

## SYNTHESIS

# Oyster shells as archives of present and past environmental variability and life history traits: A multi-disciplinary review of sclerochronology methods and applications

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### Scientific Significance Statement

Bivalve shell increments are widely used in ecology and archaeology to study growth rates and population dynamics, or past human population subsistence habits. Contrary to most bivalves, oyster shells do not exhibit clearly defined growth marks, and they are often disregarded in sclerochronological studies. This paper presents all methods to date that highlight morphological and compositional growth patterns in oyster shells and show how this information can be used in ecological, archaeological, palaeoenvironmental, and aquaculture contexts.

### Abstract

Oysters inhabit a variety of coastal and deep-sea settings over a wide latitudinal range and have a role as ecosystem engineers. They also represent an important food source for humans since hunter-gatherer times, which motivates interest in using oyster shells as environmental and life history archives. Still, oysters have often been disregarded in sclerochronology studies, although several methods based on both microtextural and geochemical approaches have successfully been investigated. We review how these methods have been used to improve

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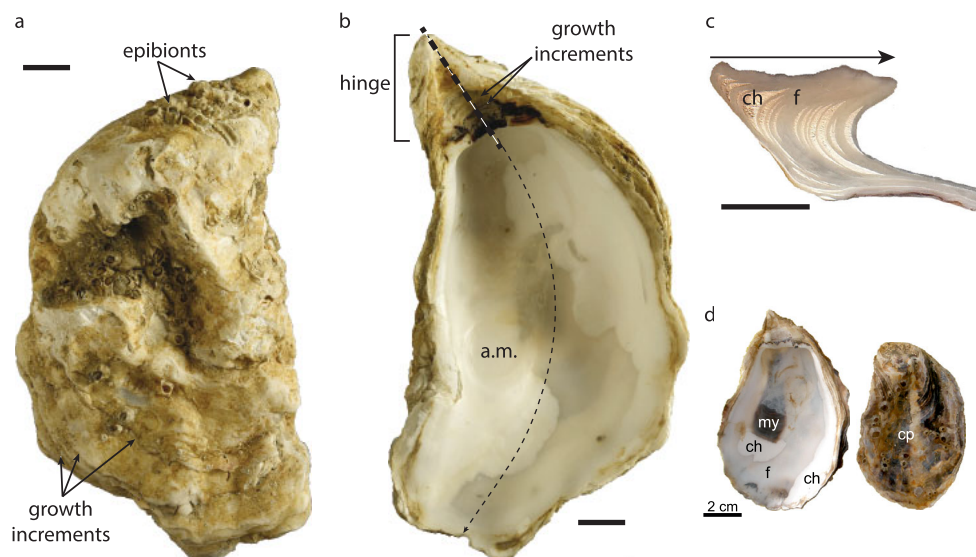
interpretations of shell records, and we identify knowledge gaps in a variety of disciplines. Those include ecology to study larval dispersal and growth rates; archaeology to determine shell midden constructions and site occupations; and palaeoenvironmental and palaeoclimate reconstructions from tidal to annual timescales. We also suggest standardizing sclerochronology procedures to improve palaeoenvironmental reconstructions and biophysical models on oyster larval dispersal.

Growth incremental analyses (sclerochronology) of mollusk shells can be used to gain a basic understanding of the animal's life span, growth rate, time of death, and general growth structure. The underlying principle is the sequential deposition of carbonate structures, easily visible on shell surfaces in most mollusk species (Hallmann et al. 2009; Schöne and Surge 2012), into individual increments whose size correspond to the same time unit and is linked to external and internal factors. However, oysters do not present the relevant growth increments on the surface, as their shell is brittle enough to easily break along these increments (Fig. 1a). This results in this group to be excluded from sclerochronological interpretation in a variety of disciplines, in favor of other bivalves like clams or mussels. However, several methods exist to determine the temporal calibration of oyster shells.

Most often, analysis is conducted in the hinge plate (e.g., Richardson et al. 1993; Fig. 1b), a denser area gathering all shell increments, but some studies analyzed growth lines in cross section of the adductor muscle scar area (e.g., Arkhipkin et al. 2017). A significant correlation has been reported between shell length and hinge length for *Magallana*

*gigas* (Lartaud, de Rafelis, et al. 2010), enabling measurements on the hinge area, which generally presents less damage and no contaminating sediment between increments (Fig. 1).

As part of the special issue “Expanding the Horizons of Sclerochronology: New Perspectives for Life History and Environmental Monitoring,” this manuscript aims to highlight the usefulness of oyster sclerochronology—rarely applied to its full potential—in a variety of disciplines. We first expose the knowledge gaps and uncertainties of applications of oyster sclerochronology in the fields of (palaeo-)environmental and climate reconstruction, archaeology, ecology, fisheries, traceability, and chronobiology. We then present the crystallographic evidence that allows for the formation of incremental structures, before listing the existing methods for oyster sclerochronology. The common name “oyster” is a polyphyletic group comprising the “true oysters,” namely Ostreidae, as well as Gryphaeidae (e.g., deep-sea oysters and numerous extinct species in the fossil record) and other Pteriomorpha such as Pteriidae (pearl oysters) and Spondylidae. This study introduces available oyster sclerochronology studies, focusing on information on Ostreidae and Gryphaeidae. Ostreidae are economically important and palaeoenvironmental studies



**Fig. 1.** *Magallana gigas* shell. **(a and b)** Left valve of an oyster shell (a: external view; b: internal view) showing the section plane direction to expose the umbo. The dashed line (on b) represents the growth direction. The position of the adductor muscle scar (a.m.) is indicated. Scale bar is 1 cm. **(c)** Section of the umbo following direction in b, exhibiting dense foliated (f; slightly translucent) and porous chalky (ch; milky white) calcite. The arrow indicates the growth direction. Scale bar is 1 cm. **(d)** Other *M. gigas* individual exhibiting pigmented myostracum (my). Note irregular distribution of the chalk (ch) and foliated layers (f). The dark coloration of the exterior of the right valve is due to the columnar prismatic layer (cp).

have often referred to both Ostreidae and Gryphaeidae as “oysters” because similarities in their shell structure caused them to be treated in similar ways and taxonomy may be unclear for some species. We decided to discard pearl oysters and Spondylidae from this synthesis, as they have for most disciplines a relatively low impact compared to Ostreidae and Gryphaeidae and are not part of Ostreoidea.

## Part 1: Applications of oyster sclerochronology

### Paleoenvironmental and paleoclimate reconstructions

Oyster shells are among the most stable archives of short-term climate and environmental variability because their shells consist predominantly of low-magnesium calcite (Brand and Veizer 1980). Nevertheless, screening protocols based on elemental composition or microscopy remain essential to assess the preservation of original shell material, preventing biased reconstructions (Ullmann and Korte 2015).

### Spatiotemporal coverage

Oysters are particularly common in the fossil record, with early members of Ostreidae appearing in Europe in the Middle Triassic and close ancestors found during the Late Permian in Oregon (USA), Japan, and China (Márquez-Aliaga et al. 2005). Jurassic oysters spread from the circum-Arctic to the equator during the Mesozoic Revolution (Harper and Skelton 1993; Li et al. 2021). Their fossils record variability in Mesozoic seasonality and climate over time and space (Alberti et al. 2017; Brigaud et al. 2008; Korte et al. 2009; Petersen et al. 2016). The opening of the North Atlantic Ocean in the mid-Cretaceous allowed oysters to colonize the margins of the Atlantic, Tethys, and later Indian Ocean, where thick-shelled taxa (e.g., *Crassostrea*, *Ostrea*, and *Pycnodonte*) record Cretaceous to early Cenozoic hothouse climates (e.g., de Winter et al. 2018; de Winter, Dämmer, et al. 2021; de Winter, Müller, et al. 2021; Jones, Petersen, and Curley 2022). Since then, oysters spread to shallow marine waters from the Arctic to southern South America with common occurrences throughout the Cenozoic (Bougeois et al. 2018; Huyghe et al. 2015; Li et al. 2021).

### Environmental parameters

Geochemical analysis of oyster shells yields information about past climate, most notably seasonal variations in (paleo) temperature. The oxygen isotope ratio ( $\delta^{18}\text{O}$ ) of a shell increment can be mathematically linked to seawater temperature at the time of formation of that increment. However, the seawater  $\delta^{18}\text{O}$  ( $\delta^{18}\text{O}_w$ ) also impacts the shell  $\delta^{18}\text{O}$  and is challenging to assess in palaeoenvironmental contexts. Most studies either from Ostreidae (Harzhauser et al. 2011, 2016; Huyghe et al. 2012, 2015) or Gryphaeidae (Brigaud et al. 2008; Mettam et al. 2014) have used  $\delta^{18}\text{O}$  analyses for temperature reconstructions, constraining the  $\delta^{18}\text{O}_w$  from other independent proxies. Other works used elemental measurements as paleothermometers (Mg/Ca, Mn/Ca) to circumvent the dependence

on  $\delta^{18}\text{O}_w$  (Bougeois et al. 2014, 2016). More recently, clumped isotope ( $\Delta_{47}$ ) analyses were successfully applied to oyster shells (including *Pycnodonte*) to reconstruct past seawater temperatures (Briard et al. 2020; de Winter et al. 2018; de Winter, Müller, et al. 2021; Ghosh et al. 2018).

Recent studies promote the combination of different proxies for the reconstruction of both paleotemperature and paleosalinity in the living environment (Bougeois et al. 2014; Briard et al. 2020). The combination of  $\delta^{18}\text{O}$  measurements with strictly temperature-dependent proxies (e.g., Mg/Ca,  $\Delta_{47}$ ) provides information on  $\delta^{18}\text{O}_w$ , which relates to the amount of global ice volume and the local evaporation/precipitation balance. Combined with estimates of global ice volume, these coupled measurements allow seasonal scale reconstructions of (paleo)salinity (Bougeois et al. 2014; Briard et al. 2020; de Winter et al. 2018; Ghosh et al. 2018). Indirectly, the combination of  $\delta^{18}\text{O}$  and  $\Delta_{47}$  proxies has also been used to constrain rainfall in India during the Cretaceous (Ghosh et al. 2018).

### Resolution

Oyster shells record high-resolution paleoclimate variability that is not recorded in other geological archives (e.g., foraminifera and sediment cores). The seasonal range, a temporal frame mostly inaccessible in the fossil record but essential in the climate system (IPCC 2007), has been widely studied (Bougeois et al. 2018; Brigaud et al. 2008; Harzhauser et al. 2011; Huyghe et al. 2015).

Beyond the seasonal scale, cathodoluminescence (CL) images of *Crassostrea aginensis* from the early Miocene and *Ostrea bellovacina* from the late Paleocene reveal intra-seasonal growth structures (Lartaud et al. 2006). Through comparison with modern specimens, these growth units could be related to lunar, semi-lunar, or shorter growth rhythms (Huyghe et al. 2019). de Winter, Ullmann, et al. (2020) identified circadian rhythms in the shells of Cretaceous *Rastellum diluvianum*. High-resolution growth increments may fill the gap in reconstructions between climate and weather (e.g., cyclones, storms, cold surges). Oyster shells thus record past meteorological events in addition to triadacnids and rudists (de Winter, Goderis, et al. 2020; Yan et al. 2020). Such fine temporal scale is made possible by relatively high growth rates in certain species, both for the total shell length (e.g.,  $> 10 \text{ cm yr}^{-1}$  for *Crassostrea gigantissima* from Oligocene and *Crassostrea titan* from the Miocene; Kirby 2000, 2001) and in the umbo area (e.g.,  $> 8 \text{ cm yr}^{-1}$  for *C. gigantissima*, Oligocene,  $> 4 \text{ cm yr}^{-1}$  for *Magallana gryphoides*, middle Miocene and  $> 2 \text{ cm yr}^{-1}$  for *Crassostrea virginica*, Pleistocene; Durham et al. 2017; Harzhauser et al. 2011; Kirby 2000). Beside *Neopycnodonte zibrowii* reaching  $> 500 \text{ yr}$  old in submarine canyon ecosystems (Wisshak, López Correa, et al. 2009), oysters do not tend to be long-lived. Some fossil species exceed several decades, such as *O. bellovacina* and *C. titan* (Kirby 2001; Lartaud et al. 2006), providing reliable paleoenvironmental reconstructions over decadal time-scales.

### Outlook

Future paleoclimate studies could leverage these developments in the accuracy and precision of sclerochronological reconstructions in two key directions. First, using fossil oyster shells to reconstruct accurate seasonal temperature ranges in dissimilar climate periods will illuminate the response of seasonality to climate change. Second, using detailed sclerochronological studies will enhance the resolution of climate reconstructions to the daily or even weather scale. Also, a combined approach using geochemistry and sclerochronology may shed light on the temperature tolerance of extinct species.

### Archaeology applications

Oyster shells are common mollusk remains in coastal archaeological sites in many locales (see reviews in: Andrus 2012; Colonese et al. 2011; Gutiérrez-Zugasti et al. 2011; Habu et al. 2011; Winder 2017). Archaeologists employ sclerochronology primarily to address questions related to the season of capture and detect past climate and environmental change. Emerging techniques focus also on determining provenance, assessing catchment area, evaluating resource management strategies, and reconstructing site formation processes.

Season of capture (i.e., timing of death) determination using growth increment analysis and/or  $\delta^{18}\text{O}$  profiles is frequently applied to archaeological mollusk shells (West, Burchell, and Andrus 2018). As later described here (see Parts 2 and 3), visual incremental analysis of oyster shells for age and growth studies is limited by complex shell architecture and irregular periodicity of growth structures. Therefore, few archaeologists conduct such analyses, with notable exceptions such as *Ostrea edulis* in England and Denmark where seasonal growth increments were noted (Milner 2013; Robson et al. 2021). In most other regions, such as Atlantic North America where *C. virginica* is the most common species found in archaeological sites, no broadly reliable incremental interpretation for season of capture has been identified (e.g., Andrus and Crowe 2000; Kent 1989; Surge, Lohmann, and Dettman 2001). Age and growth data may be interpreted (see Part 3) in some cases using ligamental increments (Milner 2013) and foliated layers (Savarese et al. 2016) but with limited success. Therefore,  $\delta^{18}\text{O}$  profiles are the most widely applied age and season of capture method. Season of capture results can be interpreted further to infer site occupation patterns, subsistence strategies, and ritual activity (e.g., An and Lee 2015; Blitz, Andrus, and Downs 2014; Colclasure, Andrus, and Blair 2023; Hadden et al. 2022; Thompson and Andrus 2013).

Recently, oyster sclerochemistry proved useful in determining site formation processes. For example, Mouchi, Emmanuel, et al. (2020) analyzed oxygen and carbon isotope profiles in shells grown on amphora fragments found beneath a riverbed in France. Estimated salinity indicated they grew in a marine environment, implying the site had originally been farther away from the river output. A similar situation occurred in Florida, USA where oysters were found growing

on human bone eroding from the Gulf of Mexico sea floor. Oxygen isotope profiles were interpreted to estimate salinity, documenting how sea level rise inundated what had been a freshwater mortuary pond (Price 2023).

Salinity of the habitats from which ancient oysters were collected can be estimated, which in turn may give insight into the distances people traveled to collect food. The technique was first proposed in the southeastern USA using  $\delta^{18}\text{O}$  profiles in *C. virginica* (Andrus and Thompson 2012) and has since been applied to a great extent there, resulting in regional synthesis papers (e.g., Garland et al. 2022). The rationale is based on seasonal cycles in  $\delta^{18}\text{O}$  oscillating around mean values that vary along estuarine salinity gradients. A related application is to infer trade networks. This has been accomplished using elemental fingerprinting in *O. edulis* to detect the origin of oysters excavated in Lyon, France (Mouchi et al. 2021; see “Provenance” section). Similarly, sequential Mg/Ca coupled with stable carbon and oxygen isotope data has been used to infer the existence of multiple Mediterranean collection localities (Mouchi et al. 2018). Oyster sclerochronology may reveal certain paleoenvironmental and paleoclimate conditions. A major challenge of this approach is that many oyster taxa are estuarine, thus past  $\delta^{18}\text{O}_w$  values were likely variable and unknown, precluding calculation of paleotemperatures. An exception includes limited *Ostrea angasi*-based temperature estimates from Southeast Australia (Tynan, Opdyke, Dutton, et al. 2017). Most oyster paleoclimate research instead focuses on estimating past salinity and relating it to precipitation variation and/or sea level flux (e.g., Garland et al. 2022; Harding et al. 2010).

Conservation paleobiology research using archaeological oysters relies on a number of measurements, such as shell size and morphology, but often includes sclerochronology to assess harvest age and sometimes habitat conditions including overharvesting (Hesterberg et al. 2020; Milner 2013; Savarese et al. 2016). In turn, such data can contribute to large-scale syntheses. For example, oyster data from multiple sites on the east coast of the USA suggest active oyster management by prehistoric Native Americans (Thompson et al. 2020). A synthesis of indigenous oyster harvest data in North America and Australia relied in part on sclerochronology research, arguing that stewardship by ancient peoples should inform current practice (Reeder-Myers et al. 2022).

Emerging applications of oyster sclerochronology in archaeology include expanding the spatial and temporal scale of established techniques, such as large-scale conservation paleobiology studies to establish pre-industrial baseline population demographics (e.g., Reeder-Myers et al. 2022) and creating regional syntheses of season of capture and subsistence strategies (e.g., Garland et al. 2022). To accomplish this, new low-cost, high-throughput techniques will be of broad benefit. Thus, fundamental validation of methods to permit visual or simple chemical assessment of shell growth in multiple oyster taxa would be valuable.



## Ecology

### Life span and growth rates

Although reading growth lines on the oyster shell surface is difficult (Fig. 1a), sclerochronological methods on the umbo can provide an efficient assessment of oyster growth dynamics and estimation of their life span. A majority of extant oysters are considered relatively short-lived, as their life span rarely exceeds a decade (see Moss et al. 2016). However, it was reported that although modern *C. virginica* from Chesapeake Bay (USA) generally live up to 5 yr, their Pleistocene counterparts from the same region could live up to 21 yr (Lockwood and Mann 2019). Size-selection overharvesting is advanced as the cause for the decreased life span and abundance, significantly reducing ecosystem services. Finally, the life span and growth rates of *Gryphaea* were assessed along Jurassic sequences to study heterochrony (D. S. Jones and Gould 1999).

Oxygen isotope analysis has been successfully applied for evaluating the growth rate and life span of several oyster species (e.g., Doldan et al. 2018; D. H. Goodwin, Gillikin, and Roopnarine 2013; Zimmt et al. 2019). Cyclic patterns of  $\delta^{18}\text{O}$  were used on *M. gigas* shells of invasive populations in southern San Francisco Bay to estimate the year of the invasion and the number of larval cohorts per year in the area (D. H. Goodwin, Cohen, and Roopnarine 2010). Durham et al. (2017) determined the lifespans and growth rates of modern and fossil *C. virginica* and *M. gigas* through Mg/Ca ratios. The spatial imagery of Mn distribution, observed under CL microscope, was revealed as a powerful tool for both estimating life span and growth rates of oyster species, including for high-resolution changes, such as in *Ostrea puelchana* and *M. gigas* (Doldan et al. 2018; Huyghe et al. 2019). Cathodoluminescence was used to determine the ontogenic age of wild *M. gigas* in France and the Netherlands to study the reproduction output and potential further colonization in the North (Cardoso et al. 2007). Finally, for long-living species, such as deep-sea oyster *N. zibrowii* (> 500 yr; Wisshak, Neumann, et al. 2009), radiocarbon analysis is required to provide insight into life span as in these ecosystems the seasonal trend is classically reduced or absent.

Growth rates were estimated for a variety of species. Oysters present growth cessation or at least reductions during cold months (*C. virginica* below 10°C: Kirby, Soniat, and Spero 1998; *M. gigas*, confirmed growth increments as low as 6°C: Lartaud, de Rafelis, et al. 2010) and/or above a certain temperature (*C. virginica*: Surge, Lohmann, and Dettman 2001; *Saccostrea cucullata*: Arkhipkin et al. 2017). There is evidence that oysters reach their maximum heat tolerance while being exposed during low tides. This tends to indicate that shell growth stops are controlled by temperature tolerance for each species.

Changes in the incorporation of carbon sources and metabolic and kinetic effects can be inferred with the estimation of metabolic carbon in shells by  $\delta^{13}\text{C}$  analyses. This was applied to track changes in the food supply in modern and fossil adult oyster shells (Harzhauser et al. 2011;

Lartaud, Emmanuel, de Rafelis, Pouvreau, and Renard 2010; Surge, Lohmann, and Goodfriend 2003) and also in larval specimens (Waldbusser et al. 2013).

### Planktonic larval duration

Contrary to juveniles and adults, the oyster larvae exhibit growth increments on the shell surface. The sclerochronology of larval shells can provide valuable information on the dispersal history of individuals, in particular the determination of the planktonic larval duration (PLD), which is used by all biophysical models to infer the trajectory and distance traveled by larvae and study connectivity (Swearer, Trembl, and Shima 2019). Currently, calibration of larval sclerochronology has been performed on two oyster species (*O. edulis*: Millar 1968; *C. virginica*: Miller et al. 2020), although larval shell increments were also observed without temporal calibration on *Ostrea lutaria* and *Ostrea chilensis* (Millar 1968). Still, most models only use PLD estimations without appropriate constraints (e.g., *C. virginica*: J. D. Goodwin et al. 2019; Powers et al. 2023; *Ostrea lurida*: Lawlor and Arellano 2020). The accuracy of dispersal modeling would largely benefit from PLD inferred from (low-cost) larval sclerochronology on juvenile specimens collected over the region of interest.

An interesting approach would involve using backward biophysical models (Briones-Fourzan, Candela, and Lozano-Álvarez 2008; Calò et al. 2018), used to back-tracking the dispersal of larvae and identify the geographic origin of migrants, with the exact PLD of specimens collected on each site of interest. That approach could also be used consecutively on the same site, if different PLDs were measured from different specimens on that same site, to identify the various source locations. This has never been attempted so far.

Another possible avenue for future research on larval dispersal would involve high-resolution elemental fingerprinting (see “Provenance” section) over a transect following larval shell growth from collected juveniles. This approach would theoretically provide information on the water masses crossed by the larva during dispersal, in particular the identification of riverine influence and the associated watershed. This information may be compared to dispersal trajectories reconstructed from biophysical models. The sampling resolution of this work would require cutting-edge analytical equipment, such as synchrotron light or high-precision femtosecond LA-ICP-MS to avoid overheating and destroying substantial parts of the larval shell before the desired information can be obtained.

### Fisheries and aquaculture

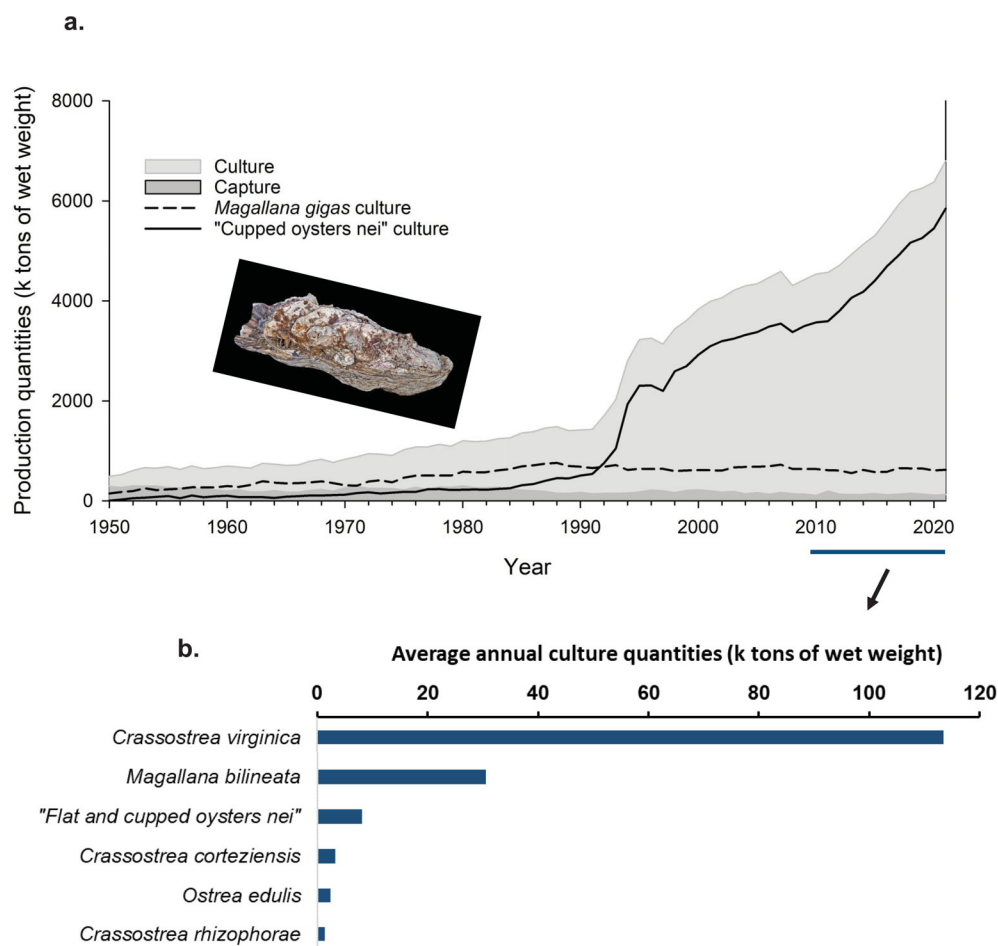
Bivalves represent an important food source for the growing human population and oysters are considered one of the most valuable taxa, both in terms of their quantity as well as quality (FAO 2022). Oyster aquaculture has a long tradition, and through past centuries and decades, it increased in production quantities as well as diversified with respect to species and geographic locations (Botta et al. 2020, and references within).

The importance of aquaculture, in relation to capture of wild oysters (fisheries) is clearly visible from low capture quantities—as during 2010s, oyster fisheries constituted less than 3% of total oyster quantities (Fig. 2a).

On the global scale, bivalve fishery and aquaculture are still dominated by very few species, and the most important ones, in terms of production quantities, are *C. virginica* and *M. gigas* (see Fig. 2b). Since the late 1980s, a pronounced decrease in the contribution of *M. gigas* in total oyster aquaculture is coupled with an increase in the production of the FAO category “Cupped oyster nei.” This is a consequence of the pronounced increase in oyster aquaculture in China and changes in data collection, where the category “Cupped oyster nei” most likely dominantly represents the culture of *M. gigas*. Other commercially important species from the family Ostreidae, include *Crassostrea rhizophorae*, *Magallana bilineata*, *O. chilensis*, *O. edulis*, and *O. lurida*.

Bivalve aquaculture has a large potential for expansion, in more environmentally friendly and sustainable way than for

example fish or crustacean aquaculture, and there is a great potential for interdisciplinary researchers and industry to work together (Willer, Nicholls, and Aldridge 2021). Offshore wind farms have been suggested potential locations for oyster restoration, and it has been suggested that further interdisciplinary research is needed to assess conservation and commercial potential of combining oyster restoration and oyster culture at such locations (Kamermans et al. 2018). The need for interdisciplinary research is also driven by anthropogenic climate change, especially in relatively shallow coastal areas where both bivalve fishery and aquaculture activities usually take place. Both regional and global environmental stressors have been identified as threats for oysters, such as algal blooms, floods, diseases, ocean acidification, and rising seawater temperatures (Neokye, Wang, Thakur, Quijón, et al. 2024; Neokye, Wang, Thakur, Quijón, et al. 2024). Sclerochronology research has a great potential to contribute to sustainable management, as well as further development, of oyster aquaculture. Previous studies have clearly demonstrated that  $\delta^{18}\text{O}$



**Fig. 2.** (a) Statistics on oyster capture and culture. (b) The annual production average contribution of other oyster taxa and categories to aquaculture in 2010–2020 period. Average annual contribution of *Ostrea chilensis*, *Crassostrea gasar*, *Ostrea lurida* and *Saccostrea cucullata* was less than 0.1 k tons in total. Data extracted from FAO statistics database ([www.fao.org/fishery/statistics-query/en](http://www.fao.org/fishery/statistics-query/en)).

is a powerful tool for reconstructing the seasonality of shell growth (e.g., Lartaud, Emmanuel, et al. 2010).  $\delta^{15}\text{N}$  analysis in shell carbonate material (e.g., Darrow et al. 2017) can provide an important insight into environmental conditions and can assist with habitat selection. Sclerochronology also helped select new potential sites of interest for farming *S. cucullata* in Madagascar (Andrisoa et al. 2024).

Furthermore, shell appearance was recently recognized as a commercially important trait, and the enhancement of shell shape is considered one of the traits adding competitive advantage to reared oysters (Mizuta and Wikfors 2019). Knowledge gained through sclerochronology research, on biomineralization and shell deposition process (e.g., Banker and Sumner 2020), can potentially contribute to the enhancement of shell shape. Sclerochronology research can also contribute to oyster reef restoration efforts, which are being expanded in different parts of the world (e.g., Smith, Cheng, and Castorani 2023).

### Provenance determination and traceability

Oyster shells can provide some indication of their geography, that is, where they lived. This information can be particularly important in archaeology to identify trade routes (Bardot-Cambot 2014; Chaufourier, Busson, and Dupont 2015), in ecology to determine the birth locality of recruits (Carson 2010), or in food control to check the correct label of aquaculture products. Several geochemical methods have been investigated to fulfill this goal, in order to determine “signatures” or “fingerprints” specific to a locality to use as references for samples of unknown origin, and reconstruct potential transfers along growth. This specific chemistry is governed by complex physicochemical and biological processes, based on the chemical composition of riverine water-carrying weathering products of the watershed. In the absence of close river output, oyster shells get their fingerprint from the seawater body (Mouchi et al. 2021).

Most data reported in the archaeology literature on provenancing shell remains from geochemical measurements consist of  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  measurements, but not on oysters (on *Spondylus*: Bajnóczi et al. 2013; Shackleton and Renfrew 1970; on *Olivella biplicata*: Eerkens et al. 2005). These isotope ratios however are driven by environmental parameters (Lartaud, Emmanuel, de Rafelis, Pouvreau, and Renard 2010; Lartaud, Emmanuel, et al. 2010), and not geography. Therefore, several distant localities with similar environmental settings would present similar oxygen and carbon isotope signatures, which increases the error on provenancing a specimen. This method should therefore only be used when region of provenance is already known, and precise locality (based on the type of environment, i.e., lagoon, bay ...) is the target (Mouchi, Emmanuel, et al. 2020). Another aspect not always considered is the sampling strategy: a strong seasonal influence is expected, and measurements performed on summer and winter parts of a shell will have very distinct signatures (Lartaud, Emmanuel, et al. 2010).

A promising method for provenance uses strontium isotope ratios. This method has been widely used on continental biominerals (Bentley 2006) but marine organism remains have been poorly studied in that regard. El Meknassi et al. (2018) noted significant differences in localities of several oyster species (*Pycnodonte* sp., *M. gigas*, *Saccostrea* af. *cucullata*, *Ostrea* sp., *Crassostrea* sp.) living in coastal settings with continental input from rivers or groundwater springs. No study so far reported oyster shell Sr isotope data in archaeological or ecological contexts.

The last method currently investigated gathers multiple elemental concentrations instead of isotope ratios. By combining several measured elements, the accuracy for determining an “elemental fingerprint” increases (i.e., the uncertainty between distinct groups of specimens is reduced or removed entirely). This method was successfully used to differentiate multiple groups of modern and archaeological oyster shells from France and identify a Mediterranean origin for a group of shells found at Lyon (200 km from the nearest shore; Mouchi et al. 2021). Distinct fingerprints were however reported between *M. gigas* and *O. edulis* from the same localities (Mouchi et al. 2021; Mouchi, Godbillot, et al. 2020) and additional data are required to study the impact of phylogeny on this approach.

### The role of chronobiology on biomineralization—oysters as a perfect model?

The drivers that trigger incremental growth during shell mineralization are still under debate. The direct role of environmental parameters is opposed to endogenous time-keeping mechanisms, called biological clocks. In sclerochronology, the clock hypothesis was introduced by Richardson, Crisp, and Runham (1980), based on the observation of the maintenance of semi-daily increments in the shell of *Cerastoderma edule* when transferred to a laboratory under constant immersed conditions. The clock is set and reset by environmental cues called zeitgebers (such as photoperiod, temperature, food), and can be self-regulated to keep oscillations under constant conditions. A review from Louis, Besseau, and Lartaud (2022) highlighted how clock genes could create rhythmic biomineralization of bivalve shells. Tidal and synodic patterns have been described in the shell increments of *M. gigas* (Huyghe et al. 2019) and in its valve activity (Tran et al. 2011), suggesting a possible relationship between these two physiological features. Interestingly, valve activity is described as a typical output of biological clocks in bivalves, and particularly for oysters. The molecular clockwork system has been well studied in *M. gigas*, showing that circadian clock genes can run at tidal frequency and drive valve activity at the same rhythm (Tran et al. 2020). Although to date, no direct relationship between clock behavioral outputs, such as valve activity, and shell biomineralization has been described, oysters can be serious candidates to fill this knowledge gap. Observations of various growth rhythms from a single species (i.e., *M. gigas*), with daily increments in shells from the

Mediterranean lagoon characterized by reduced tidal regime (Langlet et al. 2006), and tidal increments in shells from the English Channel exposed to high tide range (Huyghe et al. 2019), suggest that biomineralization might be controlled by the strongest clock driver present in the area.

## Part 2: Oyster shell formation and mineralization

Oysters, like scallops, are exceptional among bivalves in their predominantly low-Mg calcite mineralogy. Aragonite is restricted to myostracal areas (i.e., areas where the muscles attach to the shell, characterized by a special prismatic microstructure, the myostracum) and fibers within the ligament (Dungan 2008; Fig. 1d).

Shell formation starts with the formation of a thin periostracum within the periostracal groove, that is, the sulcus between the outer and middle lobes of the mantle margin (Carriker, Palmer, and Prezant 1981). At the mantle edge, the periostracum reflects back and shell calcification begins underneath (Fig. 3a).

### Microstructures

Oyster shells are made of layers with different microstructures, defined by particular sizes, morphologies, three-dimensional distributions, and modes of interlinkage of grains and, sometimes, associated organic matrices. Oysters secrete four calcitic microstructures: columnar prismatic, foliated, chalk (Ostreidae), and vesicular (Gryphaeidae) (see descriptions below), plus the aragonitic myostracum. The foliated microstructure is made of long and thin (300–500 nm thick) laths with arrowhead endings, arranged in planes, at a low angle to the growth surface (Taylor et al. 1969; Fig. 3b). Laths form bundles with changing orientations (Fig. 3c).

Columnar prisms form external columnar prismatic layers, which are thicker on the right valve. They extend at a high angle to the shell surface, have polygonal cross-sections, and are surrounded by thick (up to 1  $\mu$ m) organic membranes (Taylor et al. 1969; Fig. 3d). Prisms are internally made of folia, which are seemingly continuous into the foliated layer (Esteban-Delgado et al. 2008; Fig. 3d). Membranes confer these layers a high flexibility (Harper and Checa 2020). This provides a tight sealing of the margin, which is adaptive against predators or desiccation.

Oysters also secrete lenses of porous materials within the foliated layers. Chalk lenses are characteristically secreted by the Ostreidae (Fig. 1c,d). They consist of laths similar to those of the foliated layers (Fig. 3e), although highly inclined with respect to the growth surface, variously oriented, and widely spaced (Fig. 3e). The Gryphaeidae, instead, develop lenses of vesicular material at the margins (Fig. 3f). Vesicles are separated by thick calcitic walls, have rounded to irregularly polygonal outlines, and extend perpendicular to the growth surface (Checa et al. 2020; Fig. 3g).

Within a single shell, either the chalk or the vesicular lenses have irregular extensions and thicknesses. In cross-section, the growth lines become widely spaced from the foliated to the chalk/vesicular material (Checa, Harper, and González-Segura 2018; Checa et al. 2020; Fig. 3h). This implies a significantly higher thickening speed of the lenses compared to the foliated material. Both materials are lightweight and thick, which may be advantageous against, for example, boring predators or epibionts. Chalk lenses also serve to smooth out the shell irregularities imposed by the substrate (Checa, Harper, and González-Segura 2018; Galtsoff 1964; Korringa 1951). Both the chalk and the vesicular microstructures are unrelated structurally and morphogenetically, which implies that ostreoids and gryphaeoids reached a similar adaptive solution independently. Oysters attach to the substrate by means of a calcitic cement composed of randomly oriented crystals of high-Mg calcite (MacDonald, Freer, and Cusack 2010) that precipitates within an organic “glue.”

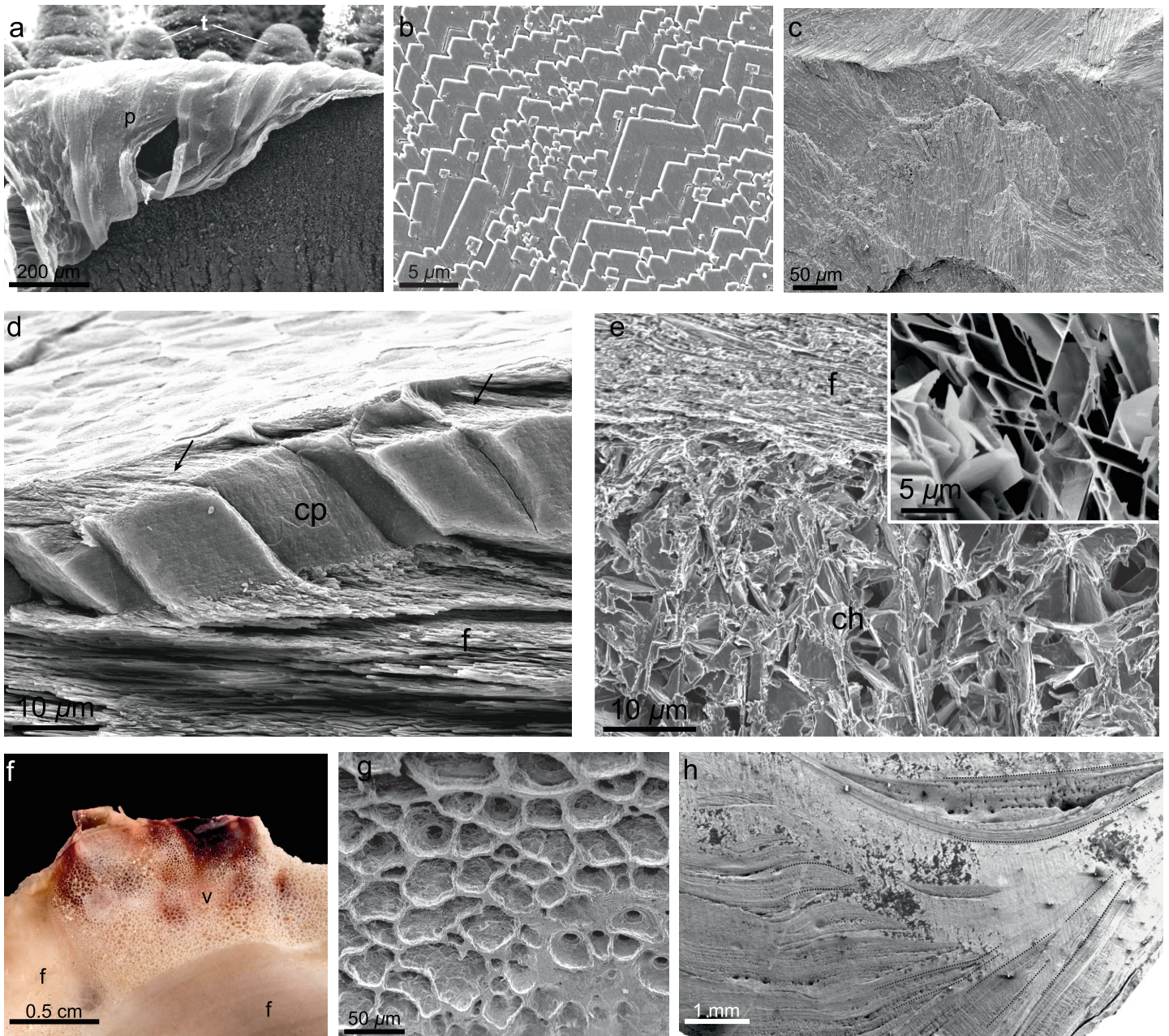
### Crystallography

Electron backscatter diffraction (EBSD) coupled with scanning electron microscopy (SEM) analyses the diffraction pattern obtained when backscattered electrons are diffracted by a crystalline material. This pattern, once indexed, provides information on the orientation of the crystal lattice. Data from different positions can either be integrated into (1) orientation maps, where different colors indicate different crystallographic orientations and (2) contoured pole figures (stereographic projections of crystallographic axes orientations), which represent the preferential orientations of crystallographic axes (the so-called texture). The  $\langle 001 \rangle$  and  $\{100\}$  pole figures provide orientations for the c- and a-axes of calcite, respectively. The foliated calcite reflects a moderate axial texture (Fig. 4) (c-axes show a cluster in one direction, a-axes orientation scatters on a great circle, perpendicular to c-axis orientation), that is, with the c-axis as fiber axis. The bundles in Fig. 4a show color gradients, indicative of internal misorientations (change in angle between adjacent locations). The surfaces of laths are very high-energy surfaces (Checa, Harper, and González-Segura 2018). This kind of surfaces hardly form inorganically but develops in biocalcite because they become stabilized by organic molecules.

Columnar prisms of the outer layer (Fig. 4b) display high misorientations and seem to be in continuity with the underlying foliated layer. Pole figures indicate that the orientations are partly preserved across both layers.

The chalk (Fig. 4c) shows no preferred orientation, except for the rough distribution of the 001 poles along a meridian. There is a drastic difference in the orientations of the c- and a-axes between the foliated and the chalk microstructures (Fig. 4c), in coincidence with the higher disorganization and inclination of the laths of the chalk (Fig. 4e). The fiber texture of the vesicular material (c-axis as fiber axis) is similar to that



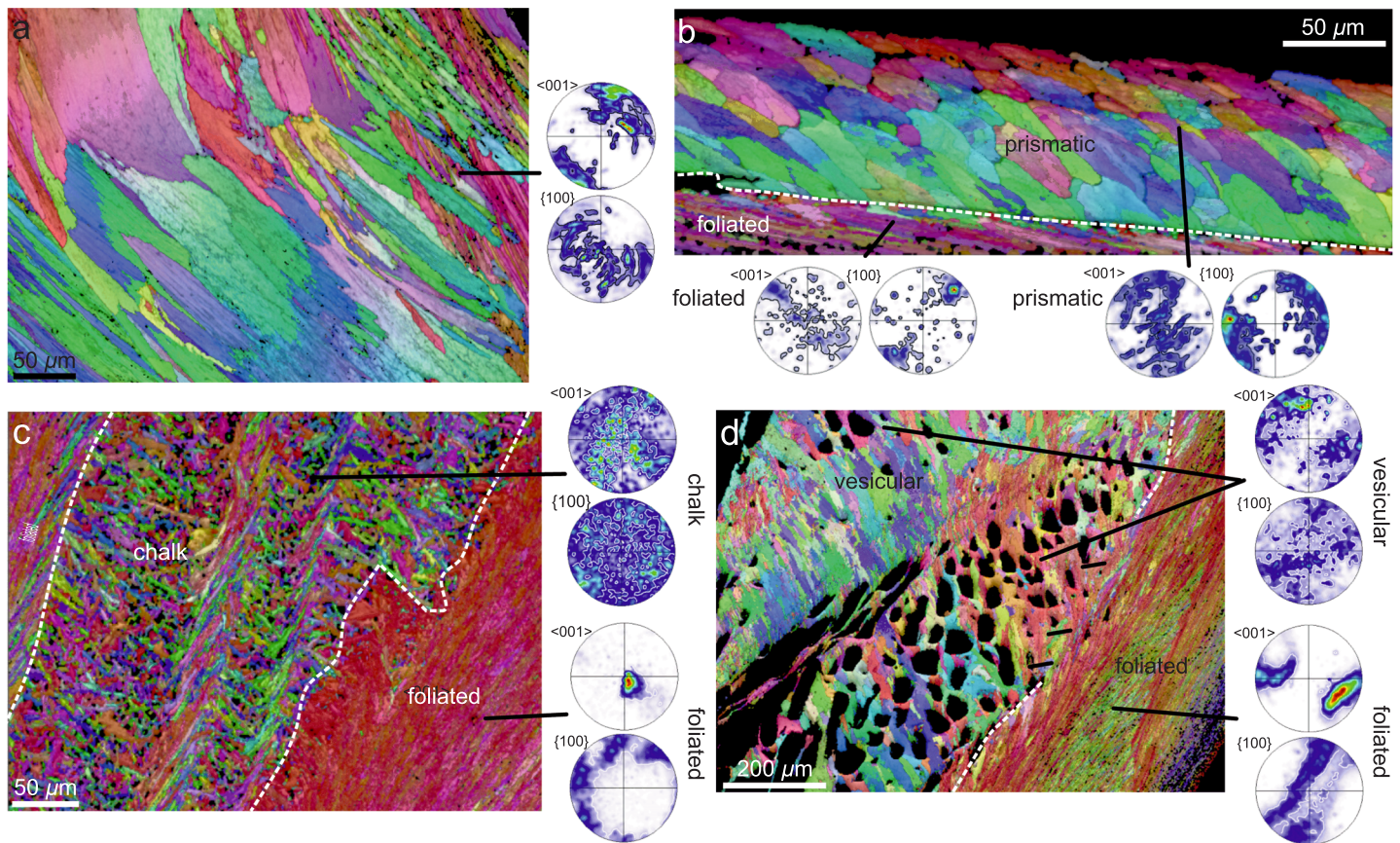


**Fig. 3.** Calcitic shell microstructures of Ostreoidea. **(a)** View of the outer mantle surface of *Ostrea edulis*. The periostracum (p) is extruded from the periostracal groove, between the outer and middle mantle folds. The tentacles (t) belong to the middle and inner mantle folds. **(b)** Foliated layer of *O. edulis*. **(c)** Far view of the foliated layer of *Magallana angulata*, showing the bundles of laths with varied orientations. **(d)** Fracture through the columnar prismatic (cp) and the foliated (f) layers of *O. edulis*. The fractures through the top part of the prisms (arrows) show their internal foliation. **(e)** Section through the foliated layer (f) and chalk (ch) of *M. angulata*. Note similarity and apparent continuity of the laths. The inset is a detail of the interior of the chalk, characterized by varied orientations of laths. **(f)** View of the interior of the upper valve of *Hyotissa hyotis*, showing the marginal distribution of the vesicular (v) material, where it alternates with foliated (f) material. **(g)** Aspect of the internal surface of the vesicular layer of *H. hyotis*. **(h)** Polished and etched cross sections of a left valve of *M. angulata*. The treatment reveals the outlines of chalk lenses, as well as the growth lines. Some growth lines have been outlined with dashed lines to show their continuity and increase in spacing from the foliated layer to the chalk lenses.

of the foliated layer, although much weaker (Fig. 4d). Crystals are continuous between the foliated and vesicular layers (arrows in Fig. 4d).

In summary, there seems to be crystallographic continuity between the different microstructures, from the shell exterior to the interior: columnar prismatic → foliated → chalk/vesicular.





**Fig. 4.** EBSD orientation maps and pole figures of the calcitic microstructures of Ostreoidae. **(a)** Foliated microstructure of *Hyotissa hyotis*. Pole figures indicate a rough fiber texture, with the c-axis approximately as the fiber axis. **(b)** Columnar prismatic (top) and foliated (bottom) microstructures of *Magallana gigas*. Note crystal continuity between layers, and similar, though not identical, orientations of pole maxima. **(c)** Alternation between foliated and chalk layers of *M. gigas*. Despite continuity of individual crystals, there is a sharp contrast in orientation and texture between both materials. **(d)** Foliated and vesicular layers of *Neopycnodonte cochlear*. Individual crystals are continuous across layers (short arrows at the transition point to some examples). The fiber texture becomes weaker from the foliated to the vesicular layer. The boundaries between layers are indicated with dashed lines in all instances.

The changes in texture and orientation are due to changes in orientation and organization of the constituent crystallites.

#### Temporality of foliated and chalky layers

The formation process of the chalk has long been subject to debate, with some suggesting the role of microbial mineralization (Vermeij 2014). Oxygen, nitrogen, sulfur and carbon stable isotope ratios of both foliated and chalky structures in *M. gigas* show no differences, which argues against microorganism activity (de Winter, Dämmer, et al. 2021). But higher concentrations of trace metals (e.g., Na, Mg, Mn, Sr) in the chalk suggest the inclusion of non-lattice bound elements or difference in mineralization rates (de Winter, Dämmer, et al. 2021; Ullmann et al. 2013). The formation of chalk laths during periods of fast growth has been described and illustrated by Checa, Harper, and González-Segura (2018) and Banker and Sumner (2020). Based on Mn labeling, a temporal continuity of deposits of foliated and chalky materials was demonstrated,

with chemical staining formed within 4 h that passes through both microstructures (Lartaud, de Rafelis, et al. 2010; Mouchi et al. 2016). The deposition of one or the other component results from distinct secretory repertoires of the shell-forming cells in the mantle epithelium (Mouchi et al. 2016). Whatever their mode of formation, the lack of chronological continuity in chalky parts and being more subject to diagenetic alterations than its foliated counterparts (Lartaud et al. 2006), a statement also observed for the vesicular structure of Grypheidæ (de Winter et al. 2018), encourage to prefer foliated microstructures for sclerochronological and microchemical analyses.

While there is hitherto a relatively wide knowledge on shell microstructures, their crystallography, mode of growth and relationships, and the functionality of lightweight, space filling chalk/vesicular materials requires more study. It would be desirable to know why their use is restricted to particular shell areas and whether and how their incidence in single species changes with environmental parameters.

### Part 3: Methods for oyster sclerochronology

Determining the timing of growth structures within oyster shells requires independent time constraints. This can be performed by labeling the shell at the start of a rearing period by using manganese- or strontium-enriched seawater baths, in high-enough concentrations to induce a label in the shell without risking toxicity for the oyster (Barbin, Ramseyer, and Elfman 2007; de Winter et al. 2023). Knowing the duration between the in vivo label and the specimen's collection (i.e., death) allows the counting of growth structures from the label to the final increment to determine the time interval represented by each increment and allows for the determination of growth rates. Here, we present the morphological and geochemical methods used to infer temporal information from growth increments in oyster shells. For a detailed explanation of methods, the reader is invited to consult the listed references.

#### Morphological and microtextural methods

The accessibility of the oyster record in terms of gaining specific information from it depends on the species and the specific individual at hand since oysters can be quite variable.

The surface of the hinge region of oyster shells may present a wave-like morphology along the growth axis that reflects consecutive winter and summer periods for concave and convex areas, respectively (Fig. 5a; *C. virginica*: Kirby, Soniat, and Spero 1998; *M. gigas*: Langlet et al. 2006). When visible, this method can provide fast screening of aging for a large number of specimens, without much sample preparation. This pattern however may be absent in specimens (Lartaud et al. 2006; Mouchi et al. 2021; Surge, Lohmann, and Dettman 2001), probably because of the shell morphology changing with substrate.

A microtextural method has also been proposed and requires making thin sections of the umbo. Annual lines commonly occur during temperature extremes, when oysters get too hot or cold (usually the latter) to grow and form denser increments in the form of organic-rich lines or thin gray/dark bands as opposed to white bands (Zimmit et al. 2019). However, other types of lines also exist, that are the result of unpredictable anomalies or disturbances interrupting the shell growth. These lines or bands are not always easy to differentiate from typical annual lines and introduce a bias toward older, slower-growing oysters that died earlier in the year (Andrus and Crowe 2000; Surge, Lohmann, and Dettman 2001). Depending on the research question these lines can have detrimental impacts on the study results and should be detected as best as possible. This can be done through the use of geochemical proxies or the comparison between rhythmic and disturbance lines based on geometric structures (Hausmann, Robson, and Hunt 2019; Robson et al. 2021; Zimmit et al. 2019). Based on modern references with known ontogeny and additional geochemical analyses, a best practice can be developed, which purely growth incremental studies can rely on.

For studies that involve geochemical analyses, a general assessment of growth incremental structures is unavoidable, as they provide the sampling strategy for the often costly geochemical samples and prevent time averaging or leaving major gaps in the geochemical record (West, Burchell, and Andrus 2018).

#### Geochemical methods

##### Cathodoluminescence

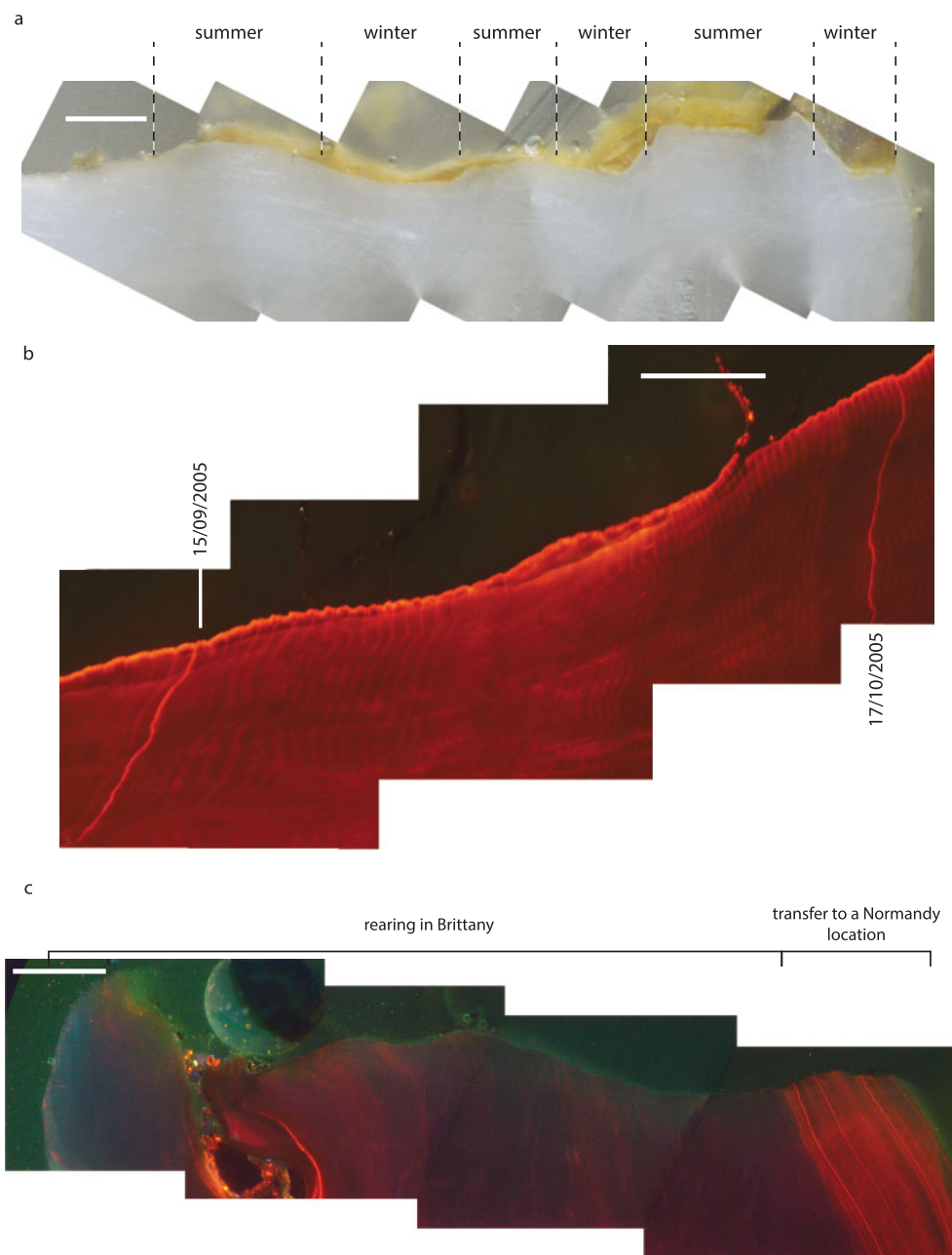
Manganese labels have been used to study growth rates and provide temporal calibration for geochemical measurements along shell growth (*M. gigas*, *O. edulis*: Barbin, Ramseyer, and Elfman 2007; Langlet et al. 2006; Lartaud, de Rafelis, et al. 2010). These markings can be found using CL microscopy. In calcite, Mn-rich growth increments appear as orange-red under CL (Fig. 5b,c).

Naturally-occurring Mn fluctuations were also discovered, firstly on the seasonal scale, with higher CL intensity in summer for *M. gigas* (Cardoso et al. 2007; Langlet et al. 2006; Lartaud, de Rafelis, et al. 2010) and *O. edulis* (Mouchi et al. 2013). However, Doldan et al. (2018) found high CL intensity in winter in *O. puelchana* specimens from Argentina, indicating that  $Mn^{2+}$  incorporation in the shell is not related to temperature but probably to the Mn concentration in seawater or metabolic activity as reported in mussels (Freitas et al. 2016). Additional data are necessary to determine if shell CL was impacted by local settings or if  $Mn^{2+}$  uptake fluctuations are a global phenomenon, and which biomineralization pathways are used by Mn for incorporation in the shell.

Monthly CL fluctuations (lunar cycles) occur in *M. gigas* (Huyghe et al. 2019) and *O. edulis* shells (Mouchi et al. 2021), probably related to food availability driven by tidal currents. The fastest CL variations observed in oyster shells correspond to single calcite increments (5 to 40–80  $\mu m$  width, Fig. 5b) and follow tidal cyclicities, with the mineralization of two increments per day in areas of semi-diurnal tidal regime (Huyghe et al. 2019). Exceptionally high growth rates (180  $\mu m$  day<sup>-1</sup>) and irregular increment mineralization (< 1 to 6 inc. day<sup>-1</sup>) independent of environmental control are observed in juvenile (< 1 yr) oysters. These newly identified high-resolution CL variations present great opportunities for high-resolution sclerochronology in oyster shells, potentially down to the hourly scale.

The CL intensity appears different depending on the locality of life (Fig. 5c) for reasons yet to be determined. Specimens from some localities present no CL variation, either seasonally or in calcite increments (*M. gigas* from Leucate in Mouchi et al. (2021)), which prevents sclerochronological assessment. This can be explained by low  $Mn^{2+}$  abundance, or the CL-inhibiting effect of elements like  $Fe^{2+}$  (Machel 1985). A thorough study on multiple localities and Mn concentrations is required to resolve this knowledge gap. Still, this cost-efficient method can provide valuable information from oyster shells when CL signal is present. Homogenous CL signal throughout





**Fig. 5.** Section of the hinge region of an oyster shell. Shell growth occurs from left to right. **(a)** Wave-like pattern on the surface of the umbo, related to season of mineralization. Scale bar is 1 mm. **(b)** Focus on a part of the umbo of modern *Magallana gigas* under cathodoluminescence. Between two consecutive Mn labels, natural luminescence occurs with a tidal rhythm. Scale bar is 200  $\mu\text{m}$ . **(c)** Cathodoluminescence observation of the umbo of a modern *Ostrea edulis* from a rearing experiment that was transferred during growth from Brittany to Normandy (France). Note the changing cathodoluminescence signal from one location to the other. Manganese labels are visible in the Normandy section. The greenish color corresponds to resin embedding the umbo. Scale bar is 1 mm.

the umbo or absence of periodic CL increments can also be used as tool for screening for diagenetic alteration.

#### Trace element ratios (Mg/Ca)

In the late 1990s, an interest in trace element ratios rose as a replacement to  $\delta^{18}\text{O}$  for temperature reconstructions. Based on

abiotic carbonates, a temperature-dependent relationship was observed for Mg/Ca (Katz 1973), later explained by thermodynamics (Lammers and Mitnick 2019). Since then, numerous studies provided temperature calibrations of bivalve shell Mg/Ca, including oysters (*C. virginica*: Surge and Lohmann 2008; *M. gigas*: Mouchi et al. 2013; *Saccostrea glomerata*: Tynan, Opdyke,



Walczak, et al. 2017), with widely varying relationships. This suggests that other parameters influence oyster Mg/Ca, such as the species (Bougeois et al. 2016), environmental settings (Mouchi et al. 2018; Tynan, Opdyke, Walczak, et al. 2017), the tidal cycles (Mouchi et al. 2013), organic-rich growth increments (inducing higher measured Mg/Ca; Hausmann, Robson, and Hunt 2019), and metabolic activity called “vital effects” (Mouchi et al. 2013; Surge and Lohmann 2008). Nevertheless, Mg/Ca variations demonstrably record the seasonal cycle, which led Durham et al. (2017) to suggest using Mg/Ca records to age specimens. Durham et al. (2017) used laser ablation inductively-coupled plasma mass spectrometry (LA-ICP-MS), but other analytical methods like scanning electron microscopy coupled with an energy-dispersive spectrometer (SEM-EDS) may be a cost-efficient, albeit slower, alternative. Recent advances in laser-induced breakdown spectroscopy (LIBS; Hausmann et al. 2017, 2023; Hausmann, Robson, and Hunt 2019) and micro-X-ray fluorescence scanning (de Winter, Dämmer, et al. 2021) constitute promising alternative approaches.

### Oxygen isotope ratios

The  $\delta^{18}\text{O}$  paleothermometer is one of the most widely used temperature proxies and was applied on mollusk shells early after its conception (Epstein et al. 1953; Hong et al. 1995; Mitchell, Curry, and Fallick 1995; Mook 1971; Urey 1948). Kirby, Soniat, and Spero (1998) and (Surge, Lohmann, and Dettman 2001) showed that fast-growing oysters precipitate their shell in equilibrium with seawater; a key assumption underlying the  $\delta^{18}\text{O}$  thermometer. Several other studies on oysters grown under monitored water temperature and  $\delta^{18}\text{O}$  compositions ( $\delta^{18}\text{O}_w$ ) allowed calibration of the  $\delta^{18}\text{O}$  proxy (de Winter et al. 2022; D. H. Goodwin, Gillikin, and Roopnarine 2013; Huyghe et al. 2020; Kirby, Soniat, and Spero 1998; Surge, Lohmann, and Dettman 2001; Tynan et al. 2014; Ullmann, Wiechert, and Korte 2010; Ullmann et al. 2013; Wisshak, López Correa, et al. 2009). The current consensus is that most oysters precipitate their shell close to isotopic equilibrium (de Winter et al. 2022; Kirby, Soniat, and Spero 1998; Ullmann, Wiechert, and Korte 2010), with the exception of juvenile *M. gigas* (Huyghe et al. 2020) and certain deep-dwelling oysters (e.g., *N. zibrowii*; Wisshak, López Correa, et al. 2009; *Neopycnodonte cochlear*; Huyghe et al. 2022).

Sample sizes required for  $\delta^{18}\text{O}$  measurements have come down from  $\sim 50\ \mu\text{g}$  to below  $5\ \mu\text{g}$  (Vonhof et al. 2020), allowing  $\delta^{18}\text{O}$  measurements of oyster shell growth increments  $< 100\ \mu\text{m}$  wide (Huyghe et al. 2020), corresponding to intervals of several days for *M. gigas* (Huyghe et al. 2019). By sampling on the high growth rate chalky structures, (Surge, Lohmann, and Dettman 2001) were able to achieve daily to weekly resolution. This allows  $\delta^{18}\text{O}$  sclerochronology in oysters to reconstruct temperature beyond the seasonal cycle, investigating weekly down to diurnal-scale variability.

In colder regions,  $\delta^{18}\text{O}$  records in oysters can overestimate winter temperature when interpreted from the minimum  $\delta^{18}\text{O}$ -

based temperature value in the shell due to slower growth in the coldest months (Lartaud, de Rafelis, et al. 2010). The  $\delta^{18}\text{O}$  thermometer is also highly sensitive to  $\delta^{18}\text{O}_w$  fluctuations (de Winter, Müller, et al. 2021; Lartaud, Emmanuel, et al. 2010; Surge, Lohmann, and Dettman 2001). Unlike other mollusks,  $\delta^{18}\text{O}$  in *C. virginica* is not biased toward a particular time of the day (D. H. Goodwin et al. 2021).

### Clumped isotopes

Alternative proxies to the  $\delta^{18}\text{O}$  thermometer have been investigated to reconstruct temperature without  $\delta^{18}\text{O}_w$  influence. Clumped isotopes ( $\Delta_{47}$ ) of carbonates predominantly depend on temperature variations (Eiler 2011), as demonstrated for a large variety of organic and inorganic carbonates on temperature, including mollusk shells and specifically modern oysters (de Winter et al. 2022; Eagle et al. 2013; Henkes et al. 2013; Huyghe et al. 2022).

This method studies the statistical anomalies in the abundance of  $^{13}\text{C}$ - $^{18}\text{O}$  bonds in carbonates. Measurements can be performed on either large ( $\sim 3\ \text{mg}$ ) or small ( $\sim 70\ \mu\text{g}$ ) samples. However, to limit the uncertainties of the calculated temperature, this approach requires the analysis of several replicates (5–20), corresponding to 1–12 mg of carbonate powder analyzed according to the protocol considered. This constitutes the main limitation of this proxy. A calibration on modern *M. gigas* specimens chemically marked and bred on the French coast demonstrated  $\Delta_{47}$  measurements yield reliable seasonal temperature estimates (Huyghe et al. 2022). However, during the juvenile ( $< 1\ \text{yr}$ ) part of oyster shells, high and fluctuating growth rates induce strong isotopic disequilibrium causing overestimated temperatures. Moreover, reduced growth rates during cold seasons in combination with the large amount of carbonate required for analysis prevent reconstructing the winter temperature minimum, limiting reconstructions to winter temperature averages. This problem is less severe in summer when more shell carbonate is produced. Multi-proxy studies by de Winter, Dämmer, et al. (2021) demonstrated that the isotopic values of foliated and chalky microstructures in *M. gigas* are similar, likely because they are mineralized under the same environmental conditions, implying that both microstructures should yield the same reconstruction result. The deep-sea *N. cochlear* seems to mineralize its shell at equilibrium for clumped isotopes, allowing for the reconstruction of deep-sea ( $\sim 300\ \text{m}$ ) temperatures (Huyghe et al. 2022).

### Conclusions

We identified several knowledge gaps in oyster sclerochronology and its applications that need to be addressed:

- To investigate the reasons for the lack of CL intensity and fluctuations hampering sclerochronology, which may provide additional information on the environment and ecology of past specimens.

- To compare the seasonality of reconstructed environmental parameters in past dissimilar climate periods.
- To continue improving the spatial resolution of geochemical sampling related to growth increments to reconstruct past climate variations and weather.
- To create regional syntheses of season of capture and human subsistence strategies.
- To use time-calibrated high-resolution elemental fingerprinting to reconstruct larval dispersal trajectories.
- To further investigate species-specific heat tolerance for growth to better constrain seasonal temperature reconstructions.
- To investigate biological clocks on shell mineralization.

In addition, some procedures should be standardized to all relevant studies to improve their qualities, by:

- Measuring PLD of migrants to feed larval dispersal models.
- Determining temporal calibration prior to any geochemical measurement for (paleo)environmental reconstruction to determine the uncertainty from sampling resolution.

These works would significantly improve our knowledge of oyster shell mineralization and its applications in a variety of research fields.

### Author Contributions

Antonio G. Checa and Erika Griesshaber acquired and processed new EBSD data. All authors contributed to the writing and editing of this manuscript.

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### Conflicts of Interest

None declared.

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