionation values across freshwater habitats and the reasons for this variation.

The stable carbon isotope ratio value of DIC is based on a relationship between different sources and sinks of DIC, which each have a different contribution to the stable carbon isotope ratio value (Campeau et al., 2017). Sources of DIC in freshwater environments include isotopic ratios of ground water or other inflowing waters, the exchange of atmospheric and aqueous CO_2, soil CO_2 (predominantly decomposing organic material), and weathering of silicates and carbonates (Błażejowski et al., 2013; Kaandorp et al., 2006; Yoshimura et al., 2015). Sinks include photosynthesis of plants and algae, outgassing of CO_2 into the

atmosphere, and fixation of carbon into calcium carbonate, such as mollusc shell (Kaandorp et al., 2006). The contribution of these factors may vary seasonally and based on location. For example, temperate lacustrine habitats are more likely to be affected by plant and algae photosynthesis compared to stream habitats because of the longer water residence time (Kaandorp et al., 2003). Photosynthetic plants preferably remove lighter isotopes (^{12}C) into their cells, resulting in closed temperate lakes often having an enriched stable carbon isotope ratio value of DIC (Apolinarska and Kurzawska, 2020).

Apart from DIC, it has been estimated that metabolic or respired carbon makes-up approximately 10% of overall carbon in aquatic molluscs (McConnaughey and Gillikin, 2008), however freshwater mollusc sclerochronology research has shown that this relative contribution can vary from <5% (Kaandorp et al., 2003; Shanahan et al., 2005), to 40% (Van Plantinga and Grossman, 2018). Metabolic carbon comes from dietary organic sources and its contribution may increase based on environmental conditions (e.g., ambient CO_2/O_2 ratio, see the respiratory gas exchange model; McConnaughey and Gillikin, 2008) or taxon (e.g., pulmonates vs. caenogastropods, differences in life history; Chen et al., 2021; Shanahan et al., 2005; Van Plantinga and Grossman, 2018). The contribution of metabolic carbon to the stable carbon isotope ratios of shell carbonate is generally though to increase through a mollusc's life (Gillikin et al., 2009; Goewert et al., 2007; Van Plantinga and Grossman, 2018; Yan et al., 2009), causing a systematic decrease in the stable carbon isotope ratio with ontogeny as metabolic carbon is generally more enriched with ^{12}C (Leng and Marshall, 2004). As a result, some studies have been able to define a relationship between shell height and the percent of metabolic carbon in the shell (Gillikin et al., 2009; Yan et al., 2012). However, several studies have shown that this
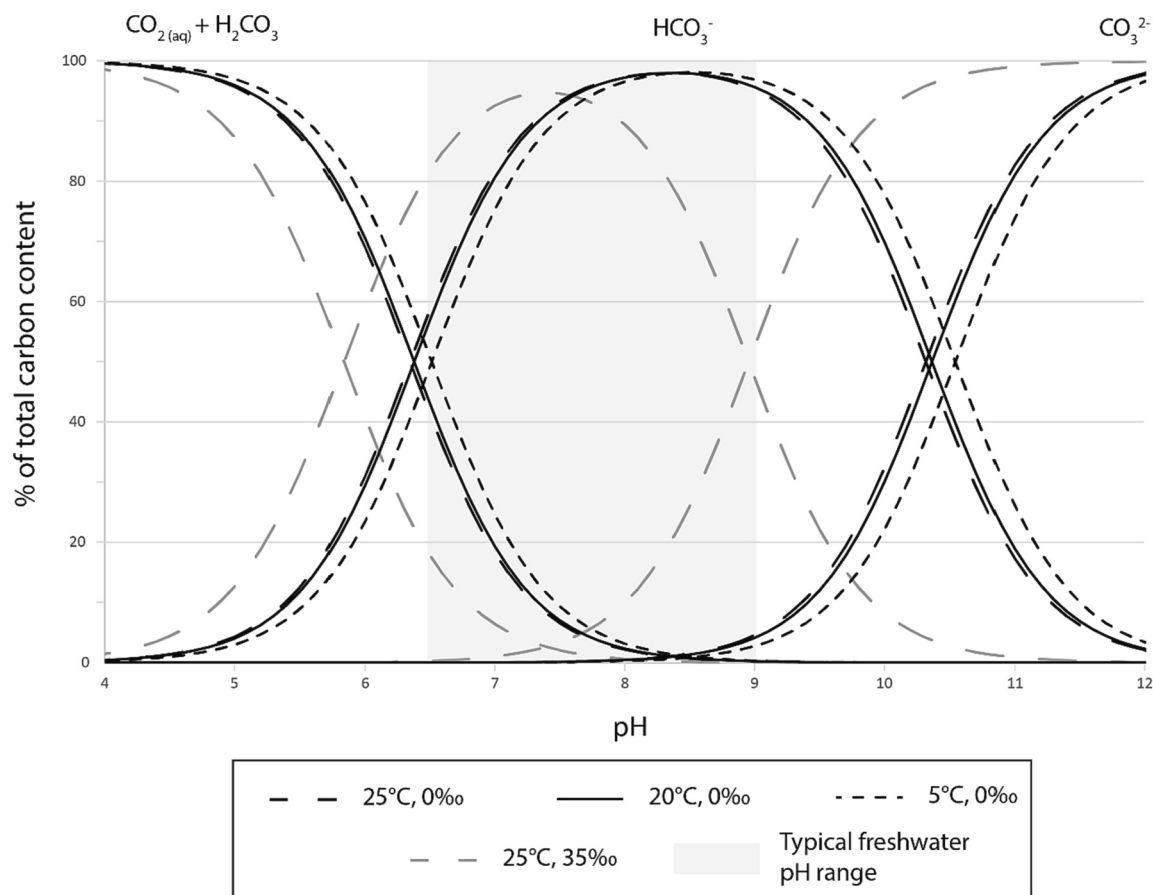

Fig. 6. Bjerrum plots modelling the speciation of DIC under different pH, temperature (25 °C, 20 °C, 5 °C) and salinity (0‰, 35‰) conditions. 0‰ salinity depicts typical freshwater conditions; 35‰ salinity is the average ocean salinity. Typical freshwater pH range for productive freshwater system based on guidelines by Robertson-Bryan, Inc (2004). Constant values according to Millero and Roy (1997).

ontogenetic trend is not universally true for all freshwater molluscs (Kelemen et al., 2017; Neubauer et al., 2014; Schöne et al., 2020; Yoshimura et al., 2015). Other life events, such as reproduction, may also affect its inclusion (Dettman et al., 1999). As such, an equation developed by McConnaughey et al. (1997) is used in the literature to estimate the relative contribution of metabolic versus DIC carbon to the stable carbon isotope ratios of shell carbonate (see Shanahan et al., 2005; Van Plantinga and Grossman, 2018, and Yoshimura et al., 2015 for application examples).

While a failure to relate the stable carbon isotope ratios of shell carbonate and DIC is often attributed to the increased contribution of metabolic carbon, the resolution of data on the stable carbon isotope ratio of water should also be considered (Versteegh et al., 2010). In fact, less than one third of studies that investigated the stable carbon isotope ratio of shell carbonate collected water data relating to the stable carbon isotope ratio of DIC. This may be due to the extra expense and knowledge involved: in the detailed study by Yoshimura et al. (2015), they collected data relating to water pH, alkalinity, and the stable carbon isotope ratio of DIC, each parameter requiring a vastly different technique. Nevertheless, future modern calibration studies should look to collect this kind of data more regularly so that the relationship between the stable carbon isotope ratios of DIC and shell carbonate can be better understood, and the relationship between different DIC sources and sinks at the site of interest can be better established.

Once the influence of metabolic carbon on the overall stable carbon isotope ratio of shell carbonate has been determined, stable carbon isotope ratios can provide useful information on a variety of environmental factors (Gillikin et al., 2009). Despite the complexity of the system, stable carbon isotope ratios in freshwater mollusc sclerochronology studies have been interpreted as a proxy for discharge regimes (Van Plantinga and Grossman, 2018), aquatic habitat (e.g. marine vs. freshwater; lake vs. river; Apolinarska and Kurzawska, 2020; Kaandorp et al., 2006; Vonhof et al., 2013) and changes in molluscan food/organic carbon sources and food availability (Bar-Yosef Mayer et al., 2012; Çakirlar and Şeşen, 2013; Goewert et al., 2007; Versteegh et al., 2010). Two studies (Goewert et al., 2007; Kelemen et al., 2017) observed that the stable carbon isotope ratios of shell carbonate may be used to identify different vegetation types (C3 vs C4 plants) within a watershed, although Kelemen et al. (2017) noted that different weathering regimes among watersheds may also be responsible. Soil weathering may also be a proxy for precipitation: Taft et al. (2012) identified that a decrease in the stable carbon isotope ratio of shell carbonate coincided with the onset of monsoon precipitation and suggested that this was due to the precipitation penetrating unsaturated soil and washing the ^{12}C enriched nutrients into the lake. Therefore, in certain cases, the stable carbon isotope ratio may be used to strengthen interpretations of the stable oxygen isotope ratio record. The relationship between the stable carbon and oxygen isotope systems also provides unique insights into hydrological habitat (e.g., river, open/closed lake; Apolinarska and Kurzawska, 2020; Buskirk et al., 2016; Vonhof et al., 2013), and the seasonality of different carbon sources (Kaandorp et al., 2006; Lewis et al., 2017). This relationship may also be used to elucidate the impact of kinetic effects on carbon and oxygen isotope fractionation in the shells (Goewert et al., 2007; Yan et al., 2012).

Finally, it is important to consider how rising CO_2 emissions have impacted the stable carbon isotope ratio value of DIC and what role the stable carbon isotope ratios of shell carbonate can play in better understanding the output of atmospheric CO_2. Researchers have hypothesised that the Suess effect should be visible in shell carbonate records of stable carbon isotope ratios as an approximate 2‰ decrease, and that this may create issues when trying to compare pre-industrial shells to modern specimens (Apolinarska and Kurzawska, 2020; Geist et al., 2005). So far, however, no evidence of this decrease has been identified in freshwater mollusc shell records (Geist et al., 2005). The various sources of the stable carbon isotope ratio of DIC are likely to make this hypothesis difficult to test, however a high-resolution study of long-lived

molluscan records which includes the collection of modern water data could help to distinguish the influence of other DIC sources and sinks on the stable carbon isotope ratio of shell carbonate. The likely increase in pollution that accompanied the post-industrial change in atmospheric carbon will probably further complicate the situation (Schöne et al., 2006). In the absence of understanding the influence of past pollution, the study by Yoshimura et al. (2015), detailed above, demonstrates how the analysis of the stable carbon isotope ratio of shell carbonate could aid current attempts to better model how rivers contribute to global carbon cycling.

5.2.1.3. Other isotope proxies. A small number of studies reviewed here have employed stable isotope ratios other than oxygen and carbon to freshwater mollusc shell sclerochronology. Stable nitrogen isotope ratios ($^{15}N/^{14}N$) were analysed by four recent studies (Fritts et al., 2017; Graniero et al., 2021; Kukolich and Dettman, 2021; Wilson et al., 2018a). Graniero et al. (2021) determined that stable nitrogen isotope ratios analysed in the periostracum and carbonate-bound organic matter in freshwater mussel shells (*Elliptio complanata*) could be used as recorders of stable nitrogen isotope ratio changes in surrounding hydrology, as was previously attested in estuarine and marine bivalve species and has been demonstrated in the analysis of freshwater mussel soft tissues. This was also supported by the findings of Kukolich and Dettman (2021), who determined that stable nitrogen isotope ratios measured in periostracum and carbonate-bound organic matter in the shell of three freshwater mollusc species recorded seasonal variability in stable nitrogen isotope ratios. This study was also able to assign calendar dates to the stable nitrogen isotope ratio variation through correlation of growth with stable oxygen isotope ratios of shell carbonate. Stable nitrogen isotope ratios are suggested to provide a proxy for land-use change, individual's trophic-level, and/or presence of industrial pollutants and sewage. These two studies validate the application of stable nitrogen isotope ratios in freshwater sclerochronology studies, although species-specific calibration studies are still recommended to account for geochemical differences seen between mollusc soft tissues and shells and species-specific vital effects. Further research needs to consider the impact of parasites on the stable nitrogen isotope ratios of shell material, as they have been shown to impact the stable nitrogen isotope ratios of mollusc tissue (Doi et al., 2008). Although studies by Fritts et al. (2017) and Wilson et al. (2018a) used stable nitrogen isotope ratios without an initial calibration study for *Amblema plicata* or *Quadrula quadrula*, in both papers the stable nitrogen isotope ratio shows a positive relationship with other proxies (Cu; Wilson et al., 2018a; mussel growth; Fritts et al., 2017) suggesting that this proxy may be an effective indicator of environmental change in these studies as well.

Strontium isotope ratios ($^{87}Sr/^{86}Sr$) in freshwater mollusc shell were investigated in three studies. Mutvei and Westermark (2001) built on previous research (Åberg et al., 1995) to demonstrate that strontium isotopes ratios analysed in *Margaritifera* sp. record changes with water pH. Additionally, Geeza et al. (2018) demonstrated that strontium isotopes ratios measured in the shell carbonate of two *Elliptio* sp. were a viable proxy of strontium isotope ratios in water and showed that strontium isotopes ratios of shell carbonate could be used to track wastewater discharge from oil and gas production. Both papers point to strontium isotope ratios as a proxy for mineral weathering, supported by previous studies of both freshwater and marine environments (Åberg et al., 1995). Finally, Maurer et al. (2012) used archaeological freshwater bivalve material alongside modern specimens to investigate short- and long-term changes in bioavailable strontium isotope ratios in river water, finding that the strontium isotope ratios for the Saale river did not change significantly over the last 2000 years, despite reported anthropogenic contamination. Strontium isotopes measured in shell carbonate may therefore serve as an effective monitor of some forms of pollution.

5.2.2. Minor and trace elements

While the static nature of marine environments has allowed for correlations to be made between different trace elements and environmental parameters in marine mollusc sclerochronology research (e.g., Freitas et al., 2006; Gillikin et al., 2006; Wanamaker Jr et al., 2008), it has also resulted in the co-variance of several geochemical, environmental and biological factors (Bailey and Lear, 2006). As such, researchers have turned to the more variable freshwater habitats to tease apart environmental and biological controls and help answer questions which are relevant to the greater discipline of mollusc sclerochronology, such as the process of trace element biomineralisation (Bailey and Lear, 2006; Izumida et al., 2011). Of the 111 research papers reviewed here, only 28% analysed the trace element composition of mollusc shell. The following section will review how the study of freshwater mussels has provided insight into biomineralisation of trace elements, the best methodologies to analyse trace elements, and the effectiveness of different elements as environmental proxies.

The process of trace element biomineralisation is explored in several studies of freshwater molluscs. Generally, it is believed that cations of the elements are pumped from the ambient environment into the extrapallial fluid before being incorporated into the shell as substitutions for Ca^{2+} in $CaCO_3$ as the crystal lattice of the shell is formed (see Zhao et al., 2017a, and Soldati et al., 2016, for an overview of these processes and related references). Various factors may impact on this process, including the individual properties of each element (e.g., ionic radius, electrochemical properties), the carbonate polymorph involved (i.e., aragonite or calcite; Izumida et al., 2011; Soldati et al., 2009; Zhao et al., 2017a), and even the microtopography of the external shell surface (Zuykov et al., 2012). The physiology of the animal itself is also important to consider; not just the influence of the life history or ontogeny of the mollusc but also how the mantle forms different layers of the shell (Carroll and Romanek, 2008). Understanding the different influences on biomineralisation is a key step before being able to tease out the environmental influences on trace elements. In particular, the chemical analysis of the extrapallial fluids of freshwater molluscs is seemingly lacking from the literature (Huang and Zhang, 2022). A study which analysed the extrapallial fluid, shell carbonate and ambient environment of freshwater mollusc would likely provide invaluable information about the biomineralisation of trace elements in freshwater molluscs.

The partitioning or distribution coefficient (D_E or Kd) is used in several studies to compare the elemental content of the shell to that of the surrounding water, and is calculated using the equation $D_E = \frac{[element:Ca]_{shell}}{[element:Ca]_{water}}$ (Carroll and Romanek, 2008; Geeza et al., 2019; Izumida et al., 2011; Markich et al., 2002; Zhao et al., 2017a). A value of 0 indicates that no element from the ambient environment is incorporated into the shell, while a value of 1 signifies that the trace element composition of the shell is the same as that of the ambient environment. Therefore, a value closer to 0 or further away from 1 may indicate that vital or kinetic effects, or other factors, have impacted the biomineralisation of the trace element into the shell so that it does not record the presence of that element in equilibrium with the surrounding environment. While values over 1 are possible, the majority of values in the literature for freshwater shells lie between 0 and 1. Review tables compiled by Carroll and Romanek (2008) and Geeza et al. (2019) demonstrated that these values provide a useful way of comparing the effectiveness of different trace elements as a proxy for various taxa and environments. Yet, these calculations require an understanding of ambient water trace element composition which was only monitored by 48% of the reviewed studies which investigated trace elements. The great fluctuations present in the freshwater environment means that the monitoring of trace element values in water needs to become more commonplace in modern calibration studies of freshwater environments in order to better understand the influence of vital or kinetic effects on trace element biomineralisation.

Methods employed for trace element analysis must allow for high resolution sampling, due to the variability of freshwater environments, with sufficient sensitivity to study the elements under investigation (Füllenbach et al., 2017; Markich et al., 2002). Most studies investigating trace elements within freshwater mollusc sclerochronology analysed micro-drilled or laser ablated samples using inductively coupled plasma mass spectrometry (ICP-MS). Phung et al. (2013) demonstrate that these two techniques show no statistical difference in the analysis of Sr, Ba, and Mn, however the results of Mg showed difference, potentially influenced by the structure of the shell. Another notable methodology applied to the analysis of trace elements in freshwater molluscs is micro x-ray fluorescence (μ-XRF) which provides fast and non-destructive analysis with the potential for a high-density of sampling spots. Leppänen et al. (2021) published the first study applying μ-XRF methods to studying freshwater pearl mussels. In particular, the authors noted the 2D elemental maps generated with this method could be valuable as pre-screening methods for the identification of detrital material or leaching metals prior to conducting any point analysis. SIMS is another alternative method for trace element used within the reviewed literature (Markich et al., 2002). This technique is particularly valuable when investigating trace elements/metals with relatively low concentrations at high resolution, which Markich et al. (2002) demonstrate in their investigation of freshwater bivalve shells as records of metal pollution. Given constant improvements in sample preparation and analysis techniques, a review of the best methods for investigating trace element composition in shells is needed to determine if SIMS is still the ideal method for such research. Future research needs to assess the strengths and weaknesses of different methods used for trace element analysis within freshwater mollusc sclerochronology, while also considering additional methods not yet applied to freshwater specimens but used with marine molluscs, even lower resolution and more affordable methods such as LIBS (Hausmann et al., 2019). In addition, there is a need for more studies evaluating the statistical modelling methods used alongside these different analytical approaches (Shoults-Wilson et al., 2014).

The following section will review the results of research investigating the use of specific trace elements as proxies of environmental or biological parameters. The section is focused on Sr, Ba, Mn, and Mg which are given the most attention in the literature.

5.2.2.1. Strontium.

Sr in freshwater habitats predominantly derives from surrounding geology and bedrock weathering (Kelemen et al., 2019; Leppänen et al., 2021). Although studies of inorganic aragonite have found a D_{Sr} coefficient value of 1 (Kinsman and Holland, 1969), in freshwater mollusc studies this coefficient generally sits around 0.16–0.29, comparing relatively well to the values seen in marine molluscs and suggesting that vital effects influence how much Sr is incorporated in the shell (Anadón et al., 2010; Carroll and Romanek, 2008; Geeza et al., 2019; Zhao et al., 2017a). The direction and severity of these biological influences appear to be species-specific (Izumida et al., 2011; Kelemen et al., 2019). Several studies have correlated Sr/Ca_{shell} with growth rate and/or ontogeny (Geeza et al., 2018; Herath et al., 2018; Izumida et al., 2011; Soldati et al., 2009) however, these effects do not appear universal, and could instead be an artefact of sampling bias (Anadón et al., 2010; Kelemen et al., 2019; Zhao et al., 2017a).

As for non-biological controls on Sr/Ca_{shell}, some relationship exists between the Sr/Ca_{shell} and Sr/Ca_{water}. Chen et al. (2016) reported varying sensitivity in D_{Sr} to changes in Sr/Ca_{water} depending on whether water has a molar ratio above or below 0.007. The tank experiment performed by Zhao et al. (2017a) also found that the amount of Sr/Ca_{shell} increased linearly with the Sr/Ca_{water}, suggesting that Sr is predominantly derived from the water. Although Sr/Ca_{shell} does not directly reflect Sr/Ca_{water}, Sr/Ca_{water} can influence its composition and even mask the controls of other parameters, therefore it is an important variable to monitor (Anadón et al., 2010; Chen et al., 2021; Kaandorp

et al., 2006; Zhao et al., 2017a). The study by Zhao et al. (2017a) determined that Sr/Ca$_{shell}$ could estimate temperature to the nearest 3.5 °C through regression analysis, if the Sr/Ca$_{water}$ is known. As unaccounted shifts in Sr/Ca$_{water}$ of as little as 0.1 mmol/mol could result in a temperature error of 0.65 °C, the researchers suggested that Sr/Ca$_{shell}$ could only be used as a reliable paleothermometer in ecosystems with low Sr/Ca$_{water}$ variability, such as estuaries. Yet, other studies have not been able to draw a similarly clear relationship between temperature and Sr/Ca$_{shell}$: while some research has suggested temperature as a probable influence on Sr/Ca$_{shell}$, although likely not the only one (Anadón et al., 2010; Geeza et al., 2019; Herath et al., 2018; Risk et al., 2010), other studies have ruled it out as a potential control (Chen et al., 2016; Izumida et al., 2011; Kelemen et al., 2019). Salinity has also been suggested as an influence on Sr/Ca$_{shell}$, although there is less research on this (Chen et al., 2016). This review demonstrates that the interaction between Sr/Ca$_{shell}$, mollusc biology, and freshwater environments is complex and not yet well understood, and further research is needed to investigate the relationship between these variables in different species and habitats around the world.

5.2.2.2. Barium. Ba enters freshwater habitats through geological and organic sources (Dalai et al., 2002). Molluscs may incorporate Ba/Ca into their shell from the ambient water or food sources (Gillikin et al., 2006; Zhao et al., 2017a). Similarities between Ba/Ca and Sr/Ca have been observed in several studies (Herath et al., 2018; Kelemen et al., 2019; Soldati et al., 2009). Research shows that Ba/Ca is connected to several intertwined factors. Compared to Sr/Ca, there is a stronger vital effect on the incorporation of Ba into the shell: D$_{Ba}$ coefficients are usually smaller than for Sr/Ca (Carroll and Romanek, 2008; Geeza et al., 2019; Zhao et al., 2017a) and studies have observed interspecies and/or interindividual variation within similar habitats (Herath et al., 2018; Kelemen et al., 2019). Furthermore, Watanabe et al. (2021) observed that Ba/Ca$_{shell}$ peaks showed a chronological offset from environmental events, suggesting that they did not precipitate Ba/Ca coincidently with the ambient environment. Like with Sr/Ca, several studies have correlated Ba/Ca with growth rate and/or ontogeny (Herath et al., 2018; Izumida et al., 2011; Kelemen et al., 2019; Risk et al., 2010; Soldati et al., 2009). These factors could also be related to metabolic rate, which is affected by temperature and food availability and may impact the shell's ability to select how much Ba/Ca is incorporated into the shell (Zhao et al., 2017a).

Ba/Ca$_{shell}$ has been suggested as a proxy for temperature (Geeza et al., 2019; Kieniewicz and Smith, 2007). Additionally, studies have recognised Ba/Ca$_{shell}$ as a proxy for river discharge (Geeza et al., 2019; Watanabe et al., 2021), precipitation (Watanabe et al., 2021), and changes in erosion (Risk et al., 2010), as these events may cause an increased amount of high barium sediment to be washed into the water. A relationship between food availability/phytoplankton productivity and Ba/Ca$_{shell}$ has also been observed in several studies, although the relationship is not always clear-cut (Carroll and Romanek, 2008; Herath et al., 2018; Soldati et al., 2009; Watanabe et al., 2021). As stated in the literature, further research into the Ba^{2+} enrichment of different phytoplankton species, along with precise studies into how much food molluscs are ingesting, could help solidify the contribution of food and phytoplankton to overall Ba/Ca$_{shell}$ (Zhao et al., 2017a).

5.2.2.3. Manganese. Mn is found naturally and abundantly in aquatic sediments as MnO$_2$, from where it can easily undergo a redox reaction into the soluble and bioavailable Mn^{2+} found in sediment pore water and organic material (Zhao et al., 2017b). D$_{Mn}$ coefficients are much higher than those for other elements, suggesting that vital effects may have less of an impact on Mn/Ca$_{shell}$ (Carroll and Romanek, 2008; Geeza et al., 2019). In fact, little connection has been made between ontogeny or growth rate and Mn/Ca$_{shell}$, although Kelemen et al. (2019) suggested that Mn may be used by molluscs in different ways during different life

stages. However, research by Soldati et al. (2016) suggests that vital effects are present in the incorporation of Mn^{2+} into freshwater aragonitic bivalve shells. This research stemmed from the observation that Mn in freshwater shells was relatively abundant, despite its uptake in non-biogenic aragonite being limited and its small ionic radius being better suited to calcite structures. Analysis of the shells of various freshwater aragonite bivalve species using X-ray absorption and X-ray emission spectroscopy found that Mn^{2+} was being held in quasi-calcitic, octahedral structures within the aragonite. This is likely to cause limitations for aragonitic organisms, especially any living in environments with high concentrations of Mn. Further studies comparing aragonitic and calcitic species in the same environment are needed to better understand how this vital effect may manifest in the record.

Some studies have observed lags between Mn/Ca$_{shell}$ and environmental conditions or other geochemical proxies (Herath et al., 2018; Kelemen et al., 2019; Watanabe et al., 2021), which have previously been explained by differences in metabolic pathways. Others have observed chemical restrictions on the uptake of Mn: Carroll and Romanek (2008) suggest that Mn would not be incorporated unless Ca^{2+} water content was >5 mmol:mol, suggesting that some of the Mn may have been used in the molluscs in a different way or eliminated, while Kelemen et al. (2019) suggest that Mn incorporation into shells may be influenced by ambient water pH. However, similar patterns in Mn/Ca$_{shell}$ among populations in multiple studies suggest that some environmental controls are at work (Kelemen et al., 2019; Shoults-Wilson et al., 2014; Zhao et al., 2017b). Mn serves as an effective proxy for fluctuations in dissolved oxygen concentration of water and/or the release of soluble Mn^{2+} as a result of anoxic events (Mutvei and Westermark, 2001; Risk et al., 2010; Shoults-Wilson et al., 2014; Watanabe et al., 2021; Zhao et al., 2017b). This may reflect changes in river flow regimes or seasonal upwellings in lakes (Langlet et al., 2007; Watanabe et al., 2021). Changes in Mn concentration of the water is also associated with phytoplankton blooms and increased water productivity (Carroll and Romanek, 2008; Geeza et al., 2019; Kelemen et al., 2019; Langlet et al., 2007; Wilson et al., 2018b). A study by Tazaki and Morii (2008) revealed that an increased accumulation of Mn in the shell of a ponded group of *Sinohyliopsis schlegeli* during the summer may be due to microbiological activity, particularly the consumption of diatom *Siderocapsa* sp.. This study, which investigated the suspended solids in the water alongside the shell and other water qualities, excelled in its consideration of how the molluscs interacted with their surrounding environment. Additionally, the reduction of MnO$_2$ is associated with the release of other trace elements, such as N and P, which may also contribute to the formation of algal blooms (Zhao et al., 2017b). However, Zhao et al. (2017b) argued that coincident peaks in Mn/Ca$_{shell}$ and chlorophyll-α, an estimate for phytoplankton biomass, is not evidence of causality and further research is needed into the uptake of Mn by bivalves and the complex cycling of Mn within freshwater systems. Nevertheless, the investigation of Mn/Ca$_{shell}$ has important implications for long-term monitoring and investigations into past eutrophication events and associated changes in water quality (Zhao et al., 2017b).

5.2.2.4. Magnesium. Most studies reviewed here suggest that Mg/Ca is strongly effected by biological controls in freshwater systems (Izumida et al., 2011; Kelemen et al., 2019; Watanabe et al., 2021) and therefore is ineffective as a proxy for environmental parameters. Research on marine mussels have also found strong biological influences on Mg/Ca$_{shell}$ (Schöne et al., 2011, 2013), however several studies have also determined a relationship between Mg/Ca$_{shell}$ and temperature, although to varying degrees of success (Schöne et al., 2011; Takesue and van Geen, 2004; Tynan et al., 2017). Within freshwater mollusc sclerochronology, Chen et al. (2021) found a significant positive correlation between Mg/Ca$_{shell}$ and Mg/Ca$_{water}$ in freshwater molluscs, and Geeza et al. (2019) found a good correlation between two freshwater specimens, suggesting that there is some external mechanism of incorporation, or perhaps a

complex mix of factors, that we don't yet understand. Therefore, a closely monitored tank experiment may be valuable for better understanding the controls on this element.

5.2.2.5. Other minor and trace elements. Several other trace elements have been explored, all with varying effectiveness. Cu, Fe, and Zn are among the most promising, with multiple studies each showing their potential role as proxies for environmental factors such as changes in anthropogenic pollution (Carroll and Romanek, 2008; Markich et al., 2002; Risk et al., 2010; Wilson et al., 2018a, 2018b). While Tazaki and Morii (2008) determined in their experiment that the increased immobilisation of Fe and Si ions in the shell may be due to the mollusc's consumption of certain diatoms, more detailed, controlled studies of each element and the mechanisms involved in their biomineralisation and presence in the environment are needed before more concrete conclusions can be made about their effectiveness as environmental proxies. Furthermore, when analysing these less common elements, considerations need to be made about the analytical techniques being used, as many of the elements fall below the detection limits for common methods such as ICP-MS and/or require much larger amounts of $CaCO_3$, creating issues for high-resolution sclerochronology research (Phung et al., 2013; Wilson et al., 2018b). Additionally, multiple studies have investigated the use of freshwater bivalves as monitors of rare earth element pollution (Lyubas et al., 2021; Merschel and Bau, 2015). These studies involve the homogenisation of whole shells and analysis of several specimens together due to the analytical method's need for a larger sample mass, therefore they are not included in the larger review. Further developments in the analytical method are required before the intra-shell analysis of rare earth elements is possible. However, such methodological improvements would be hugely valuable in our monitoring of these bioavailable elements, of which we are only beginning to understand the potential toxicity despite their identification within drinking water (Bergsten-Torralba et al., 2020; Merschel and Bau, 2015).

Overall, the study of trace elements in freshwater molluscs has the potential to provide vital insight into biomineralisation processes and environmental reconstruction for mollusc sclerochronology in general. Although much valuable research has been completed so far, more research is needed to address specific questions such as the origin of different trace elements in the immediate habitat or wider watershed, the biomineralisation processes controlling each element, and the influence of microhabitats on shell geochemistry (Leppänen et al., 2021; Zhao et al., 2017a). Furthermore, researchers need to consider the type of water monitoring that should occur in a study, extending beyond water temperature to investigate less frequently studied parameters, such as dissolved oxygen and chlorophyll α (each investigated by just 5% of the reviewed literature), alongside trace element composition of the water. Tank experiments and research which focuses on just a singular element have shown to be particularly valuable in this area, so similar research is recommended.

6. Summary and recommendations for future research

Freshwater mollusc sclerochronology is a complex, yet highly important subdiscipline within mollusc sclerochronology. The field has the potential to provide essential insight into past and present environmental conditions of different regions around the world where freshwater systems serve as a valuable resource for human populations and have done so for hundreds to thousands of years. While marine mollusc sclerochronology is more frequently investigated and reviewed, the study of molluscs from freshwater environments has been shown to provide important insights into topics such as biomineralisation and drivers of skeletal growth which are of high importance to the discipline in general (Trofimova et al., 2020). This research also contributes to pertinent questions of conservation, paleoenvironmental

reconstruction, and human-environment relationships.

While freshwater mollusc sclerochronology has demonstrated its importance and usefulness in answering myriad of questions relating to method development, conservation and paleoenvironmental conditions, it faces some critical challenges. As has been shown in this review, the high variability of freshwater systems can be viewed as both a key challenge and an opportunity for sclerochronology research. Regardless, there is a need to monitor the physico-chemical and geochemical properties of freshwater systems with higher resolution due to this changeable nature. There needs to be a shift towards higher resolution monitoring in both space and time to account for the occurrence of microhabitats, as well as rapid temporal changes in water conditions. This can become a time and financial burden for those studies where extensive, long-term water monitoring systems have not already been put in place by local institutions. This is a key challenge that needs to be overcome, and as such more effort in freshwater mollusc sclerochronology research should be diverted into establishing reliable long-term monitoring programs or determining cost-effective ways to do this. While tank experiments may offer the ideal opportunity to constrain and monitor the parameters at play and better understand specific geochemical or physical proxies, the results of these studies need to also be tested under complex, real-world conditions.

While more high-resolution monitoring is needed, a wider variety of parameters also need to be tested during monitoring, particularly water trace element values and measures of stable carbon isotope ratios in water, especially when these parameters are being analysed and interpreted in the shell. Research would also be strengthened from more detailed understandings of the hydrological context of the study region and the source of different geochemical contributors to mollusc shell, particularly different trace elements. Again, these practices face logistical barriers, but their consistent inclusion would strengthen current understandings of the interaction between freshwater molluscs and the surrounding environment.

Regarding opportunities for further research, the possibilities are many and have been suggested throughout this paper. The key areas for future research are reiterated below:

- A global review of freshwater mollusc sclerochronology research from lakes, to compliment the review by Pfister et al. (2019) on river studies. Additional research also needs to be done on the effectiveness of different techniques, such as cross-dating, on lake species in comparison to river/stream species.
- As there is a clear regional bias in freshwater mollusc sclerochronology research, there is a need for further investigations into more low-cost methodologies and workflows with the aim to make this research more accessible. Also, where a dearth of malacological research presents additional barriers, interdisciplinary projects alongside malacologists and biologists should be conducted to better understand species habitat, life history, and conchology.
- Further focus should be given to the importance of diagenesis identification when working with fossil or archaeological material, and the use of more than one method to rule out the presence of diagenesis.
- Several modern calibration studies have noted their applicability to fossil or archaeological contexts, and therefore this research is waiting to be completed. In particular, seasonality of collection investigations using freshwater archaeomalacological material have great potential to answer a variety of questions relevant to archaeologists but require further dedicated studies to test their effectiveness.
- The hydrological variability of freshwater environments makes the use of paired proxies key, therefore further studies should test the effectiveness of paired proxies, such as carbonate clumped isotopes and hydrogen isotopes.
- Further research into the diversity of carbon isotope fractionation values across different habitats and the reasons for these variations.

The incorporation of the monitoring of stable carbon isotope ratios in more research should aid in this.

- Further investigations into the application of stable nitrogen isotope ratios and strontium isotope ratios in freshwater molluscs.
- Investigations into the controls on different trace elements in shells, particularly the chemical composition of extrapallial fluid and its influence on shell biomineralisation, and the origin of different trace elements in the immediate habitat or wider watershed.
- Increased exploration of the application of minimally invasive or non-invasive analytical techniques, such as SIMS or LIBS, to the analysis of freshwater taxa, particularly where the specimen's size would usually preclude traditional intra-sampling methods, or where sampling needs to be less destructive or more considered, such as with museum specimens.

While key challenges exist within freshwater mollusc sclerochronology, these challenges breed potential for future investigations and discovery. Despite these challenges, this review has demonstrated that freshwater mollusc sclerochronology research is equipped to provide answers to significant questions about the past, present, and future condition of our world and its inhabitants.

CRediT authorship contribution statement

Chloe A. Stringer: Conceptualization, Methodology, Investigation, Data curation, Writing – original draft, Visualization. **Amy L. Prendergast:** Conceptualization, Writing – review & editing, Supervision.

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.

Data availability

All data used in this study is available online at https://doi.org/10.26188/c.6624257

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