




SYNTHESIS**Capitalizing on the wealth of chemical data in the accretionary structures of aquatic taxa: Opportunities from across the tree of life**Zoë A. Doubleday ^{1*}, Louise Hosking ¹, Jasper Willoughby,¹ Minoli Dias,² Natasha Leclerc,³ Shanie Brault Nikolajew,⁴ Melita Peharda,⁵ Arieli Tristão Rézio ¹, Clive Trueman⁶¹MARIS Lab, Future Industries Institute, University of South Australia, Mawson Lakes, Australia; ²Department of Earth Sciences, University of Toronto, Toronto, Ontario, Canada; ³Department of Archaeology, Memorial University of Newfoundland and Labrador, St. John's, Canada; ⁴Department of Earth and Environmental Sciences, University of Ottawa, Ontario, Canada; ⁵Institute of Oceanography and Fisheries, Split, Croatia; ⁶School of Ocean and Earth Science, University of Southampton, Southampton, UK**Scientific Significance Statement**

Data on aquatic environments are scarce compared to many terrestrial environments and can be expensive and challenging to collect. However, chemical data extracted from the accretionary structures of aquatic organisms, like shells and skeletons, can provide a wealth of information about an individual's life history and its surrounding environment. These chemical datasets can be obtained from an extraordinary range of species, covering almost all aquatic habitats and biogeographic provinces; however, much of the research has focused on three dominant taxonomic groups. In this synthesis, we showcase the untapped potential of lesser-known taxa, from gorgonians to turtles, and coralline algae to octopuses, to collect critical data on aquatic environments and help us assess and manage human impacts.

Abstract

Aquatic organisms are natural data loggers and record chemical variations within hardened accretionary structures like shells and teeth. Chemical sclerochronology is the study of these chemical variations through time and how they are used to understand environmental change and the physiology and ecology of species. While sclerochronology research has largely focused on bivalves, teleost fish, and hard corals, there are many other aquatic taxa rich with time-resolved chemical data. To expand focus to these "other" taxa and determine the state-of-play, we compiled a database of chemical sclerochronology studies spanning nine living phyla and 19 classes. We then examined research trends and knowledge gaps across these taxa and showcase their exciting potential to collect critical data and address pressing

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Additional Supporting Information may be found in the online version of this article.

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environmental and ecological challenges. We hope this synthesis will encourage further research on species across the tree of life, as well as foster collaboration among the established and lesser-known fields of sclerochronology.

Effective conservation actions in response to environmental change depend on our ability to monitor the environment and collect data at different spatial and temporal scales. Many have noted, however, that we lack ongoing in situ monitoring of marine, coastal and freshwater environments (i.e., aquatic environments), and that there is a strong research and investment bias towards terrestrial systems, likely due to the many challenges and costs of collecting aquatic data (Richardson and Poloczanska 2008; Darwall et al. 2011; Di Marco et al. 2017). In fact, as signaled in the United Nations' 2021 World Oceans Assessment, there has been little progress made over the past 5 yr in the development of innovative and cost-effective technologies that could increase our capacity to monitor our oceans (United Nations 2021). However, monitoring is critical to assess and prioritize the effectiveness of environmental regulation and investment. Therefore, addressing the lack of aquatic data is an important step towards rectifying this bias in conservation management and policy.

Opportunistic data collection has emerged as a means of widening spatial coverage and temporal resolution of the natural environment, and effectively means taking advantage of new or unplanned opportunities for data collection, particularly when resources are limited (i.e., repurposing existing samples) (Jarvis et al. 2023). Where instrumental or ecological data are lacking, chemical sclerochronology can increase our capacity to collect aquatic data opportunistically (Roman Gonzalez 2021). Chemical sclerochronology is the study of chemical variations in the accretionary structures or tissues of organisms and how those variations relate to time, with a traditional focus on stable isotopes and element markers (Oschmann 2009; Gillikin et al. 2019). In other words, organisms log data on environmental conditions within their accretionary structures as they grow, and chemical sclerochronology involves collecting that data, calibrating it, and understanding what it means. Sclerochronological data are used in two key disciplines, paleoclimatology and ecology, with a focus on environmental and life history reconstruction, respectively. While sclerochronology itself is opportunistic in nature with data quality and type dependent on species distributions and accessibility, accretionary structures can be collected by analyzing historic samples held in museums and research agencies or via new samples collected for other purposes (i.e., stomach content analysis or benthic surveys), or even from accidental deaths (i.e., whale strandings). Furthermore, many sclerochronological samples can be readily reanalyzed and repurposed as resources and new technologies become available and new research questions or challenges arise.

Sclerochronology studies have largely focused on three taxa—hard coral, bivalves, and fish (specifically otoliths). Hard corals and bivalves are established environmental archives,

largely providing proxy datasets of past climatic conditions in tropical and non-tropical regions, respectively (Lough and Cooper 2011; Butler and Schöne 2017). However, these organisms can also provide ecological data. Both taxa are sessile and have periodic (typically annual) growth increments which allows precise dating of each increment and the creation of high-resolution chemical time series that span decades, centuries, and even millennia. Many coral and bivalve paleoclimate records now exist, extending the instrumental record and providing critical insights into climate variability and change. In contrast, fish otoliths have evolved as a tool to understand fish ecology, as well as aid fisheries science and management (Reis-Santos et al. 2023). While otoliths do have annually resolved growth increments, fish are mobile and generally shorter lived and are traditionally used to understand how an individual or population moves through the environment, rather than providing proxy environmental data per se (Elsdon and Gillanders 2003). However, otoliths are also being increasingly recognized as a tool to collect environmental data (Izzo et al. 2016). As a whole, these three taxa dominate the literature and academic symposia and drive methodological advancements, as well as the research direction of sclerochronology (Oschmann 2009; Wang et al. 2019; Roman Gonzalez 2021). Furthermore, there are many relevant reviews on bivalves (e.g., Jones 1983; Peharda et al. 2021), fish otoliths (e.g., Campana 1999; Elsdon and Gillanders 2003; Reis-Santos et al. 2023), and hard corals (e.g., Druffel 1997; Lough and Cooper 2011; Thompson 2022) across the decades, highlighting the progression, dominance, and application of these research fields. It is no surprise, therefore, that there is a strong research community on otolith and bivalve sclerochronology with 100s of chemical sclerochronology studies on each of these taxa (see Supporting Information Table S1 for estimates) (Oschmann 2009; Wang et al. 2019).

While corals, bivalves, and fish have undoubtedly changed how we collect data and understand the natural world, a diverse range of other sessile and mobile taxa generate accretionary structures and reveal unique insights into past climates and species ecology. Accretionary structures from under-sampled taxa not only include biomineralized carbonates (like bivalve shells, corals, and otoliths), but a broader range of inorganic and organic materials. Therefore, working with these taxa and structures enables opportunistic data collection on a broader range of (i) poorly understood aquatic species, (ii) environments where traditional taxa do not occur or are relatively difficult to obtain, and (iii) environmental data or chemical proxies, which can be limited by the size, composition, or biology of the traditional taxa or structure in question. Research on under-sampled taxa can also be used to

strengthen or validate environmental data obtained from traditional archives and enrich our understanding of fundamental processes like biomineralization, which is crucial for the ongoing development of sclerochronology as a whole (Butler and Schöne 2017; Wang et al. 2019).

Here we aim to expand the focus of chemical sclerochronology to under-sampled taxa and determine the current state-of-play, the knowledge gaps, and identify opportunities for the field. While we recognize the rich body of sclerochronology literature that focuses on deep geological time and paleoenvironments (Ferguson et al. 2019; Peharda et al. 2021; Taylor et al. 2021), here we focus on modern-day species and environments. In doing so, we compiled a database of chemical sclerochronology studies that spanned two kingdoms (plants and animals) and nine phyla (such as mollusks, arthropods, and vertebrates), highlighting the true diversity and breath of sclerochronological records, and how these records can help address our growing data needs for monitoring marine, coastal, and freshwater environments.

Search methods

We searched for literature examining chemical variations in the accretionary structures of modern aquatic organisms (mineralized and organic), with definitions provided in Supporting Information Table S2. In brief, we included studies that analyzed chemical data in a chronological sequence along an accretionary structure or used the chronological properties of an accretionary structure by targeting a temporally explicit area within the structure (i.e., sampling the natal core). Specifically, we focused on element markers (i.e., concentration of a given element), isotope markers (i.e., stable, radiogenic, radio/radioactive, compound-specific, or clumped), and hormones (i.e., concentration of a given hormone). We also included studies that focused on method development, proxy development, or biomineralization processes if they were undertaken for sclerochronological applications. As a special case, we did include studies that generated time series data by analyzing historic accretionary structures over time from museum collections or modern archives. We excluded studies on accretionary structures that did not have any chronological context (i.e., studies that analyzed a structure in bulk without reference to its temporal growth). In addition to our sclerochronology criteria, we excluded studies that focused on bivalves, ray-finned fishes, and hard corals, as well as fossil or sub-fossil material or any material older than the Holocene. We also excluded studies that only focused on physical variations in accretionary structures, as well as laboratory or experimental studies, unpublished studies, or review papers.

We predominantly used Web of Science to search for studies using keywords and their variants relevant to each taxa, alongside other databases (i.e., Google Scholar) and search methods (i.e., papers listed in reviews) to ensure most studies were captured. As the review covered such a diverse range of taxa, search strategies varied slightly from taxa to taxa and

were refined through the authors' expert knowledge, as well as through an initial reconnaissance of the literature to identify the most useful keywords. However, overall searches included "isotope," "element," and "hormone" as well as the commonly used names for the relevant taxonomic group (i.e., squid) and relevant structure type (i.e., statolith, beak) (see Supporting Information Table S3 for search terms). Depending on taxa, some exclusion terms were also used. For each taxa, a long list of potential studies was generated by reading the titles and abstract, the long list was then refined and reduced (if necessary) by reading through individual studies and matching them against our inclusion criteria. Searches were conducted between October 2023 to September 2024 and included any year up until, and including, 2023.

Once the literature search was complete, we recorded a range of metadata for each study including phyla and class (plus order for Chordata), accretionary structure, chemical marker category and stable isotope type, temporal breadth and resolution, location of study (country of origin of first author), and journal. Marine and estuarine studies were categorized by marine ecoregion as defined by Spalding et al. (2007), with wholly freshwater studies designated as "freshwater." If studies focused on species that lived in marine and freshwater environments, they were categorized by marine ecoregion. Lastly, we grouped all studies according to six broad, research topics (e.g., movement ecology, environmental reconstruction). Then, we grouped relevant studies according to the modern environmental or ecological challenge they sought to address (e.g., understanding global environmental change, managing commercially exploited populations); however, for some studies, this categorization was not relevant nor defined and therefore no categorization was given. While multiple categories were relevant for some studies, we chose the single most dominant topic or environmental challenge. For all categorizations, we did not extend beyond the information provided in each study (i.e., collect additional information or draw on our own opinions).

At a class level, we identified broad life history characteristics relevant to the taxonomic scale examined, as well as whether a class was used to obtain ecological data, environmental data, or both.

The trends

Our literature search collated data on 519 studies that spanned two kingdoms, nine phyla, and 19 classes, which highlight the true breadth and diversity of sclerochronology research in aquatic ecosystems (Fig. 1) (see database of studies: Doubleday et al. 2024). Valuable ecological data were obtained from all classes highlighted in Fig. 1, except for crinoids, and were predominantly derived from the mobile vertebrate classes, cephalopods, gastropods, and sessile barnacles. Barnacles were the only taxon that provided ecological data on another phyla or class (e.g., reptiles). Environmental data were obtained from

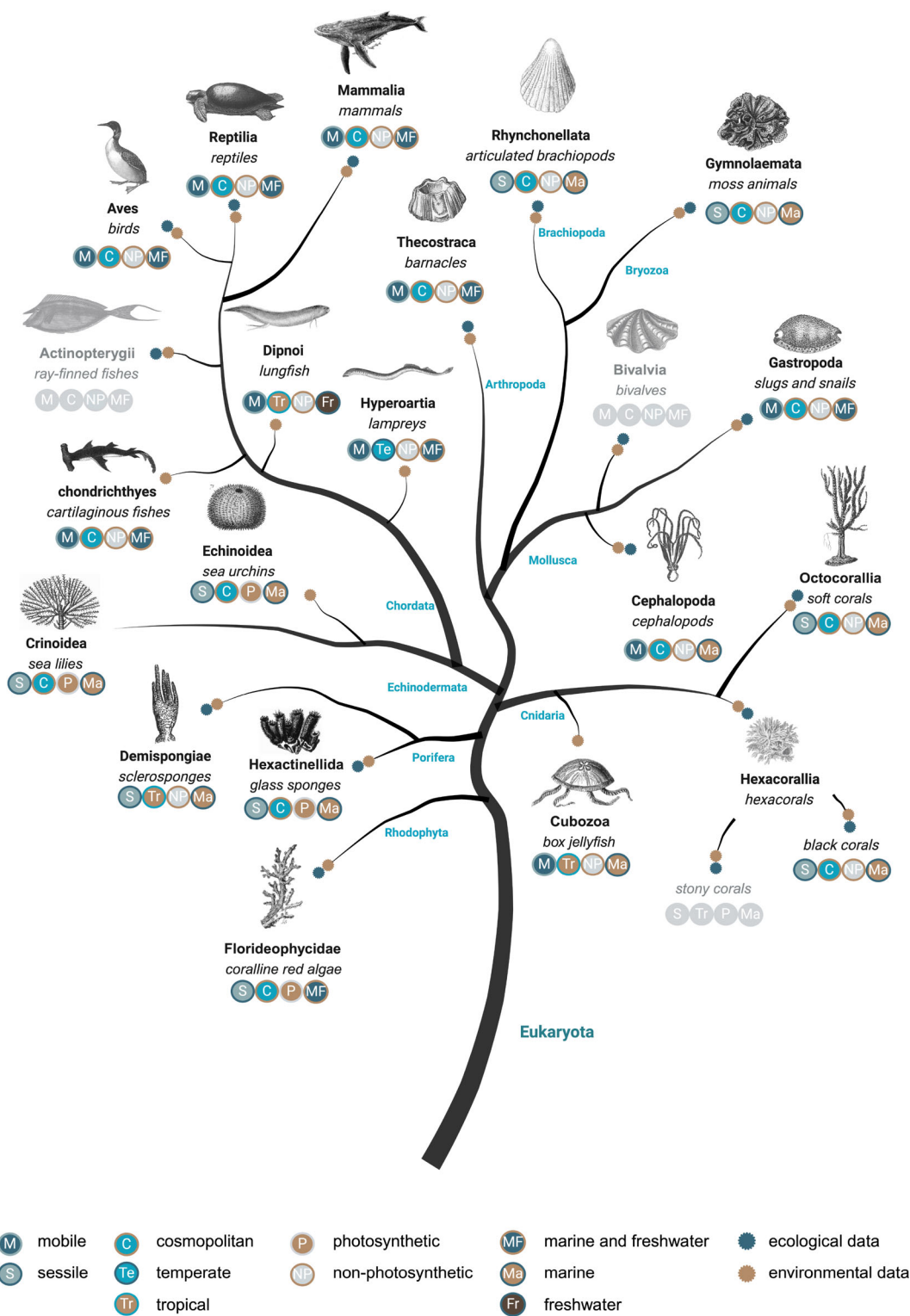


Fig. 1. The taxonomic breadth of chemical sclerochronology studies across the aquatic tree of life, including under-sampled taxa identified in our literature review (represented in black and color) and traditional taxa (represented in light gray). Taxa are identified by phyla (blue text) and class (black text) and are grouped into four broad categories. Blue and brown circles represent whether a class has been used to collect ecological data, environmental data or both. The tree of life is illustrative rather than an accurate phylogenetic representation.

12 of the 19 classes but were predominantly derived from the seven sessile classes and gastropods. The use of crinoids was examined as an environmental proxy, but was not deemed to be useful due to the strong physiological influence on chemical composition (Gorzela et al. 2012).

Studies were dominated by Chordata or vertebrates, which, in turn, were dominated by Mammalia and the orders Carnivora (e.g., seals, sea lions, and walrus) and Cetacea (e.g., baleen and toothed whales) (Fig. 2). This trend is no surprise given the persistent focus on vertebrate species in ecological and conservation research, compared to invertebrates (Collier et al. 2016; Donaldson et al. 2017). Additionally, the dominance of Carnivora may also reflect the relative ease of sampling and preparing whiskers from living animals (Lübcker et al. 2016). No studies were found for the classes Malacostraca or Amphibia, and only two studies for Echinodermata. This may reflect a lack of need, or limited sample material, or that the respective accretionary structures are challenging to work with (e.g., material prone to degradation), or that chemical markers are under a high level

of physiological regulation, such as in crinoids (Gorzela et al. 2012). However, it could also mean that the structure is relatively new to sclerochronology, and chemical markers have yet to be explored (e.g., gastric ossicles in decapod crustaceans). Our review also highlights the diverse array of accretionary structures that are used to collect data on aquatic species (Fig. 2C), which were dominated by mollusk shells and skeletons of sessile organisms, as well as teeth, whiskers, and baleen plates. The structures represented a diverse array of inorganic and organic materials from calcite, aragonite, and apatite to collagen, keratin, and chitin (Supporting Information Table S4).

Studies spanned four decades; however, there was only a handful of studies published prior to 2005, with an uptick in publications in 2005 and 2015 (Fig. 2D). Studies on coralline algae (Rhodophyta) did not appear until 2000 and subsequently picked up momentum in 2007. Meanwhile, studies on proteinaceous octocorals and black corals (Cnidaria) only appeared in 2010. This is likely driven by the increasing need to collect data on relatively inaccessible environments (e.g., the

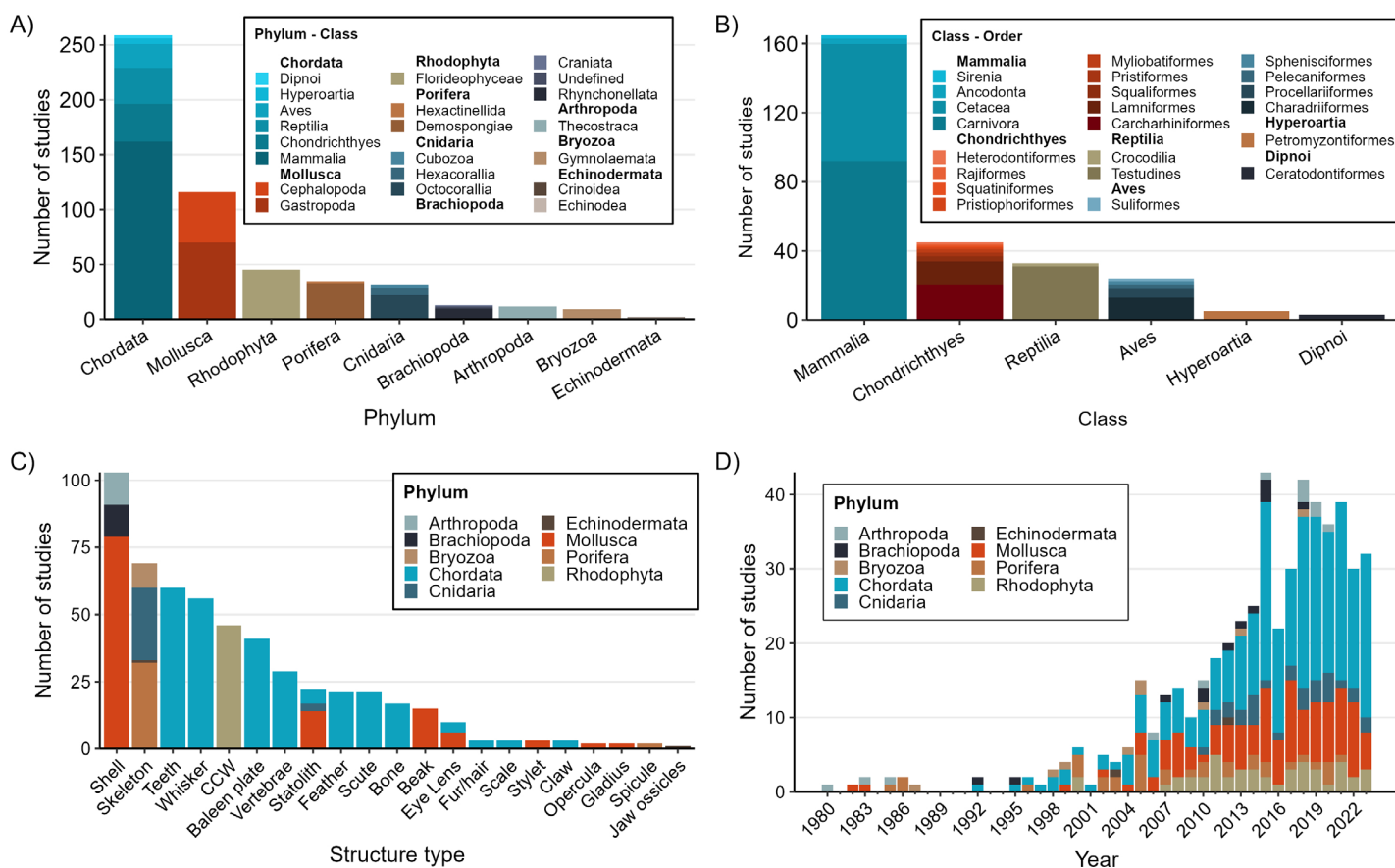


Fig. 2. Number of chemical sclerochronology studies from 1980 to 2023. Graphs represent (A) all studies by phylum and class, (B) studies on Chordata by class and order, (C) studies by type of accretionary structure, and (D) studies through time. Noting that ray-finned fishes are excluded from Chordata, bivalves from Mollusca, and hard corals from Cnidaria. A small number of studies included multiple classes or orders; these studies were duplicated across categories. CCW, calcified cell walls.

high Arctic and deep sea) (Halfar et al. 2000), as well as increasing recognition of proteinaceous corals as valuable chronological archives (e.g., for collecting data on nutrient pollution) (Baker et al. 2010). However, after 2018, research effort has appeared to plateau and even decline for some taxa, particularly mammals and gastropods (Supporting Information Fig. S1); a trend that may have been exacerbated by the COVID-19 pandemic.

The bulk of the studies were undertaken on samples collected in temperate and polar marine regions in the northern hemisphere, with most of the research conducted in either the United States (32%) or Europe (24%) (Fig. 3; Supporting Information Fig. S2). This trend is broadly reflective of trends observed for sclerochronology research on bivalves and ecology in general, where much of the research effort stems from more populated, wealthy nations (Martin et al. 2012; Peharda et al. 2021). The focus on the Global North may reflect proximity to research expertise and sample archives in museums, research agencies and private collections, as well as the need to collect data from polar regions that are particularly vulnerable to climate change (Halfar et al. 2000). There were fewer studies from the tropics, except for the tropical Atlantic (particularly the Caribbean and American coast), and the central Indo-Pacific. Research on sponges (Porifera) has been largely restricted to these regions, with all 30 odd studies largely focused on only 2 tropical species. This may reflect the accessibility of the species from the United States (i.e., in the Caribbean) and extensive research extending back to the 1980s. Temperate Australasia had relatively few studies despite having the research infrastructure and being home to many taxa analyzed in this review.

Species from wholly freshwater environments only made up 4% of all studies, which in part reflects the dominance of marine-only classes (Fig. 1), as well as our classification system (e.g., river otters were assigned to a marine eco-region as they reside in both marine and freshwater environments). However, lack of freshwater representation is a recognized gap in sclerochronology (Stringer and Prendergast 2023), and, in our study, freshwater studies were still relatively limited in taxonomic groups with freshwater representation.

Seven broad chemical marker categories were identified within the literature, dominated by stable isotopes which were analyzed in 73% of studies and represented all phyla (Fig. 4). Fifty-five percent of all studies had analyzed stable carbon isotope ratios and 42% analyzed stable nitrogen isotope ratios, which were largely used to understand movement and foraging ecology, habitat use, dietary change, and ontogenetic shifts in vertebrates and cephalopod mollusks. Oxygen isotope ratios were analyzed in 24% of all studies, which were predominantly analyzed in the gastropod mollusks for environmental reconstruction, as well as aging work. The dominance of carbon, nitrogen, and oxygen isotope analyses also likely reflects the relative ease with which they can be analyzed using

established and accessible methods, as well as a well-established mechanistic understanding of isotopic variation. The use of more novel stable isotope systems (e.g., sulfur and boron), radiogenic isotope pairs (e.g., $^{206}\text{Pb}/^{207}\text{Pb}$, $^{208}\text{Pb}/^{207}\text{Pb}$), clumped isotope markers, and compound-specific isotope ratios was relatively rare. This may reflect the fact that these markers are generally more expensive, complex, and time consuming to analyze, as well as require more specialist expertise, sample preparation facilities, and instrumentation. Radioactive or radio isotopes (6% studies) were largely used for aging work (i.e., radiocarbon and uranium-series dating), particularly in accretionary structures that have no apparent growth increments (i.e., sclerosponges). The use of element markers was relatively low (30% of all studies). Element markers are relatively easy to analyze using laser ablation ICP-MS, and dominate otolith-based research, but mechanisms responsible for variation in element markers are poorly understood. Consequently, element markers were often used to track anthropogenic pollution inputs in the environment or to track movement of species across strong environmental gradients. Element markers were notably more prevalent in coralline algae (Rhodophyta), as Mg/Ca and other element markers are established environmental proxies. Hormone-based markers were relatively new (3% of studies with the earliest from 2014) and were used to understand the health and reproductive biology of marine mammals.

More than 70% of studies spanned years to decades, providing data at temporal scales relevant to both ecology and modern environmental change (Fig. 5). Most datasets were calibrated to absolute time and had a defined temporal resolution (e.g., annual); however, for some studies, resolution was undefined (e.g., periodicity of growth unknown or undefined) or focused on relative time (e.g., adult vs. juvenile life history stages).

The greatest proportion of studies focused on understanding the ecology and life history of species (e.g., movement ecology, age and growth, reproductive biology), with a smaller proportion focused on environmental reconstruction (Fig. 6A). This is largely reflected by the journal profile of the database, which were dominated by marine ecology, geochemistry, and aquatic science journals, as well as multi-disciplinary journals (Supporting Information Fig. S3). However, there were many papers also focused on method and proxy development for the collection of both ecological and environmental data. Studies were used to address six broad environmental challenges, with more than half focused on collecting critical data on endangered and inaccessible species, as well as understanding modern environmental change (Fig. 6B). Studies also focused on fisheries management, pollution, and collecting paleoclimate data from inaccessible and poorly studied environments. A consistent theme through these studies was that chemical sclerochronology enabled the collection of data that would be otherwise difficult to collect via other means.

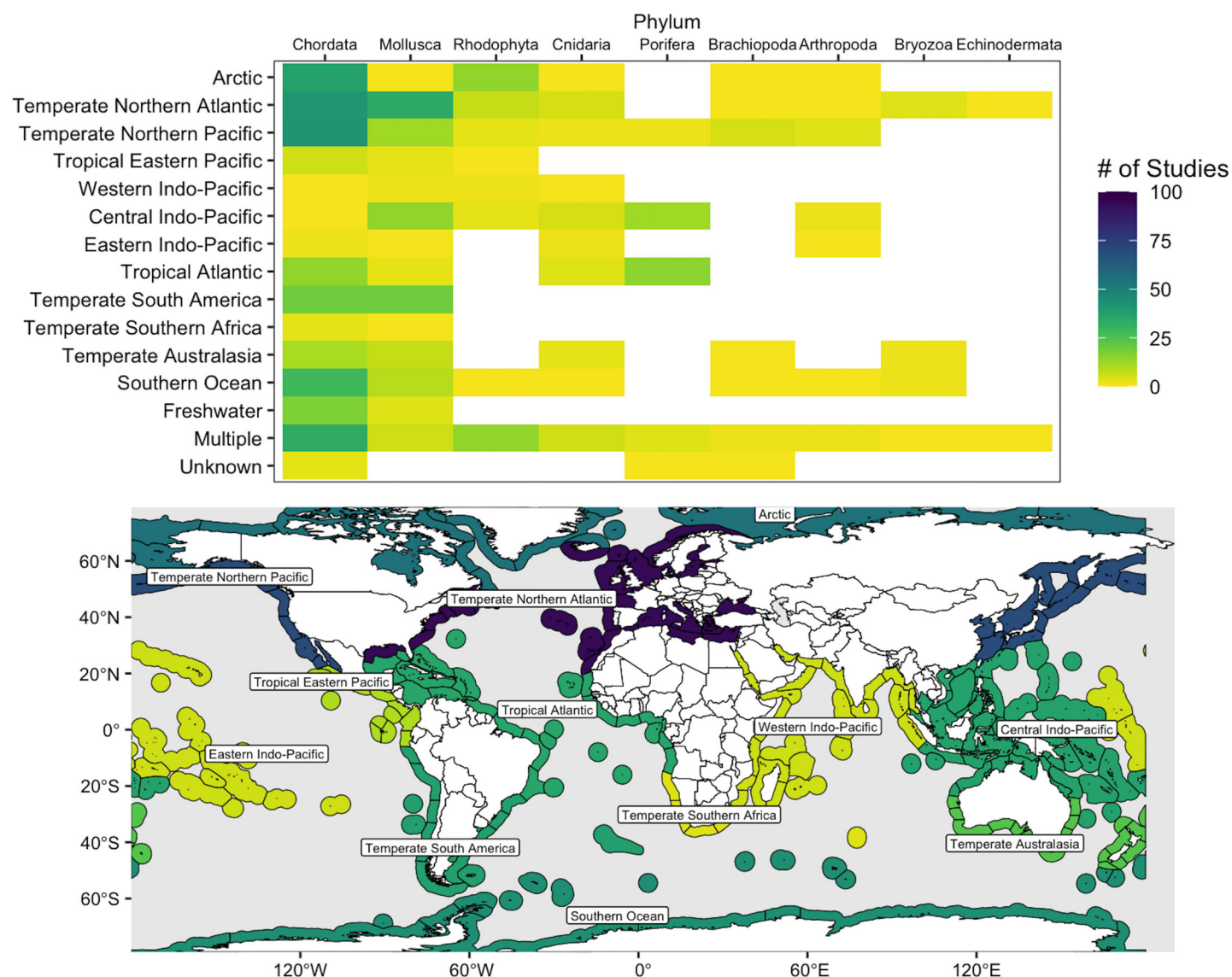


Fig. 3. Number of chemical sclerochronology studies by phyla associated with each marine eco-region or other grouping. Freshwater studies are simply classified as “freshwater” and are not associated with an eco-region. Some studies were global or represented multiple eco-regions; these were classified as “multiple.” Marine eco-regions are defined by Spalding et al. (2007) and are presented in the map. Colors in the map are also scaled quantitatively, representing the total number of studies per eco-region. Noting that studies on ray-finned fishes, bivalves, and hard corals are excluded from the analysis.

Using chemical sclerochronology to collect critical data and help address environmental challenges

Our review has revealed a wide diversity and breadth of research, as well as key areas of focus. Here we focus our discussion on how researchers have used these chemical datasets to address modern environmental and ecological challenges, drawing on six broad, inter-related categories derived from our literature review (Fig. 6).

Understanding modern environmental change and impacts

Understanding past environmental conditions is crucial for managing future change. Under-sampled taxa, such as

black and soft corals, gastropods, seals, brachiopods, sponges, and coralline algae have all been used to reconstruct past environments in recent time. For example, brachiopod records have revealed multi-decadal changes in sea surface temperature and CO₂ levels in the Subarctic and found the region was warming six times the global average (Brand et al. 2014), and soft coral and seal teeth records have revealed multi-decadal regime shifts in nutrient regimes and primary productivity in western North Atlantic and Barents Sea, respectively (Sherwood et al. 2011; de la Vega et al. 2022). Importantly, under-sampled taxa can help fill gaps where instrumental or proxy data from traditional sources are scarce (see “Collecting critical data from

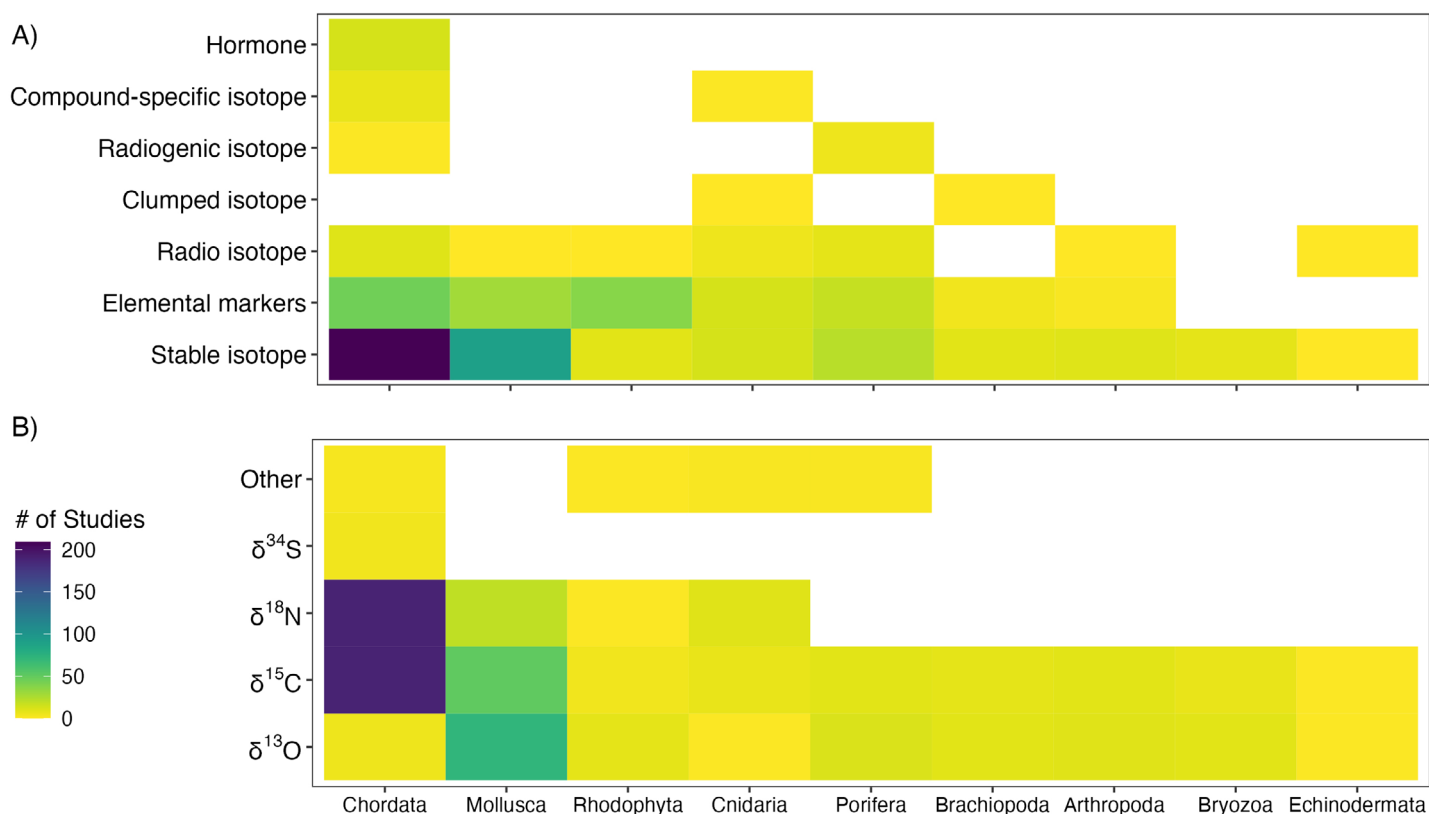


Fig. 4. Number of chemical sclerochronology studies by phyla associated with (A) different chemical marker categories and (B) specific stable isotope markers, with “other” representing six markers with only one or two studies each ($\delta^{11}\text{B}$, $\delta^{30}\text{Si}$, $\delta^2\text{H}$, $^3\text{He}/^4\text{He}$, $\delta^{44}/^{42}\text{Ca}$, and $^{88}\text{Sr}/^{86}\text{Sr}$). Studies were duplicated across categories if a study analyzed more than one chemical marker category or stable isotope. Noting that ray-finned fishes are excluded from Chordata, bivalves from Mollusca, and hard corals from Cnidaria.

inaccessible or poorly studied environments and time periods” section for a detailed discussion). Furthermore, by working with a range of under-sampled and traditional taxa, multi-taxa approaches can also be used to calibrate and verify proxy environmental records (Schöne et al. 2006).

While chemical sclerochronology has traditionally focused on reconstructing changes to the physical environment it can be an equally powerful tool for reconstructing biological change at a species, community, and ecosystem level. For example, isotope records have identified long-term, climate-driven shifts in the diets, migration patterns, distributions, and weaning age of apex species (York et al. 2008; Quillfeldt et al. 2010; Lowther et al. 2017; Matthews et al. 2021), which, in turn, can reveal regime shifts (i.e., a persistent change in ecosystem structure and function). Furthermore, by analyzing a range of taxa, community-level changes can be revealed, such as trophic dynamics, resource partitioning and niche segregation among sympatric species (Hobson et al. 2004; Botta et al. 2018).

Climate change remains a dominant theme in sclerochronology, but by sampling a broader range of taxa, sclerochronology can also be used to understand other facets of environmental change, such as the legacy of commercial

whaling (Buss et al. 2022), hydrological modification of rivers (Olden et al. 2019), impacts of aquaculture (Sepúlveda et al. 2015), and nutrient and metal pollution (see “Pollution monitoring and impacts” section).

Collecting critical data from inaccessible or poorly studied environments and time periods

Working with a range of taxa can improve our understanding of global environmental change by expanding our capacity to collect proxy environmental data where data are scarce or difficult to collect using traditional taxa. Coralline red algae is a striking example whereby an alternative taxon has been used to collect data from the high Arctic—one of the most rapidly warming regions in the world. While a key bivalve species, *Arctica islandica*, can also provide Arctic environmental records, *A. islandica* has a relatively habitat-limited distribution and optimal growth temperatures of 6–16°C, which has restricted its use as an archive for Arctic environmental conditions and motivated the search for more suitable archives (Halfar et al. 2000). In contrast, the coralline algae, *Clathromorphum compactum*, is abundant across Arctic and Subarctic habitats, can live for hundreds of years, and has

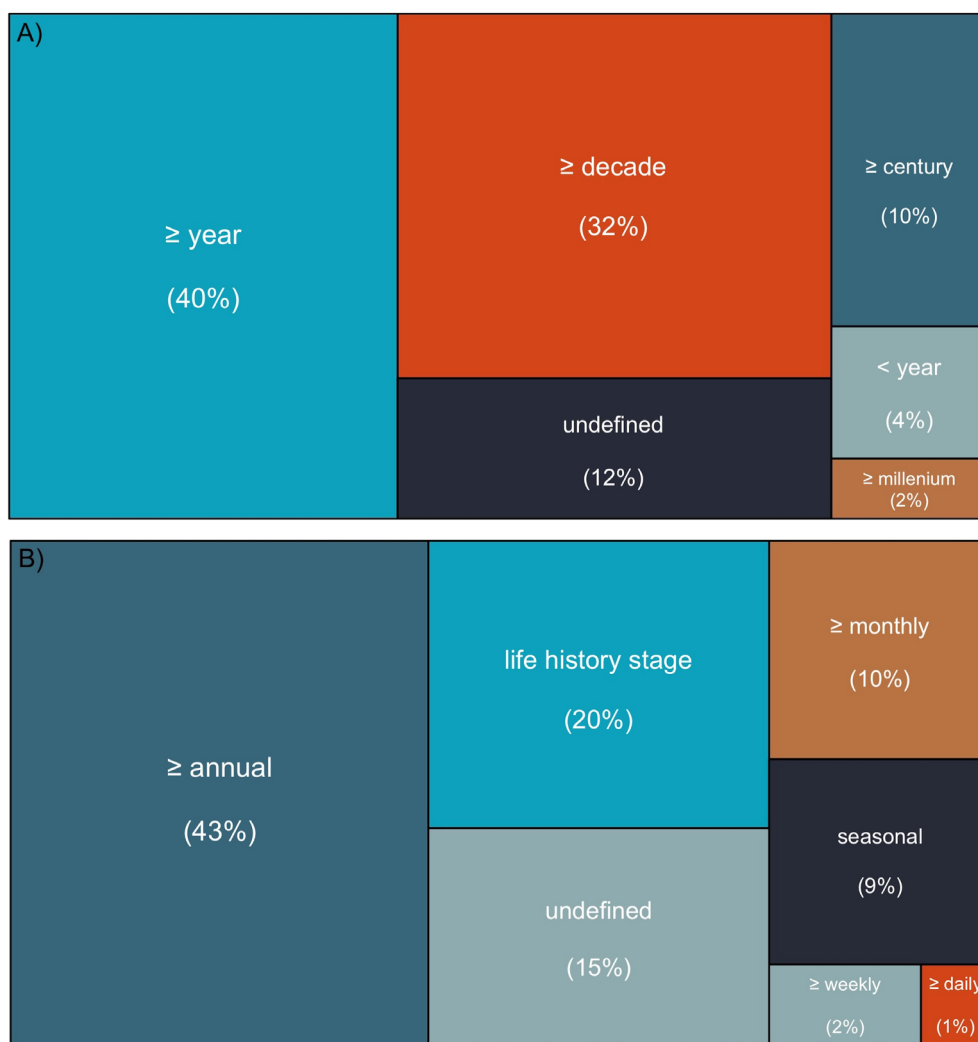


Fig. 5. Breakdown of chemical sclerochronology studies by (A) temporal breadth of datasets and (B) temporal resolution of datasets. A small number of studies were duplicated across categories if a study included datasets representing more than category. Life history stage refers to studies that specifically focus on analyzing chemical markers from different life histories stages (i.e., juvenile vs. adult). Undefined studies were largely associated with method development papers whereby temporal information is not critical, or studies that analyzed chemical markers along an ontogenetic growth axis, but periodicity of growth was not known or defined.

been found to grow through winter water temperatures as low as -1.8°C (Hetzinger et al. 2011; Halfar et al. 2013). Furthermore, as coralline algal growth and elemental uptake is highly dependent on environmental conditions including temperature and light availability, they are suitable for continuous, high-resolution geochemical sampling. To date, algal proxy-based reconstructions have provided continuous, annual data spanning centuries on preindustrial sea surface temperature (Williams et al. 2017), sea-ice cover (Halfar et al. 2013; Leclerc et al. 2022), glacial runoff (Hetzinger et al. 2021), and primary production (Hou et al. 2019).

There are numerous other examples of under-sampled taxa expanding paleoclimatic datasets. As highlighted in Fig. 1, photosynthetic hard corals are restricted to sunlit

tropical environments, and other sessile taxa like black corals, octocorals, and sclerosponges have a wider distributional range. Therefore, such taxa can provide data on colder, darker or deeper sea environments, such as biodiverse sea mounts and hydrothermal vents, mesophotic coral reefs, and submarine caves (Raimundo et al. 2013; Coppari et al. 2019; Asami et al. 2021). For example, one study suggested that soft corals are an untapped record of intermediate and deep ocean variability, due to the taxon's cosmopolitan distribution, depth range, and longevity (Kimball et al. 2014). Barnacles have also proved useful for collecting data from relatively inaccessible environments, such as under an Antarctic ice shelf (Burgess et al. 2010), as well as open-ocean environments as they can attach to mobile species or debris (e.g., oxygen isotopes in

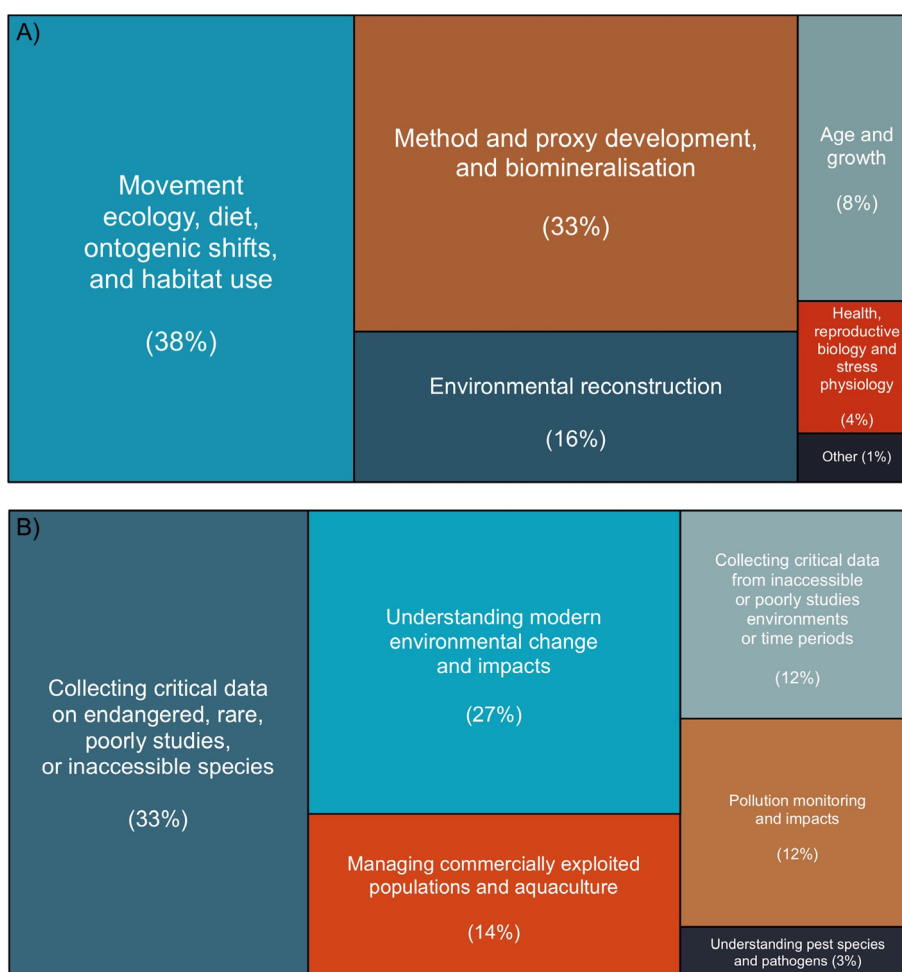


Fig. 6. Breakdown of chemical sclerochronology studies by (A) key research topics ($n = 519$ studies) and (B) environmental and ecological challenges (only if identified by authors, $n = 286$ studies). “Other” includes environmental forecasting, archaeology, and species identification.

turtle barnacles, Detjen et al. 2015). In a freshwater example, the gastropod species, *Radix*, is one of few aquatic taxa widely distributed on the Tibetan plateau, a region that influences global climate and the intensity of monsoon rains, which are critical to the livelihoods of billions of people (Taft et al. 2012). As such, research was conducted on the species to determine its suitability to reconstruct climatic and hydrologic variability in the region (Chen et al. 2016).

In addition, slow growing taxa like sclerosponges, black coral, and coralline algae, can help fill in temporal data gaps (Lazareth et al. 2000; Halfar et al. 2013; Wu et al. 2021). For example, one study suggested there are opportunities to expand shorter coral records with longer sclerosponge records to verify the stability of sea surface salinity over longer time-scales (Wu and Grottoli 2010). Another study also suggests that sclerosponge records provide a more complete view of century-scale, subsurface ocean dynamics in the tropics, relative to corals (Moore et al. 2000). The authors go on to state that while corals can be used, multi-centennial coral colonies

are rare below 15 m and dangerous to core at such depths. And, in an extreme example, research on the giant basal spicules of a deep-sea glass sponge suggested that the species could provide environmental data that span the entire Holocene (i.e., 10,000 yr) (Jochum et al. 2012). There are also more opportunities to target different temporal resolutions with different taxa. For example, corals are excellent long-term proxies of mean annual sea surface temperature in the tropics, but high-resolution, climate data in inter-tidal zones are lacking (Mau et al. 2021). As such, Mau et al. (2021) investigated the use of tropical, inter-tidal limpets to fill this data gap.

Pollution monitoring and impacts

Sclerochronology is particularly useful for collecting temporally explicit proxy data on environmental pollution, and subsequently, understanding how that pollution impacts the study organisms or the ecosystem more broadly. Again, under-sampled taxa can help fill gaps where data on pollution are lacking. For example, soft corals or octocorals are excellent

archives of nutrient pollution based on their unique composition. Unlike hard corals or other traditional calcareous organisms, soft corals are proteinaceous with a high nitrogen content. As such, they are excellent recorders of anthropogenic nutrient pollution, whereby nitrogen isotope profiles can be used to monitor the source and levels of nutrient pollution over time. Much of this research has been focused in the Caribbean (Baker et al. 2017); however, nutrient pollution profiles in soft corals have also been used to assess the impact of tourism in the Philippines (Wong et al. 2019) and Madagascar (Baker et al. 2013).

Our review also revealed that under-sampled taxa are excellent archives of metal pollution. For example, one study used seal teeth to examine long-term heavy metal contamination in Russia's Lake Baikal seals (Ozersky et al. 2017). The authors concluded that mercury contamination from atmospheric emissions in eastern Europe, was likely influencing the rapid changes to the lake's food webs. Furthermore, Schneider et al. (2015) found that growth rings in freshwater turtle scutes were useful for estimating mercury accumulation over time. In the marine realm, a range of vertebrate, invertebrate, and algal species have been used to monitor heavy metals including squid beaks (Queirós et al. 2020), whelk shells (Mayk et al. 2022), walrus teeth (Clark et al. 2021), rhodoliths (specifically associated with mining pollution) (Darrenougue et al. 2018), and sclerosponges (Lazareth et al. 2000). While well-known heavy metals, such as mercury and lead, dominate the literature, a recent study explored the use of penguin feathers to record trends in rare earth metals, which are now increasing in the environment due to the manufacture of smart phones, electric vehicles, and other products (Celis et al. 2023). Another novel study also looked at the level and sources of aluminum using marine mammal bones, which is increasing rapidly in the environment and may be harmful to marine species if it accumulates (Borrell et al. 2023).

Nutrients and metals aside, reptiles have also been used to monitor novel pollutants. One study analyzed uranium radio isotope contamination in turtle and tortoise scutes at nuclear sites and found that the scutes were valuable archives of nuclear activities (Conrad et al. 2023). A second study suggested that carbon isotopes in turtle scutes may be useful markers of oil spill exposure (Reich et al. 2017).

Collecting critical data on endangered, rare, poorly studied, or inaccessible species

A common theme throughout many studies was that sclerochronology is an ideal tool for collecting temporally explicit ecological data that would be otherwise too difficult or expensive to collect using other methods, such as tagging, visual observations, or stomach content analysis. This is particularly critical for species that live in largely inaccessible environments, such as the deep-sea, open-ocean, and polar regions. The dominance of chordates, as well as carbon and nitrogen isotope markers, in the review reflect the many

studies that were designed to fill critical data gaps on the migration patterns, foraging ecology, and habitat use of inaccessible and poorly understood vertebrate species (e.g., turtles, whales, dolphins, sharks, seabirds, sea lions, otters, and polar bears). Many of these species were also rare or endangered, highlighting the advantages of using accretionary structures as an opportunistic, and often non-lethal, and non-invasive data source. For example, chemical markers in the rostral teeth of a critically endangered sawfish were developed because conservation efforts are hampered by lack of data on critical habitats, and rostral archives are available in museums and research agencies worldwide (Hegg et al. 2021). An interesting suite of studies have also used hormone markers in whale baleen and seal whiskers to reconstruct species' reproductive biology and stress levels through time (Keogh et al. 2020; Lowe et al. 2021b), as well as physiological responses to stressors such as ship strikes or entanglement (Lysiak et al. 2018; Lowe et al. 2021a). Such data would be near impossible to collect by other means, and is made possible by analyzing organic, rather than traditional carbonate structures.

While the bulk of the studies on endangered or rare species are focused on charismatic vertebrates, sclerochronology is a useful tool for collecting data on invertebrates. Studies have used isotopes to understand the diet, age, and growth of long-lived, deep-sea cnidarians (black coral and sea pens), which not only provide critical habitat but are vulnerable to fishing and mining (Coppari et al. 2019; Marriott et al. 2020), as well as data on hydrothermal vent (Bojar et al. 2018) and high Antarctic shelf (Brey et al. 1998) communities. Furthermore, chemical sclerochronology has provided a wealth of data on cephalopods, including rarely encountered Antarctic and deep-sea species (Queirós et al. 2018). Such data can also be obtained opportunistically by analyzing cephalopod beaks collected from predator stomachs, rather than direct capture, which is difficult for many species.

Understanding pest species and pathogens

While sclerochronology is not traditionally used to study pest species, researchers have investigated whether trace element chemistry in lamprey statoliths (which are different in structure and mineralogy to teleost fish otoliths) can identify the natal origins and source of the parasitic sea lamprey, which has invaded the Great Lakes in the United States via shipping canals. For example, in one study, it was evident that a population of lampreys completed their life history within a tributary of the Great Lakes, indicating the population could be likely eradicated through control measures like lampricides and trapping (Johnson et al. 2016). Furthermore, stable isotope markers in feathers have been used to examine the impact of anthropogenic food sources on superabundant, yellow-legged gulls and develop measures to reduce their population size (Pedro et al. 2013; Ouled-Cheikh et al. 2021), as well as understanding the relationships between bird migrations and the spread of avian influenza (Chang et al. 2008).

Finally, chemical sclerochronology could help reduce interactions between potentially harmful species and people. In Australia and Hawaii, for example, element markers in jellyfish statoliths have been used to identify the movement ecology of the Irukandji and box jellyfish, two species that cause extremely painful and, sometimes, fatal stings (Mooney and Kingsford 2012; Morrissey et al. 2020).

Managing commercially exploited populations and aquaculture

For over a century, fish otoliths have underpinned fisheries science (Reis-Santos et al. 2023). However, accretionary structures from other taxa can be used for fishery applications, particularly to identify stock structure, natal grounds, dispersal, and migration, which is essential for the management of commercial populations. We found a range of structures used for such purposes including shark vertebrae (Magozzi et al. 2021), octopus stylets (Doubleday et al. 2008), squid statoliths (Li et al. 2023), and gastropod shells (Manríquez et al. 2012). Age data are also critical for managing commercial populations and chemical aging methods have been used to support the management of gastropods harvested for food, ornamental purposes, and the aquarium trade (Herbert et al. 2022, 2023), as well as assess the suitability of species for mariculture (Radermacher et al. 2009). Another example of chemical aging comes from one of the only two studies found for echinoderms. The authors used bomb radiocarbon and jaw ossicles to age commercially exploited red sea urchins in the Mediterranean. The radiocarbon data confirmed that the species lives for over 100 yr (Ebert and Southon 2003), which has implications for how the species is managed.

Lastly, in novel applications, isotope profiles in abalone shells have been investigated as a tool to identify the success of abalone culture and release programs (i.e., stock-enhancement), to counteract the impacts of overfishing and poaching (Lee et al. 2002); and, isotope profiles in sea lion whiskers have helped determine the impact of salmon aquaculture and non-native prey on the species' foraging ecology, as well as the impact the species has on the salmon industry (Sepúlveda et al. 2015).

Future directions, knowledge gaps, and opportunities

By harnessing taxa from across the tree of life, our review highlights how sclerochronology can be used to collect critical data on many species and environments and help tackle modern scientific challenges. Many of the sclerochronology studies we collated followed a well-established methodology and chemical marker profile that enabled the collection of data that would be otherwise impossible or difficult to collect by other means (e.g., using carbon and nitrogen stable isotopes to understand the foraging ecology of threatened species). The dominance of these established methods and markers, suggest their wide-ranging utility and ease of use, and could be readily deployed to expand our data collection needs.

In addition to these well-established applications, our review highlights areas of potential expansion, thereby increasing the number of environments and species we can monitor, and the type of data we can collect. For example, some studies highlighted the potential of sclerochronology to understand novel taxa such as sawfishes (Hegg et al. 2021) and rays (Feitosa et al. 2021), as well as assess impact of human activities that are not typically assessed using sclerochronological methods, such as tourism (Baker et al. 2013), oil spills (Reich et al. 2017), and invasive species (Johnson et al. 2016). There is also potential to develop chemical markers to monitor the impacts of emerging stressors, such as deep-sea mining, renewable energy infrastructure, increased use of rare earth metals, pharmaceuticals or persistent organic pollutants (Le Goff et al. 2019). While sessile taxa are largely used for environmental reconstruction and mobile taxa for ecological information, our review shows that the reverse can be applied. For example, chemical data can be used to understand the age, growth, and diet of vulnerable black corals (Coppari et al. 2019) and mobile species like seals can be excellent recorders of environmental change (de la Vega et al. 2022). While commonly studied accretionary structures, like pinniped whiskers, highlight their ease of use and usefulness, there are avenues to expand research on novel structures. For example, eye lenses and gladii are proving to be valuable new structures for targeted and opportunistic sclerochronological analysis in fish, sharks, and squid due to their protein-rich composition and accretionary growth (Li et al. 2017; Quaeck-Davies et al. 2018; Meath et al. 2019).

Our review highlights the future potential of novel chemical markers, such as the use of rare earth metals to track pollution (Celis et al. 2023), and calcium isotopes as markers of birth and weaning in mammals (Martin et al. 2023). Other little-used chemical markers also offer new avenues for exploration. For example, sulfur isotopes and radiogenic strontium isotopes are extensively applied to study fish and bird movements or foraging between freshwater and marine environments (Walther and Limburg 2012; Doubleday et al. 2018), but we found that these markers were rarely applied to other taxa. While underused chemical markers can be technically challenging and expensive to analyze, advances in analytical technology, like multi-collector ICPMS, are making them increasingly accessible (Martin et al. 2023). Furthermore, hormone markers may reveal the reproductive histories, health status, and stress physiology of many aquatic species beyond mammals. While research on hormone markers in other taxa is in its infancy, hormone profiles have been successfully obtained from fish opercula (Charapata et al. 2022) and, recently, cephalopod beaks (Durante et al. unpublished data). There also are opportunities to develop more common element markers for vertebrate species, given they are widely used for teleost fish and that they are relatively easy to analyze using established methods (i.e., laser ablation ICP-MS). For example, strontium and barium concentrations were successfully used to track movements in baleen whales (Vighi

et al. 2019) and determine the weaning age in walrus (Clark et al. 2020). Finally, our review highlights how more well-known markers can be used in a novel way, such as using radiocarbon to study the feeding ecology of humpback whales (Eisenmann et al. 2017) or Mg/Ca in coralline algae to track atmospheric wind patterns affecting sea ice movement, instead of just sea ice (Leclerc et al. 2024). There is also much scope to explore carbon isotopes as a proxy for metabolic rate in under-sampled taxa. Such proxies have been developed from fish otoliths (Martino et al. 2020; de Groot et al. 2024) and are beginning to be explored for other taxa such as cephalopods (Chung et al. 2021; Durante et al. 2024).

Lastly, one notable study, used sclerochronology not to reconstruct the past per se, but to predict the future. Specifically, they showed how noble gas records (helium isotopes) in black corals could be used to predict a submarine volcanic eruption, with potential future applications for eruption forecasting (Álvarez-Valero et al. 2018). While this is a niche application, perhaps there are other opportunities to use chemical sclerochronology to forecast other environmental events like extreme weather.

Ideally, extensive method development is first required to use new or lesser-known structures, taxa, and chemical markers, as well as develop novel applications. This can be achieved via controlled laboratory studies, field studies, or comparison to instrumental data. However, laboratory studies are impractical for some species and the lack of long-term or in-situ instrumental data to calibrate and verify the accuracy of chemical proxy data can hamper the development of proxy archives, such as coralline algae. In the accretionary structures of some under-sampled taxa, the periodicity of growth increments may need to be precisely verified so chemical data can be calibrated against absolute time. For accretionary structures with no apparent growth increments (e.g., sclerosponges, seal whiskers), growth rates can still be verified using methods such as radio isotope dating and chemical staining. Also, for biomineralized structures, etching and staining methods can enhance or reveal growth increments in a range of taxa (Schöne et al. 2005; Hegg et al. 2021). However, even if growth is not calibrated to absolute time, assigning chemical data to relative time (i.e., younger vs. older life history stages) is still useful in ecology and commonly used. Although we have focused on modern-day organisms and research questions in this review, preservation potential of different structures and materials is also an important point to consider when working with new or under-sampled structures. For example, echinoderm skeletons are renowned for their poor preservation and are readily altered post-mortem (Gorzalak et al. 2012). In contrast, Antarctic barnacles were identified as a suitable alternative taxon for environmental reconstruction as they secreted a low-Mg calcite shell that was robust to diagenesis (Burgess et al. 2010). Similarly, gorgonians (soft corals) have been identified as a useful environmental archive as their proteinaceous skeleton is resistant

to decomposition and diagenesis (Baker et al. 2010; Sherwood et al. 2011). Using a range of accretionary structures across the tree of life can also be advantageous. For example, for chemical markers with lower concentrations, larger accretionary structures, such as squid gladii or feathers, can be more useful than smaller structures, like statoliths, where there may be not enough sample material to undertake a chronological analysis. Furthermore, elemental concentrations can also vary considerably between different materials and organic and inorganic structures, thereby opening new avenues for analysis (e.g., proteinaceous materials have a high nitrogen content relative to structures largely composed of carbonate biominerals).

Concluding remarks

With increasing need to monitor, assess, and manage aquatic environments, taxa from across the tree of life can act as natural data loggers and collect proxy data on the ecology of species and physical environment. Traditional taxa aside, our review shows that we can collect ecological data from 18 taxonomic classes, as well as increase the spatial and temporal breadth of environmental datasets and the type of proxy data we collect. However, as emphasized by numerous method and proxy development studies collated in our review, validation and calibration are required alongside analytical development for accurate and successful interpretation and subsequent application of sclerochronological data. Chemical datasets are also not always clearly correlated to a single environmental or biological variable, and maybe influenced by a range of inter-related or unverified factors. As such, there is call to acknowledge this complexity when drawing conclusions, particularly for conservation and management applications (Christiansen et al. 2015). Despite some of these challenges, collecting data via sclerochronological records can be cost-effective, enabling the collection of data that would be otherwise impossible or unfeasible to collect. Expanding the spatial and temporal coverage of environmental and ecological records is necessary for accurate representation and successive data applications from modeling to policy. To this end, we encourage researchers to make the most of the many existing biological archives across the tree of life and take advantage of unexploited opportunities in ongoing sample collection programs.

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