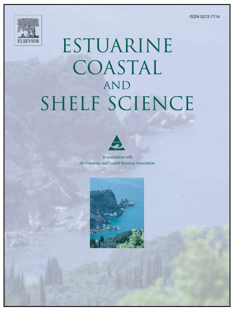

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Fundamental Questions and Applications of Sclerochronology: Community-Defined Research Priorities

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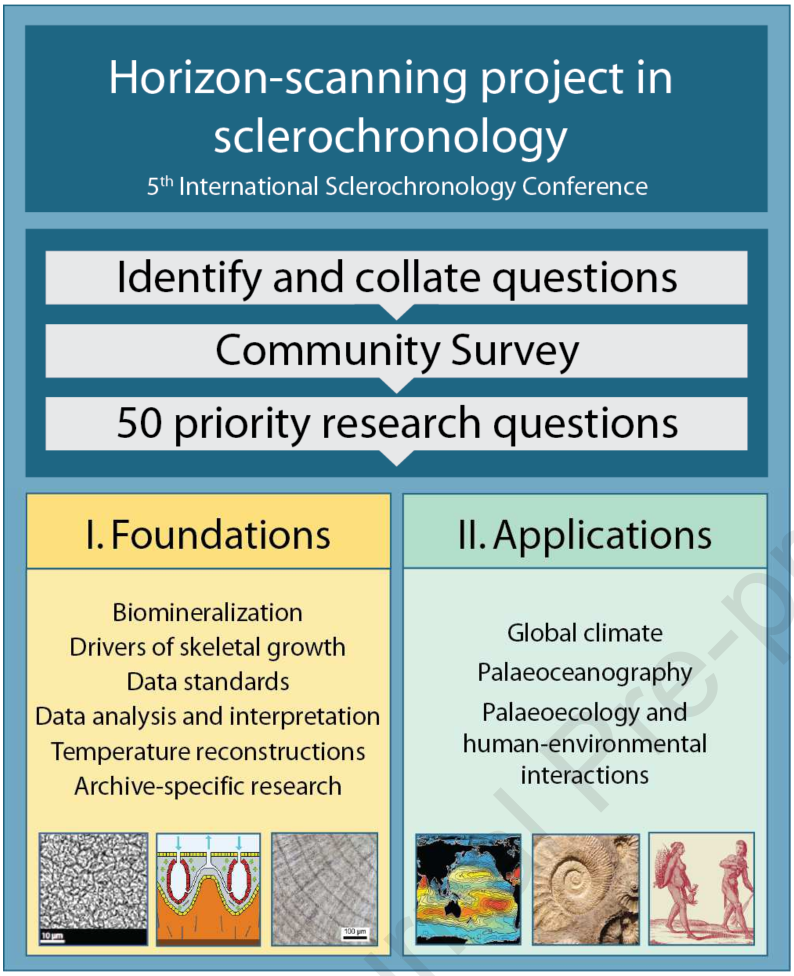
Graphical Abstract



Abstract

Horizon scanning is an increasingly common strategy to identify key research needs and frame future agendas in science. Here, we present the results of the first such exercise for the field of sclerochronology, thereby providing an overview of persistent and emergent research questions that should be addressed by future studies. Through online correspondence following the 5th International Sclerochronology Conference in 2019, participants submitted and rated questions that addressed either knowledge gaps or promising applications of sclerochronology. An initial list of 130 questions was compiled based on contributions of conference attendees and reviewed by expert panels formed during the conference. Herein, we present and discuss the 50 questions rated to be of the highest priority, determined through an online survey distributed to sclerochronology community members post the conference. The final list: (1) includes important questions related to mechanisms of biological control over biomineralization; (2) highlights state of the art applications of sclerochronological methods and data for solving long-standing questions in other fields such as climate science and ecology: and (3) emphasizes the need for common standards for data management and analysis. Although research priorities are continually reassessed, our list provides a roadmap that can be used to motivate research efforts and advance sclerochronology toward new, and more powerful, applications.

1. Introduction

Sclerochronology is a rapidly developing field of research. While growth bands in hard tissues of some organisms have long been observed and studied (e.g., Pulteney, 1781; Maton, 1805; Isely, 1914; Ma, 1934; Davenport, 1938; Adams, 1940; Kohler, 1964; Clark, 1974; Jones, 1981, 1983), the term "sclerochronology" was first introduced to the published literature in the 1970s. Analogous to the long-established field of dendrochronology (e.g., Fritts et al., 1971), sclerochronology was originally defined as "the study of growth patterns in calcareous exoskeletons and shells" (Buddemeier et al., 1974) and was first applied to coral research (Buddemeier et al., 1974; Hudson et al., 1976). The term has since been broadened to include various terrestrial and aquatic taxa with growth patterns, whereby the most common examples are fish (e.g., Coulson et al., 2014; Martino et al., 2019), coralline algae (e.g., Halfar et al., 2011; Williams et al., 2017), gastropods (e.g., Surge et al., 2013; Prendergast and Schöne, 2017) and bivalves (e.g., Jones et al., 1989). The list of sclerochronological archives is continuously expanding as more species are being assessed for their utility in sclerochronological studies. The term was redefined during the First International Sclerochronology Conference held at St. Petersburg, FL, USA in 2007 as "…the study of physical and chemical variations in the accretionary hard tissues of organisms, and the temporal context in which they formed…" (Oschmann, 2009).

Today, sclerochronology is an increasingly diverse and interdisciplinary field. Apart from utilizing a wide array of archives, sclerochronology employs a suite of morphological, geochemical, microstructural and crystallographic techniques. The data provided by sclerochronological studies have shown clear application across a range of fields, including ecology (e.g., Rhoads and Pannella, 1970; Rhoads and Lutz, 1980: Black et al., 2018), geophysics (e.g., Wells, 1963; Rosenberg & Runcorn 1975; Zachariasen et al., 2000), archaeology (e.g., Coutts 1970; Andrus, 2011; Wang et al., 2013), climate reconstruction (e.g., Jones et al., 1989; Butler et al., 2010; Tierney et al., 2015), and environmental (e.g., Steinhardt et al., 2016) and fisheries (e.g., Campana et al., 2001) sciences. Crossdated sclerochronological records, in particular, can provide powerful archives of past spatiotemporal environmental variability on local to hemispheric scales (Black et al., 2019). Advances in sclerochronological methods continually open up new applications, indicating that the full potential of sclerochronology has yet to be realized.

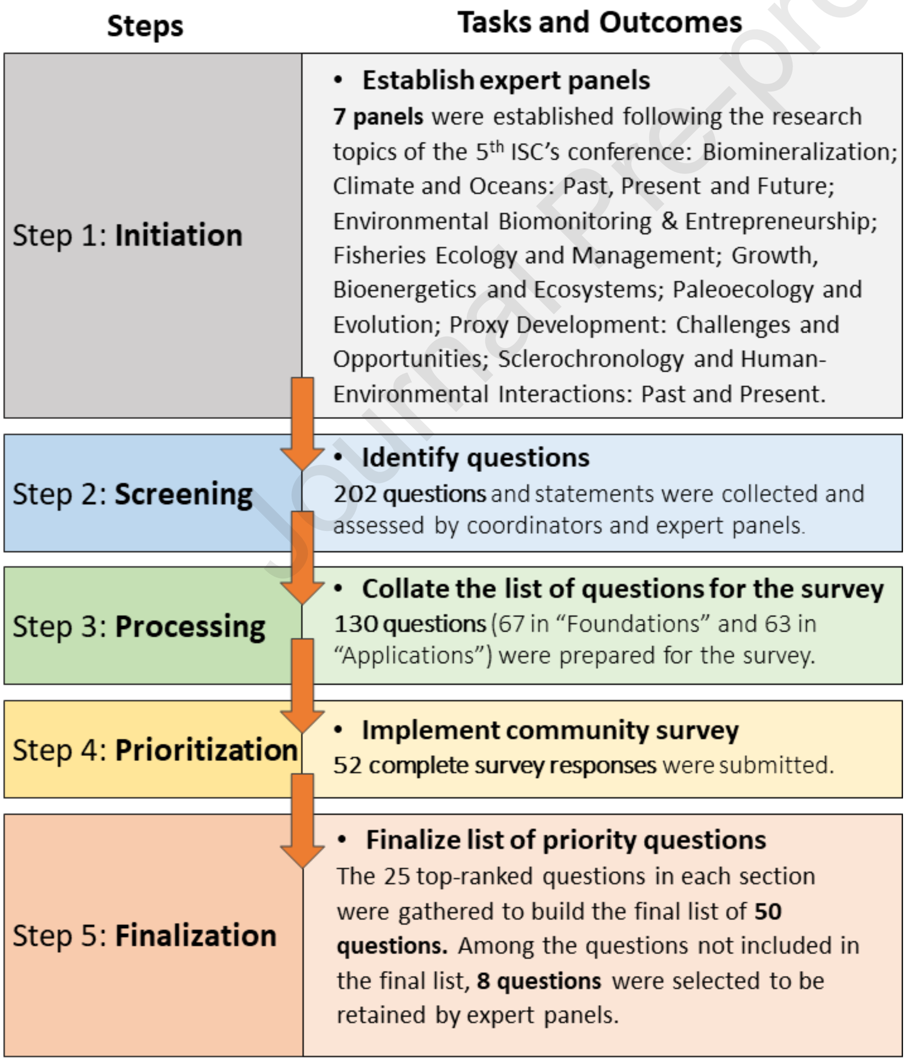
The triennial International Sclerochronology Conference (ISC) and other regular meetings with a sclerochronology component have played an important role in the development of the field. Journal special issues associated with such meetings have provided regular overviews of the most recent results and demonstrations of the potential of sclerochronology (Schöne and Surge, 2005; Gröcke and Gillikin, 2008; Oschmann, 2009; Wanamaker et al., 2011; Schöne and Gillikin, 2013; Butler and Schöne, 2017; Prendergast et al., 2017; Gillikin et al., 2019). Although significant effort has been made to review and synthesize recent findings, the sclerochronology community faces a variety of challenges and opportunities to be addressed in future work.

Now, 46 years after the term "sclerochronology" first appeared in the literature, and more than a decade after the first ISC, we have reached a timely moment to evaluate existing challenges and the most promising research directions. Inspired by previous examples from other research fields (e.g., Sutherland et al., 2011; Seddon et al., 2013; Patiño et al., 2017), the coordinating authors (Trofimova, Alexandroff, Mette, and Tray) initiated this community effort at the 5th ISC held in Split, Croatia in June 2019. The aim of our project is to advance the field and support its progress by identifying key research needs and providing an overview of persistent and emergent research questions. Due to the connection to the 5th ISC, the main focus of this article is on the sclerochronology of invertebrates and fish.

2. Methodology

Our project employed a horizon-scanning approach to identify community-defined priority research directions (for details see Supplementary Material 1; Fig. 1), adapted from similar studies performed in other research fields (e.g., Sutherland et al., 2011; Seddon et al., 2013; Patiño et al., 2017). At the initial stage, the coordinators (first four authors in the author list), in collaboration with expert panels and with the input from the wider research community, collected and curated a list of questions addressing fundamental knowledge gaps (Section Foundations) and promising applications of sclerochronological methods (Section Applications). In total, 202 questions and statements were submitted. Based on these contributions, we formulated an initial list of 130 questions (see Supplementary Material 2) that met previously outlined criteria (see Supplementary Material 3; adapted from Sutherland et al., 2011). An anonymous survey was launched and distributed to the sclerochronology and paleoclimatology communities through email list-servers and social media. Participants were asked to rate each question on a 5-point Likert scale (Zero/Low/Neutral/High/Top Priority) in response to ‘Considering how fundamental the question is for sclerochronology, what should its priority be for future research?’.

In total, 52 complete survey responses were submitted. The top 25 questions from each of the two categories (Foundations and Applications) were selected by calculating the percentage of total respondents rating the question as a priority (‘High priority’ or ‘Top priority’, without differentiation). The expert panels reviewed the questions that did not make the final list to retain those that addressed underexplored research directions with potential to widen the horizon of sclerochronology (presented in section 3.3).



- **Establish expert panels**

7 panels were established following the research topics of the 5th ISC’s conference: Biomineralization; Climate and Oceans: Past, Present and Future; Environmental Biomonitoring & Entrepreneurship; Fisheries Ecology and Management; Growth, Bioenergetics and Ecosystems; Paleoecology and Evolution; Proxy Development: Challenges and Opportunities; Sclerochronology and Human-Environmental Interactions: Past and Present.

- **Identify questions**

202 questions and statements were collected and assessed by coordinators and expert panels.

- **Collate the list of questions for the survey**

130 questions (67 in “Foundations” and 63 in “Applications”) were prepared for the survey.

- **Implement community survey**

52 complete survey responses were submitted.

- **Finalize list of priority questions**

The 25 top-ranked questions in each section were gathered to build the final list of **50 questions.** Among the questions not included in the final list, **8 questions** were selected to be retained by expert panels.

Figure 1. Conceptual scheme illustrating the methods employed to identify fundamental questions and priority applications in sclerochronology.

2.1 Limitations of this study

As a horizon scanning project, the present study relies heavily on the expertise, interests, and skills of the participants. Continual efforts to exchange input and feedback from a diverse array of sclerochronological expertise were made throughout the development of the project in an attempt to maintain a wide perspective on the field and reduce bias. Even so, the fundamental questions identified by this exercise cannot be wholly separated from the research interests of the participants. While the final list of questions presents a community-informed perspective on priorities within sclerochronology, the rankings were determined by a relatively low number of participants (n=52) with potentially strong geographical, archive-based, and research-based bias (see Supplemental Material 4). Additional bias was introduced during the preparation stage, as questions were collected via input from participants in the 5th ISC. While the ISC invites participation of sclerochronologists from all fields and regions, some archives are more highly represented than others. This is particularly the case for fish otoliths and mollusk shells, as the research utilizing these archives dominated the scientific presentations at the conference. This bias was also evident in the survey, where otoliths and mollusks were the primary or secondary expertise of all participants. Similarly, the most common applications of sclerochronology presented at the ISC were related to scientific inquiries in (paleo-)ecology and climate science. In addition, the location of the conference and associated travel, as well as other expenses, are contributing factors to regional bias. Thus, the final list by no means reflects the true boundaries of the extended field covered by the term “sclerochronology”. The 130 identified questions (see Results and Supplementary Material 2) represent a wide-ranging, but far from exhaustive, overview of possible future research directions and priorities. As this project was initiated to stimulate discussion among researchers, encourage collaboration, and spur new ideas for scientific advances, the results presented here, despite the inevitable biases, reflect a unique community-based insight.

3. Results

Below, we present 50 priority questions identified by this study. The questions are divided into two categories that identify (1) fundamental knowledge gaps (Foundations of Sclerochronology, 25 questions) and (2) promising applications (Sclerochronology application, 25 questions). In this section, we also discuss the general motivation and background behind the questions. Due to the high diversity of archives and proxies, techniques, and research topics within sclerochronology, we aimed to provide a general overview, fully acknowledging that there will be exceptions to the rule. The literature cited in our paper deliberately represents a mixture of seminal papers, highlights in the field, and unique applications spanning a range of research groups and archives. These references are meant to point the reader to useful or interesting examples, and by no means represent a comprehensive review of the state-of-the-art on a particular question. We have grouped the 50 questions into topics to avoid repetition in the discussion and provide an outline of the general themes evident in the collection. In addition, eight questions not included in the list of the leading 50 questions, but highlighted by the expert panels as cutting-edge ideas, are presented in the final section of the results.

3.1 Foundations of Sclerochronology

This section presents the highest ranked questions addressing knowledge gaps in our understanding of sclerochronological archives. It covers a range of topics, including but not limited to physiology, biomineralization, interpretation of sclerochronological data, development of standards, and establishment and calibration of new proxies.

3.1.1 Biomineralization

1. How, and to what extent, do vital effects influence biomineral stable isotope composition, elemental distribution, and elemental concentration?
2. What controls the incorporation of trace and minor elements into biogenic carbonates and how do these processes affect distribution of different trace elements between crystal lattice and organic phases?
3. Are there differences in biomineralization processes across ontogeny and between species and/or populations that affect skeletal isotopic composition and elemental concentrations?
4. How might climate and environmental change (e.g., ocean acidification) be altering processes of biomineralization?

A sound understanding of biological mineralization is fundamental to sclerochronology and the establishment of geochemical proxies in various contexts. Yet, the exact mechanisms driving biomineralization are not fully characterized, which is reflected in the questions in this topic [Q1-4]. The hallmark of biomineralization, as opposed to its abiogenic counterpart, is the remarkable control that organisms can exert over mineral formation (Weiner and Dove, 2003). These so-called “vital effects” (Urey et al., 1951), including kinetic and taxonomic effects (Weiner and Dove, 2003), can obscure the environmental signal in geochemical proxies, and thus confound proxy interpretation. An understanding of the role of vital effects in biomineralization is a major challenge for sclerochronology, as highlighted by Questions 1-3.

Whereas the relationships of some geochemical properties and environmental variables are well established for sclerochronological archives (e.g., stable oxygen isotope value of biogenic carbonate ($\delta^{18}O_c$); see Topic “Temperature reconstructions”), other properties are often difficult to interpret due to taxon-specific physiological effects. For example, previous studies have demonstrated that Mg-to-Ca ratios in coralline algae (e.g., Nürnberg et al., 1996; Kamenos et al., 2008), and Sr-to-Ca ratios in tropical shallow-water corals and sclerosponges (e.g., Beck et al., 1992; Rosenheim et al., 2004) are robust temperature recorders, but are currently still difficult to interpret in otoliths (e.g., Campana, 1999) and bivalves, specifically those with aragonitic shells (e.g., Zhao et al., 2017a; Gillikin et al., 2019). Stable carbon isotope values ($\delta^{13}C$) of coralline algae (Williams et al., 2011), corals (Swart et al., 2010; Dassié et al., 2013), and sclerosponges (Druffel and Benavides, 1986; Böhm et al., 1996) have been successfully used for environmental reconstructions, e.g., as a proxy for the $\delta^{13}C$ value of dissolved inorganic carbon in ambient water. However, vital effects on the $\delta^{13}C$ signature are suspected among corals, fish otoliths, and some mollusks (Kalish, 1991; Iacumin et al., 1992; McConnaughey et al., 1997; Lorrain et al., 2004; McConnaughey and Gillikin, 2008). Further characterization of the mechanisms controlling the isotope and element chemical variability in biominerals will improve the usability of proxies across various taxonomic groups and therefore is crucial for future sclerochronological studies [Q1].

While biomineralization processes differ among taxonomic groups, they can also vary through an individual’s lifetime, even within skeletal structural layers, and between individuals. Apart from environmental factors, the chemical composition, as well as microstructure, of biominerals is affected by genetics (Carter, 1980; Clarke et al., 2010; Norrie et al., 2019) and can vary throughout ontogeny (Marshall and McCulloch, 2002; Elliot et al., 2003; Gillikin et al., 2007; Nishida et al., 2011; Grammer et al., 2017; Reynolds et al., 2019). The role of these factors in biomineralization is not well understood in the broad context of archives and proxies, representing a significant knowledge gap for sclerochronology [Q3]. In the case of element proxies, additional complexity may result from the presence of non-lattice bound trace elements (e.g., Takesue et al., 2008). Mechanisms of elemental incorporation into biogenic carbonates, therefore, require a special focus in future research to improve application of trace element records in sclerochronology [Q2].

Development of biophysical models coupling metabolism, biomineral growth, and elemental and isotopic dynamics could provide much needed mechanistic insights into vital effects in terms of their effects on environmental proxies, and the use of elemental and isotopic compositions of biominerals as physiological tracers. This will require experimental and theoretical modelling work, but frameworks such as Dynamic Energy Budget theory provide a platform suitable for model development (e.g., Fablet et al., 2011; Spalding et al., 2017) [Q1-3].

Modern climate change and associated ocean acidification can pose major threats to marine calcifying organisms due to their potential effects on biomineralization. Changes in biomineralization can have consequences for the survival of species, as well as the applicability of proxies, and therefore require further research [Q4]. In the context of sclerochronological research, it is particularly important to understand natural variations in biomineralization across different physical and biotic stressors (e.g., Telesca et al., 2019; De Noia et al., 2020), and physiological responses and adaptations leading to changes in biomineralization rate, mineralogy and geochemistry of skeletal structures. Although the effects of ocean acidification on biomineralization are increasingly studied (e.g., Checkley et al., 2009; Ivanina et al., 2013; Fitzer et al., 2014; Milano et al., 2016; Cornwall et al., 2018; Cross et al., 2019), the results suggest variable responses among taxa (e.g., Zhao et al., 2018, 2020), likely depending on the degree of biological control over biomineralization and variable compensatory mechanisms and their energetic costs (Kleypas et al., 2005; Spalding et al., 2017; Melzner et al., 2020, and references therein). More research is needed to fully understand potential outcomes and identify possible patterns. Furthermore, growing concerns about the overall effects of acidification on marine ecosystems call for reliable proxies for past ocean acidification events. Boron isotopes ($\delta^{11}B$) and U/Ca have recently shown potential as proxies for pH levels (Hönisch et al., 2012; Raddatz et al., 2014; Foster and Rae, 2016; Jurikova et al., 2019). However, more research is needed to evaluate the broad applicability of these proxies across sclerochronological archives, which is intimately linked to the understanding of biomineralization processes under changing environments.

3.1.2 Drivers of skeletal growth

5. What are the specific processes by which climate signals are translated into growth of calcified structures?
6. What determines the timing of the growth season and does it vary throughout ontogeny?
7. Are the growth/chemical responses to specific environmental drivers consistent/stationary over geologic time?
8. How can we predict the sclerochronological patterns (growth and/or chemical records) expected under differing combinations of movement, physiology, and environmental change?

Measurement of growth patterns and structures within skeletal archives is a standard procedure for sclerochronological work. Whereas the growth record serves as an age model to anchor geochemical or other proxies, individual or population-averaged growth variability is itself often a valuable environmental or ecological proxy (e.g., Halfar et al., 2011). For population-averaged records, the process of crossdating to produce absolutely dated growth increment width chronologies hinges on the assumption that common environmental drivers impart a shared growth response within a population (Black et al., 2019). However, questions remain regarding the mechanistic pathways leading to growth responses from environmental and biological drivers [Q5]. Combinations of food availability and quality, temperature, and light intensity are commonly identified as primary environmental drivers of year-to-year increment width variability that differ among sclerochronological archives (for a brief overview, see Schöne and Surge, 2005).

Structural properties of biominerals provide other promising proxies reflecting interactions between biology and environment (e.g., Füllenbach et al., 2014; Milano et al., 2017; Höche et al., 2020). The process by which environmental signals are translated into microstructure variability also informs mechanisms of biomineralization, and is increasingly being studied (e.g., Nishida et al., 2015; Checa, 2018). More detailed insight into the archive-specific drivers behind increment width and microstructural variability will enable robust linkages between growth proxy records and environmental variability. It will also contribute to a better understanding of the synchrony or lack of synchrony among individuals in a population (Marali and Schöne, 2015; Muslic et al., 2013; Rountrey et al., 2014). Finally, the question whether drivers of growth are constant and stationary over geologic time should be considered [Q7]. Proxy records collected from sub-fossil material for which a precise calendar date cannot be attached ("floating" records) offer windows into past time intervals (e.g., Kilbourne et al., 2004; Scourse et al., 2006). However, the discussion of potentially variable growth drivers in past time intervals or across the lifetime of an individual, and the resulting impact on proxy reconstructions, has received little attention.

A common approach to the determination of the timing of the growing season for sclerochronological archives is analysis of seasonal oxygen isotope ($\delta^{18}O_c$) profiles within annual increments (Weidman et al., 1994; Schöne and Surge, 2005; Mannino et al., 2008; Judd et al., 2018) or trace elemental ratios (e.g., corals, DeLong et al., 2011; coralline algae; Williams et al., 2014). Because many sclerochronological archives exhibit decreasing growth rate as they age (e.g., bivalve shells, fish otoliths), accurate determination of the full range of the growing season is best accomplished by sampling the wider, juvenile increments (Goodwin et al., 2003). Extrapolating these findings throughout the life of the animal, however, is problematic if there are ontogenetic effects on the duration and or timing of the growing season. Such effects are not consistent among species (Goodwin et al., 2003; Schöne et al., 2005), warranting further investigation [Q6].

The translation of climate and environmental signals into growth and geochemical signatures is further complicated in the case of mobile organisms. The environment experienced by an animal may vary across large-scale migrations as well as differing habitat utilization across its life history (e.g., Gillanders et al., 2015; Roberts et al., 2019). Disentangling interpretations of environmental change from interpretations of animal movement is a difficult task. Modeling provides a powerful tool to predict the effects of differing combinations of life history patterns, environmental change, and potentially adaptive drivers of growth, as discussed above [Q8]. Whereas research in this area has advanced in recent years (e.g., van der Sleen et al., 2018; Hobbs et al., 2019; Trueman et al., 2019), it is still recognized as a priority research question in the field.

3.1.3 Data standards

9. What common data standards should be adopted to improve our ability to compare sclerochronological datasets with each other and with other datasets?
10. What level of sample replication is required for geochemical records for sound estimation of uncertainty associated with inter-individual variability and ensuring comparability between records?

Variability in sclerochronological methods and reporting standards can affect the quality and comparability of datasets, representing a major challenge for the field [Q9, Q10]. Whereas the tree-ring community has agreed-upon methods and reporting standards for data sharing (e.g., International Tree-Ring Data Bank (ITRDB)), similar agreements are missing in the sclerochronological community. The issues with data reporting and sharing became apparent during the various PAGES2k projects that brought together publicly shared paleo data from a variety of archives to build global databases (e.g., PAGES2k Consortium, 2013; Tierney et al., 2015; Emile-Geay, et al., 2017; Konecky et al., 2020). Recently, global efforts have been made to improve scientific data interoperability and reusability (Wilkinson et al., 2016; McKay and Emile-Geay, 2016). Initiatives to provide growth, geochemical, microstructural, or other proxy data in common formats have also begun within the sclerochronology community (Dassié et al., 2017; Khider et al., 2019; Tray et al., 2020). Collaboration among sclerochronology researchers to standardize data collection methods and data reporting, as well as standards for archiving physical samples, are needed to address these issues. Some studies comparing multiple, inter-species sclerochronology datasets with varying temporal resolutions provide examples of progress in this area (Matta et al., 2010; Ong et al., 2016; Peharda et al., 2018), however, further extensions of such work is a priority for future research.

At present, various statistical methods are used to account for inter-individual variability within sclerochronological datasets, one of the most commonly used being mixed-effects models (Weisberg et al., 2010; Morrongiello and Thresher, 2015). Additionally, power analyses can be used to estimate appropriate sample sizes (Toft and Shea, 1983). Whereas these are acceptable methods for studies that address individual-level variation, there is less certainty about their applicability to geochemical data [Q10] (e.g., stable isotope and trace element records; but see Grammer et al 2017 and Macdonald et al 2019). Correlation coefficients paired with significance levels (i.e., *p*-values) are typically used to determine robustness of environmental reconstructions (e.g., Montagna et al., 2014 for seawater temperature). Still, there are arguments against using these metrics, due to the short length of marine instrumental records available for calibration (Crowley et al., 1999, Corrège 2006; Finney et al., 2010) and problems with statistical inference (Wasserstein et al., 2019). In addition to correlation, coral replication studies have used expressed population signal (EPS), absolute differences, and root mean squared statistical tests to assess replication and reproducibility at the intra- and inter-coral colony levels and between species at the same location (DeLong et al., 2007; 2011; Wu et al., 2014; Dassié et al., 2014). Chronological uncertainty, especially in non-crossdated reconstructions, needs to be better understood and assessed in the various sclerochronological archives (e.g., Comboul et al., 2014). There is, therefore, a need to define and clarify the types of data and analyses that constitute a sclerochronological reconstruction, and to further develop and standardize statistical techniques to quantify and account for uncertainty.

3.1.4 Data analysis and interpretation

11. What methods can we use to better assess the leads, lags, and synchronicities in sclerochronological records across large spatial regions?
12. How can we disentangle the separate and combined effects of multiple causal factors in sclerochronological records?
13. How can common environmental signals be identified in multiple records which have different spatial and temporal scales and resolutions?
14. How can we disentangle multiscale spatial and temporal variability within sclerochronological records?
15. To what extent do variations in multiannual to multicentennial growth patterns represent a community/ecosystem response to changing environmental conditions?

Interpretation of environmental signals in sclerochronological records is not a trivial task, and this is reflected in the questions in this topic [Q11-15]. Linked with the issue of standardizing data sharing (see Topic 3.1.3), these questions highlight methods and strategies for sclerochronological data analysis that require further development and standards for sharing data that have been agreed upon by the community.

Sclerochronological archives provide high-resolution (e.g., daily, annual) environmental proxy data, which, provided that live-collected samples are used, are absolutely dated. This makes them uniquely suited for studies of spatiotemporal heterogeneity in the response of different components of the Earth system to forcing factors (e.g., Evans, 1972; Ohno 1989; Black et al., 2014; Reynolds et al., 2016; Black et al., 2019). Therefore, the development of methods and strategies for the determination of leads and lags across different spatial scales is an important avenue for future research [Q11]. Methods used by tree-ring (e.g., Cook et al., 2004) and PAGES2k communities (e.g., Tierney et al., 2015; Atsawawaranunt et al., 2018; Konecky et al., 2020) in their compilation studies could be assessed and applied to sclerochronological reconstructions.

An understanding of the extent to which individual or population-averaged growth records represent a community or ecosystem response to a changing environment is crucial for interpretation of climate signals [Q12]. Sclerochronological records (e.g., growth records and geochemical data) often encapsulate a response to a suite of environmental factors which, importantly, can act on different biological and temporal scales (e.g., Morrongiello et al., 2019). Disentangling these influences is of major importance for interpreting environmental signals [Q13] at different resolutions and scales [Q14] within one record, and for identifying common signals across multiple records [Q15]. To deconvolve this complexity, past studies have employed multiple linear regression (e.g., Mette et al., 2016), principal component analysis (e.g., Black et al., 2014), univariate and multivariate mixed-effects models (e.g., Morrongiello et al., 2015; Macdonald et al., 2019), dynamic energy budget models (e.g., Pecquerie et al., 2012), and Bayesian hierarchical modelling (e.g., Helser et al., 2012). Further assessment of these tools and the adoption of new statistical techniques for time series analysis of sclerochronological records will undoubtedly improve the interpretation and impact of sclerochronological studies.

3.1.5 Temperature reconstructions

16. How can we improve estimates of past water isotopic composition to increase accuracy of temperature reconstructions?
17. Why do we often observe an offset between seawater temperature reconstructed from oxygen isotope values (using widely applied paleotemperature equations) and those measured *in situ*?
18. How can we determine if species-specific paleotemperature equations are a valid and necessary approach to increase the accuracy of paleotemperature reconstructions?
19. What are the limitations of using clumped-isotope paleothermometry to constrain isotopic paleotemperature estimates from fossil organisms?

Oxygen isotope values of biocarbonates (δ^{18}Oc) have long been used to reconstruct temperatures (Urey et al., 1947; Epstein et al., 1953). Sclerochronological archives allow the construction of highly resolved δ^{18}O records, which have important applications in many research fields, such as climatology, physiology, anthropology, paleoceanography, and ecology, among others. The applicability of $\delta^{18}O_c$ as a temperature proxy has been established for all sclerochronological archives, including scleractinian corals (e.g., Weber and Woodhead, 1972), fish otoliths (e.g., Devereux, 1967), mollusks (e.g., Weidman et al., 1994), and coralline algae (e.g., Halfar et al., 2008), among others. The premise for using $\delta^{18}O_c$ to study temperature is that the fractionation of oxygen isotopes during biomineralization is temperature-dependent and in (near) equilibrium with the ambient water (Grossman and Ku, 1986; Kelemen et al., 2017; Thorrold et al., 1997; Weidman et al., 1994; but see Smith et al., 2000). The accuracy and reliability of this method depend on knowledge of (1) the δ^{18}O value of the ambient water ($\delta^{18}O_w$) and other site-specific physical and chemical properties [Q16-18], and (2) the specific biomineralization processes within the chosen archive [Q17, 18].

Question 16 raises a well-known and pertinent issue in δ^{18}O paleothermometry and its application in sclerochronological studies (Prendergast and Stevens, 2014; Yan et al., 2014). Given that $\delta^{18}O_c$ is a function of

$\delta^{18}O_w$ and temperature-driven fractionation, independent estimates or measurements of $\delta^{18}O_w$ are crucial. In studies of modern samples, $\delta^{18}O_w$ is often estimated using a region-specific relationship between salinity and $\delta^{18}O$ (i.e., mixing lines) (LeGrande and Schmidt, 2006). However, the accuracy of mixing lines in local studies needs to be scrutinized, especially at locations where freshwater input causes high $\delta^{18}O_w$ variability (e.g., Wagner et al., 2011). One approach to overcome the issue of unknown $\delta^{18}O_w$ is to use paired proxies to constrain temperature with the element-to-element ratio and solve for $\delta^{18}O_w$. Examples for such paired proxies in aragonitic sclerochronological archives are Sr/Ca and $\delta^{18}O$ in corals and sclerosponges (e.g., McCulloch et al., 1994, Gagan et al., 1998; Ren et al., 2002; Rosenheim et al., 2004), $\delta^{13}C$ and $\delta^{18}O$ in bivalve shells (e.g., Reynolds et al., 2019), and $\delta^{18}O_w$ in otoliths paired with $\delta^{18}O$ in bivalve shells (Wang et al., 2011), among others. Carroll et al. (2006) suggested another approach, using hydrogen isotope values (δD) within the organic matrix of freshwater bivalves to independently estimate $\delta^{18}O_w$. Carbonate clumped isotope values (Δ_{47}; Δ_{48}) provide an avenue to circumvent this question altogether, as this method does not require an estimate for $\delta^{18}O_w$ (Eiler, 2007; Fiebig et al., 2019). This is especially useful in studies where $\delta^{18}O_w$ uncertainty is high, for example in estuarine environments or deep-time marine settings (e.g., Martin and Letolle, 1979; de Winter et al., 2018), or where kinetic effects are present. However, as Question 19 shows, limitations of the Δ_{47} value as a paleothermometer have yet to be fully assessed. One drawback is the requirement for relatively large sample sizes; conventional carbonate clumped isotope techniques require 3-7 mg of carbonate sample, while recent techniques have been able to lower the number to 14-20 replicates of 100 µg (Meckler et al., 2014; Müller et al., 2017). This size requirement limits high-resolution temperature reconstruction, and most archives will have specific limitations due to the overall size of the calcified structure. Additionally, yet-to-be assessed taxon-specific vital effects may be a limiting factor (Eiler, 2011). Other limitations of clumped isotope paleothermometry are its time-consuming and demanding analytical methods and its sensitivity to diagenetic overprint (Leutert et al., 2019).

Offsets between the $\delta^{18}O$-derived temperatures and measured *in-situ* temperatures have been reported for different archives and locations (e.g., Weber 1970; McConnaughey 1989; Bonitz et al., 2017; Dunbar and Wefer, 1984; Kelemen et al., 2017). In response to this issue, species-specific or site-specific calibrations are often formulated [Q17, 18]. However, performing new and specific calibrations might lead to false conclusions, e.g., a steeper slope between $\delta^{18}O$ and temperature can mask the real temperature amplitude (Waite and Swart, 2015). It is therefore crucial to understand what causes the observed offsets and eliminate inaccurate $\delta^{18}O_w$ assumptions [Q16] or sampling methods as potential sources of error. Suspected sources of unexpected offsets or observed variability in $\delta^{18}O_c$ include (1) isotopic alteration caused by mechanical sampling or analytical methods (Tobin et al., 2011; Waite and Swart, 2015; but see Foster et al., 2009), (2) signal aliasing as a result of limited sampling resolution (Goodwin et al., 2003; DeLong et al., 2007; Gagan et al., 2012), (3) sampling imprecision considering layers of different architectural structures, which can influence $\delta^{18}O_c$ (Leder et al., 1996; DeLong et al., 2016; Mette et al., 2018; Trofimova et al., 2018), and (4) cleaning methods altering primary mineralogy and $\delta^{18}O$ signal (Boiseau et al., 1997; Wierzbowski, 2007; Holcomb et al., 2015, Grottoli et al., 2005), and vital effects (McConnaughey, 1989). One way to more accurately quantify $\delta^{18}O$-temperature relationships is through experiments in controlled or closely monitored settings (e.g., Wanamaker et al., 2007; Ford et al., 2010; Nishida et al., 2014, 2015; Sakamoto et al., 2017). It is crucial to improve our understanding of oxygen isotope dynamics in organisms and the biominerals they synthesize in the effort to explain offsets between reconstructed and *in-situ* temperatures, while sampling methods and local context also have to be taken into account.

3.1.6 Archive-specific research

20. What not-yet-identified long-term sclerochronological archives exist, especially outside of the North Atlantic region?

21. What environmental parameters can be reconstructed from trace element concentrations and ratios within mollusk shells, and why are some trace element proxies unreliable?

22. Through which pathways are trace and minor elements transported into mollusk’s extrapallial fluid, and from where are they sourced (e.g., digested food, directly from water)?
23. Why is it that sometimes within the same population of bivalves, not all of the individual growth patterns from live-collected specimens crossmatch and how should we deal with such inter-individual variability?
24. What drives the formation of annual growth increments in fish otoliths?
25. How does inter-individual variation in growth patterns in fish affect long-term growth time series?

Newly identified archives or proxies are often sought to address geographic, environmental, and/or temporal gaps in earth system research (e.g., Peharda et al., 2016; Milano et al., 2017). Established, long-lived (>100 years), sclerochronological archives have limited geographic ranges, resulting in a high density of research focused in certain regions. This is particularly true in the North Atlantic Ocean, where studies using mollusk shell archives, especially *Arctica islandica*, dominate the literature (Steinhardt et al., 2016). The western tropical Atlantic and Pacific are hotspots for research using reef-building coral archives, representing another geographic bias in the availability of long-term proxy archives (Corrège, 2006). Some long-lived species are becoming well-established sclerochronological archives applicable in other regions (e.g., Tridacna sp., Jones et al., 1986; Elliot et al., 2009; Killam et al., 2020; geoducks, Strom et al., 2004; Black et al., 2009; coralline algae, Williams et al., 2017; deep sea corals, Robinson et al., 2014). However, to better address past climate and environmental research questions outside of the tropics and the North Atlantic, in particular, the search for long-lived archives from other regions is a priority [Q20].

Mollusk shells and fish otoliths are among the most frequently used sclerochronological archives. Several mollusk- and fish-specific issues were highlighted in the community survey. In particular, trace element concentrations, a reliable geochemical proxy among many archives, have been shown to be problematic or inconsistent within and across most mollusk species (see Topic “Biomineralization”). Little is known about the uptake of elements from the ambient water to the site of biomineralization, the transport mechanisms and pathways of elements within the body, nor the specific incorporation mechanisms of elements in the skeletal hard parts (Suzuki et al., 2009; Zhao et al., 2017b). Solving these questions will likely require heavy involvement from cell biologists and geneticists to improve our understanding of elemental proxies among molluscan species [Q21-22].

Synchronous growth is remarkably prevalent among mollusks (Jones et al., 1989; Weidman et al., 1994; Black et al., 2019), meaning it is unusual to encounter an individual that does not match the population growth pattern. When such individuals are identified, it is important to assess the quality of the material and clarity of the increment boundaries, and the geographic extent over which the samples were collected, as well as the experience of the worker with the particular population, to establish whether the shell truly exhibits a unique growth pattern. However, the reasons why some shells have unclear or irregular growth and do not easily crossmatch with the local population growth pattern are poorly understood [Q23] and could be biologically based. The extent to which difficult-to-crossdate individuals within a population is a problem has not been addressed within the literature, revealing an opportunity to improve understanding of molluscan growth records, and other crossdatable archives, as environmental proxies. While some research utilizes the varying strength of the common signal as an environmental record in itself (Marali and Schöne, 2015), more work is needed to assess the scope and implications of individual growth variability.

Fish otolith growth increments form with an annual periodicity in almost all fish species, even if the species lives in a relatively constant environment, such as the deep sea (Cailliet et al., 2001; Campana, 2005). Photoperiod, temperature, growth, sexual maturation, feeding, migration and other processes have all been linked to annual increment formation (Campana and Thorrold, 2001; Grønkjær, 2016), but the ubiquity of these increments suggests that there is an innate physiological mechanism involved (e.g., circadian periodicity). Many analytical approaches to otolith sclerochronology average out individual-level variation in growth and focus on the mean population trends. As fish otolith sclerochronologies continue to develop, it is critical to understand the mechanisms driving otolith growth increment formation [Q24]. Furthermore, between short- and long-lived species, attempts to crossdate individuals within a population produce varying results in terms of synchrony and environmental relationships (Rountrey et al., 2014). Understanding the occurrence and drivers behind individual growth variability [Q25] is a priority for advancing research using long-term growth series from otoliths (Morrongiello and Thresher, 2015; Morrongiello et al., 2019). For example, understanding temporal growth variability within otolith time series could aid fisheries management by improving stock discrimination methods (Denechaud et al., 2020) and assessing the impact of harvest on populations (Morrongiello et al., 2019).

3.2 Application of Sclerochronology

This section presents the highest-ranked questions addressing potential applications of established sclerochronological archives and techniques to outstanding questions in a wide range of research fields, including enhanced applications for climatological, oceanographic, ecological, and cultural studies.

3.2.1 Global climate

26. How spatially heterogeneous were climate and environmental conditions under “normal” past conditions (i.e., as opposed to extreme climate scenarios, such as the Little Ice Age, Last Glacial Maximum, Younger Dryas)?
27. How did seasonality vary in the past in the temperate climate zone?
28. Can we detect changes in variability in sclerochronological records that indicate an approach to a climate or environmental tipping point?
29. How did major climate changes affect the intrinsic variability of El Nino/Southern Oscillation (ENSO) in the past?
30. To what extent do sclerochronologies covary with tree-ring data, and what does that tell us about the coherence of climate variability over hemispheric scales through time?
31. How can we integrate tropical growth-increment data with mid- and upper-latitude sclerochronologies to explore tropical-extratropical teleconnections?
32. Which sclerochronological data are most suited for climate model assimilation?

Previous work has demonstrated successful applications of sclerochronological records to questions of global climate through paleoclimate reconstruction (Eakin and Grottoli, 2006; Reynolds et al., 2018). The annual and often subannual resolution of sclerochronological records, especially when supported by a crossdated chronology, makes them uniquely suitable to address questions of seasonality, rapid climate change, tipping points, and lead-lag climate responses across the Earth system (Corrège, 2006; Butler and Schöne, 2017; Reynolds et al., 2016). Several key directions for sclerochronological climate research on these topics were identified as a priority for future research [Q26-29].

The rapidly expanding range of species, geographic, and temporal coverage represented in published sclerochronological records enables new avenues for research on long-term, high-resolution climate variability. It is now possible to address questions of climate variability across broad spatial areas to explore large-scale climate and teleconnections (e.g., northern and southern hemisphere water mass temperatures, Thresher et al., 2014; circumtropical SST, Tierney et al., 2015; Wanamaker et al., 2019) across diverse time periods (e.g., late Holocene, Black et al., 2014; middle Eocene, Bougeois et al., 2014; Paleogene, Huyghe et al., 2015; late Cretaceous, de Winter et al., 2017). Because the geographic ranges of sclerochronological archives differ, large-scale climate reconstructions often require compilation of records sourced from different species (e.g., Reynolds et al., 2018). The comparability of such records must be assessed, and limitations explored in order to apply both multispecies sclerochronology and multiproxy-based interpretations to questions of, for example, atmospheric and oceanic interactions [Q30] and tropical-extratropical teleconnections [Q31].

Additionally, much attention has been placed on how climate modeling interfaces with sclerochronology [Q32]. Many studies utilize data from climate models to inform proxy interpretations (e.g., Tindall et al., 2017; Trueman et al., 2019). However, with the exception of coral records (see Okazaki and Yoshimura, 2017), the use of sclerochronological records in large-scale proxy data assimilations, has rarely been accomplished despite its high potential value (Goosse, 2016; Pyrina et al., 2017). More work is needed to assess the quality and richness of detail provided by sclerochronological records that will enable their appropriate inclusion in paleoclimate reanalyses (see Schmidt et al., 2014). Efforts to maximize sampling resolution, improve measurement techniques, and provide a robust understanding of the mechanisms by which environmental signals are embedded within the archive will improve confidence in these modeling applications (Goosse, 2016; Butler and Schöne, 2017).

3.2.2 Paleoceanography

33. How can sclerochronological proxies be used to study historical changes in the extent of Arctic sea ice?
34. How can we use sclerochronological archives to monitor changes in the role of the oceans as a buffer for carbon emissions and heat?
35. How can we use sclerochronological archives to detect high resolution variability in strength of Atlantic Meridional Overturning Circulation (AMOC)?
36. How has the ^{14}C reservoir effect varied over time and at different temporal scales (e.g., subannual, annual, decadal)?
37. What can sclerochronological records tell us about the links between the marine carbon and nitrogen cycles in the past, especially during times of abrupt climate change?
38. How can we utilise both high resolution sclerochronological records and traditional paleoceanographic data (e.g., sediment core records) to produce spatial reconstructions of broad scale climate variability?
39. How can sclerochronological records from shelf seas be used as proxies for open-ocean conditions and what are the temporal and spatial limitations?

Questions specific to paleoceanography highlight motivations and research avenues similar to those presented in the topic “Global Climate” (section 3.2.1). The wide range of established marine sclerochronological archives and proxies enables deeper understanding of past and present oceanographic processes at high temporal resolution. The questions in this topic [Q33-39] demonstrate some of the most prominent and promising applications of sclerochronological data for solving long-standing questions in paleoceanography.

Sclerochronological data have been successfully used to study past sea ice variability in the Arctic [Q33] (e.g., Halfar et al., 2013; Chan et al., 2017; Hetzinger et al., 2019), track local oceanic uptake of anthropogenic CO_2 [Q34] (e.g., Schöne et al., 2011; Williams et al., 2011; Dassié et al., 2013), estimate oceanic heat content and temperature variability [Q34] (Linsley et al., 2015), and assess changes in past oceanic circulation [Q35] (e.g., Wanamaker et al., 2012). The ability to combine radiocarbon (^{14}C) dating and independent sclerochronological age models (e.g., growth chronologies) has been used to reconstruct local ^{14}C reservoir changes through time [Q36] (e.g., Druffel and Griffin, 1993; Sherwood et al., 2008;

Butler et al., 2009; Wanamaker et al., 2012; Hirabayashi et al., 2017). Furthermore, promising results have been obtained in studies on nitrogen isotope ($\delta^{15}N$) values in sclerochronological archives (e.g., Yamazaki et al., 2016; Sherwood et al., 2014; Gillikin et al., 2019, and references therein). There is great potential for stable nitrogen and carbon isotope records to be coupled to enable detailed investigation of marine food web links in the past, as well as other aspects of the marine nitrogen and carbon cycles [Q37].

To fully address important questions on ocean history and broad-scale climate variability [e.g., Q33-37], spatiotemporal expansion of proxy data coverage is needed. Use of paleoceanographic data based on sediment cores in conjunction with diverse sclerochronological archives represents a promising avenue for future research [Q38]. While some work has been done in this area (e.g., Reynolds, et al., 2013), literature on methods and limitations for such work is sparse. Related to this issue, the temporal and spatial limitations of sclerochronological reconstructions of open-ocean conditionsbased on archives from shelf seas (e.g., bivalves and tropical corals) should be further investigated [Q39].

3.2.3 Paleoecology and human-environmental interactions

40. How can sclerochronological tools help us to decide which time period/condition provides an appropriate baseline for studies which require "natural", "pristine" or pre-human impact data on the environment?
41. How can sclerochronology be used to assess the anthropogenic impacts on overall ecosystem process and structure throughout the Holocene?
42. How can we use sclerochronological data to detect the first signs of human impact on the marine system through fishing and climate change?
43. How can sclerochronological records be used to assess changes in fish and shellfish populations due to harvesting?
44. In the context of global climate change, which aquatic ecosystems/environments experience ecological change first or to the greatest degree (e.g., open ocean, upwelling, subtidal, intertidal, estuarine, riverine, lacustrine)?
45. How can we use sclerochronology to distinguish variations in the effects of climate change on marine ecosystems at various spatial scales (e.g., local, regional and global)?
46. How can we use sclerochronological archives to monitor the lag in the ecosystem response to climate change and other environmental change in the oceans?
47. How can we use sclerochronology to quantify the rate of recovery of marine ecological systems from natural or anthropogenic disturbances?
48. How are different classes of chemical pollutants presented in the sclerochronological record and can their temporal distribution be inferred?
49. How can sclerochronological records be used to study eutrophication dynamics in coastal ecosystems?
50. How can sclerochronological records be used to infer the frequency and intensity of hypoxia and anoxia events in the past?

It is abundantly clear that most, if not all, modern ecosystems are severely affected by human activities (IPCC, 2018). Quantifying and understanding the impact of human activities on these ecosystems in the past [Q40-43] is among the key challenges in paleoecology (Seddon et al., 2013). Climate change, pollution, and industrial fishing have been identified as major threats to aquatic biodiversity and ecosystem health. It is therefore important to monitor environmental change in order to inform the definition of goals and directives for environmental protection, health assessment, and restoration [Q44-50]. However, due to shifting baselines and scarce data, restoration targets are often based on images of ecosystems that have already been disturbed and are thus no longer pristine [Q40]. Sclerochronology provides powerful tools to extend and analyze such baselines by constructing highly resolved chronologies that span centuries or millennia.

Sclerochronological archives are often used to study the human impact on marine species and ecosystems in the past and present [Q41-43]. Fishing and shellfish harvesting, in particular, have been important sources of food for humans since prehistoric times. Shell middens (i.e., anthropogenic sites of shellfish remains) are a particularly useful resource for studies of early human-environmental interactions, as they can be found on coastlines worldwide (except for Antarctica) and have been deposited throughout the Holocene and beyond (see Erlandson, 2001). Material obtained from shell middens has been used to study season of capture, resource management, measures of overharvesting, and environmental changes (see Andrews et al., 2003; Andrus, 2011; Geffen et al., 2011; Carré et al., 2019; Butler et al., 2019). Accurate age-structured information and growth rates of commercial species are of great importance in fisheries science and have been gathered extensively from fish otoliths, and also from mollusk shells or statoliths (Campana and Thorrold 2001; Henry and Nixon, 2008; Ezgeta-Balic et al., 2011; Hollyman et al., 2018). Otolith chemistry is also used to study the thermal life history of populations, or as a geochemical tracer to determine past locations and stock identity (e.g., Campana, 1999 and references therein; Wang et al., 2016). Moreover, additional information on food-web dynamics can be gained from δ^{15}N composition in carbonate-bound organic material (e.g., Gillikin et al., 2017; Sirot et al., 2017). Sclerochronology thus offers valuable insight into the impact of human activity and climate change on commercial species as well as the wider ecosystem. Further advances in this field to inform stakeholders and management are thus a priority research area.

Carbon dioxide emissions and climate change affect marine environments in complex ways through changes in temperature, mixing regimes, circulation patterns, oxygen solubility, and carbon chemistry. Responses of marine ecosystems are manifold, interlinked, and spatially and temporally heterogeneous [Q44-47]. While single-population chronologies provide limited insight into an ecosystem, a more holistic view can be achieved by comparing sclerochronological data from archives at different trophic levels or from different regions (e.g., Black, 2009; Reynolds et al., 2017). This approach enables us to study leads and lags in response to climate change or environmental disturbances between different ecosystems, regions, or taxa. Another method used to study or predict ecosystem response to climate change is the use of sclerochronological data to parameterize forecasting models (e.g., Morrongiello et al., 2012; Barrow et al., 2018). These and other methods (e.g., dynamic energy budget models) for investigating characteristics of ecosystem response to environmental change should be further explored.

The impacts of environmental pollution on aquatic ecosystems and mixing regimes is a matter of rising concern [Q48-50]. Some studies have applied sclerochronological techniques to monitor heavy metal pollution retrospectively (e.g., Scott, 1990; Gillikin et al., 2005; Krause-Nehring et al., 2012; Holland et al., 2014), which confirms that sclerochronology can provide long-term and highly resolved records that are not obtainable by standard monitoring techniques. While elemental content alteration through diagenesis or biological control is a potential limitation of these methods, the applicability and advantages of sclerochronology in the field of biomonitoring are evident (Schöne and Krause, 2016; Steinhardt et al., 2016). Another form of pollution is the anthropological input of nutrients into freshwater and coastal ecosystems, e.g., through agricultural runoff or wastewater, which fuels eutrophication [Q49, 50]. Sclerochronological studies on deep-water corals have shown that enrichment in skeletal ^{15}N is an indicator for terrestrial runoff (e.g., Williams et al., 2007; Prouty et al., 2014). Similarly, bivalve shell δ^{15}N is increasingly used to assess human and animal waste input into waterways (e.g., Black et al., 2017; Thibault et al., 2020). While this has been predominantly done via whole-shell analysis, time series δ^{15}N data have been published in other contexts (Gillikin et al., 2017), and the potential for sclerochronological studies is evident. Cultural eutrophication is relevant to many issues within public health and ecology, such as the concern for safe drinking water and the increasing development of hypoxic areas in oceans and lakes known as ‘dead zones’ (Chislock et al., 2013; Breitburg et al., 2018). Previous studies highlight promising applications of sclerochronological methods in this area, for example, shifts in Mn/Ca of cod otoliths have been used as a proxy for exposure to hypoxia in the Baltic Sea (Limburg et al., 2011; 2015; Limburg and Casini, 2018). Given that they are (mostly) immobile and benthic bioaccumulators with worldwide distribution, bivalves might be particularly suitable to track the history of hypoxic and anoxic events (e.g., Zhao et al., 2017c; Murakami-Sugihara et al., 2019). As dead zones are rapidly increasing worldwide, it would be very beneficial to develop sclerochronological applications to assess and monitor these phenomena.

3.3 Cutting Edge Sclerochronology

This section presents questions that were not ranked in the leading 50, but were nevertheless highlighted by the expert panels as potentially groundbreaking. These questions may have been downgraded because they are very specific to particular archives, or because they were perceived as high-risk with little chance of success. After discussion, they have been resurrected by the expert panels because they were thought to have the potential to broaden the horizons of sclerochronology, leading to highly novel applications.

A. *Can we use material within the growth line to infer conditions outside the main growing season?*

This question alludes to archives with varying growth rates, in particular, bivalves from mid- and high-latitude locations. Growth lines are formed during times of slow growth, often during autumn and winter months (see Killam and Clapham, 2018). Thus, growth lines potentially contain information on the environment outside of the main growing season. Attempts to use growth lines to study environmental and climate changes are absent within the literature, most likely due to the analytical challenges that arise from the fine scale of growth lines (Shirai et al., 2014). However, some research has demonstrated potential for shell Sr/Ca and Mg/Ca proxies to reveal environmental information near the growth line (e.g., Schöne et al., 2013), despite general challenges in elemental ratio proxies within bivalve shells (see Section I, Topic “Archive-specific research”). Thus, analytical techniques making use of growth lines in bivalves is a promising avenue for studying previously inaccessible seasons, as well as improving our understanding of biomineralization processes.

B. *What approaches can we use to identify coeval shells for deep-time geological settings that will enable us to construct multicentennial crossmatched chronologies?*

Crossdating allows construction of well replicated, annually resolved, and exactly dated records that can span multiple centuries to millennia (Black et al., 2016). Also, software tools such as Shellcorr (Scourse et al., 2006) or CDendro (Cybis Dendrochronology) can assist in pattern matching among dead-collected specimens which are known to be roughly coeval. However, construction of deep-time chronologies by crossmatching shells requires the identification of fossil specimens with overlapping lifespans from accumulations and lags which may cover many thousands of years. The antiquity of these shells precludes rangefinder radiometric dating, and other methods need to be developed to identify coeval specimens in cases such as this. While stratigraphy or spatial proximity among specimens can provide time constraints in certain cases, these factors alone are not sufficient to guarantee contemporaneity — modern shell lags, for example, can contain specimens separated in time by several thousand years (Butler et al., 2010). The likelihood of contemporaneity might increase when fossils can be interpreted to have been rapidly buried in life position (e.g., bivalves with both valves still intact; Lockwood and Work, 2006) or in a calcified reef formation (Greer et al., 2006; Wu et al., 2017). A taphonomic indicator of rapid burial is good preservation of the surface structure with no signs of grazing, boring, or postmortem microboring (Vogel, 2000; Lescinsky et al., 2011, and references therein). However, even where rapid burial in life position is assumed, time-averaging effects may complicate the search for coeval specimens; this is especially true for shelly fossils in siliciclastic environments, and to a lesser degree also for shells in carbonate sediments as well as for reef coral assemblages (Kidwell et al., 2005; Edinger et al., 2007). Developing sampling strategies in the fossil record could represent a breakthrough that enables us to investigate change at high resolution over extended periods in deep-time settings.

C. *What can sclerochronological records tell us about which seasons are represented by non-sclerochronological estimates of paleo-seawater temperature - e.g., from sediment core proxies?*

Temperature estimates based on sediment core proxies (i.e., marine microorganisms and their organic residues) are an important source of paleoceanographic data. Yet, interpretation of the climate signal is often complicated by the uncertainties related to the life cycle of biological sediment core archives (i.e., planktonic and benthic microorganisms). Ecological factors, such as the length and timing of the growing season, determine whether paleo-seawater temperature estimates represent an annual mean or an average over a certain season (typically summer). Sediment traps and core-top analysis in combination with instrumental data are typically used to calibrate proxy-based reconstructions. However, this approach cannot account for changes in the growing season through time and is not applicable to extinct species. The advantage of sclerochronology for providing seasonally resolved paleotemperature records opens a possibility for comparison with contemporary non-sclerochronological estimates (e.g., de Winter et al., 2018), thus providing the means for proxy calibration. The feasibility of this approach depends on our understanding of how sclerochronological records can be used to reconstruct past open-ocean conditions [Q39] typically reflected in sediment core records. To enable calibration of proxies based on planktonic species, sclerochronological records that reflect mixed-layer temperature dynamics have to be developed. Identification of suitable sclerochronological archives and development of new methods to solve these issues can lead to a novel application of sclerochronology and improve our understanding of past climate.

D. *How can we use sclerochronology to investigate potential latitudinal gradients in the response of marine biota to climate change, in terms of species die-off or range shifts*?

An understanding of how biotas respond to climate change, to possibly predict future extinctions and species range shifts, are among the key challenges of ecology (Sutherland et al., 2013). Most of the research on this topic focuses on abundance and species distribution data, which is a coarse metric of change (Rombouts et al., 2012). For the impact to be detectable in such data, organisms have to die, stop breeding, or shift their geographic distribution. Sclerochronology provides promising tools for analyzing population metrics from both stationary (e.g., bivalves and corals) and/or mobile (e.g., fish) organisms to infer latitudinal shifts in optimal conditions and/or fisheries regime shifts in population demography (Neuheimer et al., 2011; Morrongiello and Thresher, 2015). Using sclerochronology to identify sublethal impacts of changing environmental conditions can help to recognize potential range shifts or fisheries productivity changes before distributional change has happened.

E. *Can fisheries management advice be improved by combining traditional stock assessment techniques (e.g., otolith aging) with machine learning?*

Advances in software and analytical tools have had profound impacts in the environmental sciences (Fielding, 1999). One such advancement is in the field of ‘machine learning’, which is a transformative tool across disciplines (Malde et al., 2019). Image recognition is a common application of machine learning within the natural sciences. Machine learning methods have been utilized for mollusk shell identification (Zhang et al., 2019) and geometric morphometric analysis of gastropods (Doyle et al., 2018). Furthermore, fisheries scientists have applied machine learning techniques to fish age assessment through otolith image analysis with some success (Dub et al., 2013; Moen et al., 2018). Combining machine learning with long-term historical datasets of sclerochronology images, from any species, and their associated growth and ages, could 1) automate aging, 2) reduce human error, 3) improve predictions of population growth responses, and 4) identify anomalies. Large-scale incorporation of open-source otolith image recognition software could improve stock management advice for commercially important species.

F. *What proportion of the whole ecosystem extent does the environmental DNA (eDNA) in bivalve shells capture and how can the eDNA be used to reconstruct ecosystem change?*

Technological advances in molecular ecology have led to the utilization of environmental DNA (eDNA) to detect the presence of certain taxa within aquatic environments. From a physical environmental sample (e.g., water, soil, shell), molecular markers within fragments of available eDNA are amplified and compared against a database to identify the presence of target species within the environment (Ardura et al., 2015). This tool is particularly useful for ecosystem monitoring. For example, eDNA can allow for early detection of invasive species, and the identification of vulnerable species. Sclerochronology and genetics are not traditionally paired together, but recently, the carbonate biominerals of fossilized marine mollusks have been found to contain eDNA (Der Sarkissian et al., 2017). More studies are needed to verify how successful bivalve eDNA is at reconstructing the full range of species present within the entire ecosystem, and how eDNA results may vary depending on environmental and physiological conditions. The ability to identify the timing of presence and absence of taxa within sclerochronological archives could revolutionize our understanding of ecosystem shifts during changes in global climate.

G. *How can possible effects of early human harvesting be separated from natural variability in marine fauna to better assess how changes in resources affected hunter-fisher-gatherers?*

Material from middens can be used to reconstruct past climatic and environmental change as well as human behavior (see also Q40-43). Fish and shellfish have been an important source of food throughout human history. The impact of fishing, harvesting, and maricultures on marine ecosystems can be traced back to the early Holocene and beyond - for instance, in Europe, records of shellfish harvesting date back to over 450,000 years ago (Bailey and Milner, 2008). However, natural variability also influences ecosystem change, and not all environmental changes that we see in the paleo record are anthropogenic. Thus, anthropogenic influences such as overharvesting or ancient maricultural constructions have to be separated from natural variability of ecosystems and populations. For example, regional differences in shellfish harvesting practices and underlying environmental and historical factors can be investigated by combining growth and $\delta^{18}O$ data in shells collected from archaeological shell middens in different environmental settings (Burchell et al., 2013b). Disentangling natural and anthropogenic signals recorded in middens using sclerochronological tools , would allow us to study not only how humans have impacted the environment, but in turn how environmental change has affected human societies and food security through time.

H. *How can data from sclerochronology be used to inform us about land claims by indigenous people?*

Indigenous land rights are tightly linked with physical and economic safety, as well as mental and emotional well-being, and therefore of fundamental importance for the self-determination of indigenous groups. As discussed above, many studies have used midden material to study past human-environmental interactions. Season-of-capture studies provide insight into residential mobility and sedentism of hunter-fisher-gatherers in the past (e.g., Burchell et al., 2013a). In the Americas and Australia, as well as some regions in Asia and Africa, midden archives are almost always on indigenous land. Therefore, scientists should acknowledge that these archives are the result of indigenous labor, and seek conversation and exchange with indigenous groups. Given that middens can provide continuous records that span the last 11,000 years of human history (Toniello et al., 2019), sclerochronological techniques could be applied to prove long-term land use of indigenous groups based on ancient middens. Further applications and research questions should be developed by actively involving indigenous descent groups in the scientific process (see, e.g., Kaiser et al., 2019).

4. Discussion

4.1. Priority research questions

This collaborative project was conducted to identify the state-of-the-art in sclerochronology and to reflect on existing challenges and possible future developments. The questions identified herein as fundamental and priority to the field (see Supplementary Materials for the complete list) represent a snapshot in time describing the potential and challenges of sclerochronological research as perceived by a group of leading experts and community members following the 5th ISC. The link to the 5th ISC was an advantage for this endeavor, as the conference provided an overview of contemporary research results, facilitating the compilation of well-informed contributions.

We intended to highlight research addressing promising applications of sclerochronology, as well as gaps in our understanding of archives and methods used in the field. The questions presented and discussed in this paper reveal significant knowledge gaps in our understanding of biomineralization processes [Q1-4, 22], mechanisms driving the growth of skeletal structures [Q5-8, 23, 25], and challenges in geochemical proxy interpretations [Q16-19, 21]. They also emphasize the need to identify common standards for data management and analysis [Q9-15] and introduce fundamental questions related to the use of specific archives, such as fish otoliths [Q24, 25, C, F] and bivalves [Q21-23, B, G]. Even though many of the submitted questions suggest that current tools and methods require further development, many existing techniques are sufficient to address important scientific questions in other fields. Our results highlight the potential for applying sclerochronological data and methods to answer long-standing questions in other research fields, such as climate sciences [Q26-39] and (paleo-)ecology [Q40-50].

Identification of research priorities entails certain trade-offs. The feasibility of approaches and their potential impacts are often difficult to foresee and evaluate. This complicates identification of the research directions that are not-yet established and thus truly lie on the horizon. Although our list of questions provides an overview of possibilities and challenges in sclerochronology, considering all the limitations of this study, it should be treated with some degree of caution. The questions selected by the community are largely reflective of ongoing research. As the 5th ISC conference showed, sclerochronological tools have been used in many research fields. Nevertheless, the most common applications to date are related to climate and environmental sciences, which is reflected in both the research presented at the ISC and the questions submitted to the survey that forms the basis of this paper. However, these are not the limits of sclerochronology, and applications to social and anthropological sciences, for example, are feasible and promising [e.g., Questions G, H]. Thus, the range of questions presented here by no means portrays the full diversity and potential of the field and the list of questions will require further updates as the field develops.

4.2 Future outlook

The discussion arising from this project emphasizes important issues relevant to the future of the field. While previous advances in sample preparation, observation and analysis have moved the field significantly forward and enabled new and improved applications of sclerochronological research, our results show there is still room for technical and methodological development in the field (Section 3.1), as support and motivation for applications in the field (Section 3.2). The survey participants identified common standards for data management and analysis as high priority. Similarly, identification of common terminology within and across different branches of sclerochronological research would significantly improve communication and potential collaboration. A further promising avenue for sclerochronology is future collaboration with researchers utilizing similar archives (e.g., calcium phosphates biominerals), or researchers in the social sciences. Relatively low response rates and the bias towards certain disciplines and archives in the framework of the ISC indicate that the field requires consolidation and more collaborative work. Collaboration across different disciplines would undoubtedly widen the profile of sclerochronology among the scientific community. As the field matures, it should become possible to combine climatological, ecological, biogeochemical and archaeological applications of sclerochronology to create an integrated sclerochronological approach to the study of the Earth system, covering the physical and living systems and extending to human cultural history.

5. Conclusions

This is the first effort to identify priority and fundamental research questions in sclerochronology via horizon scanning. As the field grows and advances, we recognize that research priorities will have to be re-assessed. The list of questions presented and discussed in this paper contains the highest-ranked research priorities and fundamental questions, as identified in a community-based survey. While this list should not be considered definitive, we hope that the results of this project will stimulate discussion and serve as a stepping stone to future collaborations and groundbreaking research.

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Research utilizing biomineralized structures (sclerochronology) is rapidly advancing

Horizon-scanning survey reveals community-defined research priorities

Top questions highlight persistent challenges and promising applications

Declaration of interests

☑ 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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: