Quaternary Science Reviews 350 (2025) 109068

Contents lists available at ScienceDirect

Quaternary Science Reviews

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

Molluscan isotope sclerochronology in marine palaeoclimatology: Taxa, technique and timespan issues

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ARTICLE INFO

Keywords:
Cenozoic
Marine palaeoclimatology
Global
Sclerochronology
Mollusc
Bivalve
Oxygen isotope
Clumped isotope

ABSTRACT

Study of the accretionary biomineralised hardparts of organisms (sclerochronology) can make a useful contribution to palaeoclimatology. Ontogenetic sequences of isotopic data ($\delta^{18}O$ and Δ_{47} values) from the shells of marine molluscs are a source of information on seasonal sea-surface temperatures that can be used for detailed and rigorous evaluation of the outputs of numerical climate models. In situations where there is significant seasonality, and where shell preservation is adequate, accurate information about winter and summer surface temperature can be obtained from shallow-water benthic forms (bivalves and gastropods), in particular the early ontogeny of fast-growing species. Accurate information about winter surface temperature can also be obtained from individuals that lived at mid-shelf depths (20–40 m), but summer seafloor values from these need upward adjustment to derive a plausible surface temperature if thermal stratification of the water column occurs in this season. Ontogenetic $\delta^{18}O$ profiles from planktonic pteropod gastropods are a potential source of insight into seasonal surface temperatures in the ocean basins; these organisms merit investigation for provision of information to complement shelf data.

Temperature profiles constructed from shell $\delta^{18}O$ require an estimate of the $\delta^{18}O$ value of ambient seawater, which can be derived by back-calculation from the Δ_{47}-temperature supplied by the same shell material. Alternatively, through appropriate sampling and data processing, seasonal temperatures can be obtained directly from Δ_{47} profiles. Climate parameters are defined in terms of the mean state over a period of 30 consecutive years, a statistic (e.g., for seasonal temperatures) which can be derived from the long isotopic temperature records obtainable from bivalve species that live for many tens or hundreds of years. Efforts should be made to acquire such records, especially averaged data from crossdated shells, to specify climate parameters for precise times in the past. Information for precise times would be of particular value for icehouse intervals like the late Cenozoic, characterised by high frequency (high amplitude) climate fluctuation. Short records from non-crossdated shells can nevertheless provide useful insights into climate, particularly if a large dataset is obtained, supplying a reliable picture of the mean state and range of variation in climate parameters over the interval represented by the shells.

1. Introduction

Although contemporary climate change is commonly discussed in terms of global mean surface temperature, it is more marked in certain areas of the planet, and may be manifested unevenly over the seasons. For instance, the increase in annual mean surface air temperature over the last 50 years in the Arctic is more than twice the global average, and the temperature increase there in winter is nearly double that in summer

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https://doi.org/10.1016/j.quascirev.2024.109068
Received 1 June 2024; Received in revised form 25 October 2024; Accepted 5 November 2024

(Gutiérrez et al., 2021). Detailed assessment of the accuracy of numerical climate models therefore requires comparison of their outputs with temperature data at regional and seasonal resolution, from suitable proxies for the pre-instrumental period (cf. Tierney et al., 2020).

Tree rings, speleothems and varved sediments offer scope for seasonal documentation of climate on land, but of these forms of archive, only the last exists in the marine environment as well. Notwithstanding the scope of marine varves for providing seasonal data (Hathorne et al., 2023), their localised occurrence (largely in low-oxygen settings) is a limitation. The accretionary mineralised hardparts (shells and other biomineralised parts) of a variety of organisms offer an alternative source of information, probably over a larger area. Study of the various proxy records of ambient temperature contained within these hardparts (one aspect of the science of sclerochronology; Oschmann, 2009) is now an established means of documenting marine seasonality, the biomineralised (calcium carbonate) hardparts of corals (e.g., Walter et al., 2023), coralline sponges (e.g., Rosenheim et al., 2004), coralline algae (e.g., Hetzinger et al., 2018), bryozoans (e.g., Knowles et al., 2009), brachiopods (e.g., Butler et al., 2015), molluscs (e.g., Peharda et al., 2021) and fish (e.g., Darnaude et al., 2014) having been used for this purpose. Sclerochronological evidence of absolute seasonal temperatures comes in the form of ontogenetic (or astogenetic) profiles of hardpart ultrastructure, element chemistry, and isotopic composition and 'clumping', commonly set against an independent record of elapsed time in ontogeny from growth structures of annual or sub-annual periodicity.

Use of ultrastructural evidence (biomineral-unit size and shape) is a recent development, and while the technique has yielded good results from some marine bivalve mollusc taxa (e.g., Gilbert et al., 2017; Höche et al., 2020), others do not provide a record of temperature in all settings (e.g., Höche et al., 2022). The molar ratio of strontium relative to calcium (Sr/Ca ratio) in the skeletons of reef-building corals has long been used to document seasonality but can only supply information for the low-latitude shallow seas in which these organisms occur; the same applies to coralline sponges. At high latitudes the molar ratio of magnesium relative to calcium (Mg/Ca ratio) in the skeletons of coralline algae is a promising tool, but anatomical structure is an important control additional to temperature in some species (Nash and Adey, 2018). The Mg/Ca ratio of brachiopod shells can be a good indicator of temperature (Butler et al., 2015) but is not universally so in the phylum (Rollion-Bard et al., 2019; Smith et al., 2023); for meaningful results, attention is required to shell layer (Butler et al., 2015) and crystallography (Pérez-Huerta et al., 2011). Similar attention to both physical and chemical (e.g., organic content) aspects of the material (Peharda et al., 2021), and to further factors such as the rate of crystal growth (Carré et al., 2006), may also make Mg/Ca (and Sr/Ca) a reliable proxy for temperature in molluscs—while results from laboratory studies of some species have been satisfactory (e.g., Brosset et al., 2023), results from laboratory studies of others have not (e.g., Poulain et al., 2015), and wild-grown shells of some species have also yielded unsatisfactory results (e.g., Brosset et al., 2023). Growth rate in a general sense is one of a number of factors that influences elemental ratios in bryozoan skeletons (Krzemińska et al., 2022) and fish otoliths (Hüssy et al., 2021), obscuring temperature signals. In bryozoans, (astogenetic) variation in zoecium size is a reasonably good guide to the annual range in temperature (McClelland et al., 2014). However, this morphological variable does not specify absolute seasonal temperatures and so is of limited use for assessing the outputs of numerical climate models.

Notwithstanding the applicability of ultrastructural and chemical-element evidence from some taxa, ontogenetic profiles of the oxygen isotope composition ($^{18}O/^{16}O$ ratio of the analyte vs the same ratio in a reference material, here the Pee Dee Belemnite; expressed as a $\delta^{18}O$ value) of calcium carbonate (calcite and aragonite) hardparts have been to date the main source of insight into marine seasonality from sclerochronology, at least for extra-tropical areas where Sr/Ca evidence from reef-building corals is unavailable. The $\delta^{18}O$ value of calcium carbonate is dependent on the $\delta^{18}O$ value of the fluid from which it precipitates (thought to be similar to that of ambient seawater in the case of the outer shell layer of marine molluscs; e.g., Owen et al., 2002; Curley et al., 2023) and on temperature, as noted and demonstrated by Urey (1948). Additional biological ('vital') effects were considered likely by Urey and subsequently confirmed (see below). However, they are rarely large, and where so are commonly systematic (as determined from studies of individuals that grew under known conditions), such that they can be removed by a mathematical process (e.g., Fenger et al., 2007; Prendergast and Schöne, 2017; García-Escárzaga et al., 2020; Nicastro et al., 2020). The isotopic composition of ambient seawater can be measured in modern situations but must be inferred for the past. Paired Mg/Ca and $\delta^{18}O$ measurements on deep-sea benthic foraminifers have enabled calculation of changes in deep-water $\delta^{18}O$ over time (Elderfield et al., 2010, 2012). However, these changes may not be precisely synchronous between ocean basins (Skinner and Shackleton, 2005) and the values are unlikely to be a good guide to surface-water $\delta^{18}O$, especially on the continental shelves, due to regional and local differences in such factors as evaporation/precipitation balance and amount of freshwater run-off, which cause substantial variation in surface-water $\delta^{18}O$ from place to place (e.g., Schmidt et al., 1999). Thus, for any given set of $\delta^{18}O$ data from calcium carbonate, a location- and time-specific estimate of seawater $\delta^{18}O$ is required in order to compute accurate temperatures. The advent of carbonate clumped isotope thermometry has provided a means of deriving such estimates from the calcium carbonate analysed for $\delta^{18}O$. The technique uses the degree of association ('clumping') of heavy isotopes of carbon and oxygen: specifically, the frequency of the $^{13}C^{18}O^{16}O$ and $^{12}C^{18}O^{17}O$ isotopologues (mass 47) in the CO_2 evolved from carbonate by acid digestion. Assuming no vital (or diagenetic) effects, the abundance of these isotopologues relative to their stochastic abundance (expressed as a Δ_{47} value) reflects the temperature at which the carbonate precipitated (and the temperature of acid digestion); it is not influenced by the isotopic composition of the ambient seawater (Ghosh et al., 2006; Eiler, 2007; Huntington and Petersen, 2023). The temperature indicated by Δ_{47} can therefore be used to back-calculate seawater $\delta^{18}O$ from skeletal $\delta^{18}O$ using one of the well-established $\delta^{18}O$/temperature functions (e.g., O'Neil et al., 1969, for calcite; Grossman and Ku, 1986, for aragonite), although some uncertainty is attached to the value obtained because of error propagation over the several calculation steps (see Section 3).

The above is an illustration of evolving and improving isotopic approaches to reconstructing marine climate within the field of sclerochronology. Problems remain, however. There has been extensive prior coverage of vital effects on skeletal $\delta^{18}O$ and Δ_{47} (McConnaughey, 1989a, 1989b; Weiner and Dove, 2003; Huyghe et al., 2020, 2022; Wierzbowski, 2021, Curley et al., 2023), and likewise of diagenetic effects (Henkes et al., 2014; Ullmann and Korte, 2015; Ritter et al., 2017; Fichtner et al., 2018; Coimbra et al., 2020; Fernandez et al., 2020; Ingalls and Snell, 2021; Forjanes et al., 2022; Jones et al., 2022). Here we focus on three other issues: (1) the suitability of taxa according to their habitat and habits; (2) the most appropriate isotopic techniques (including sampling and data processing); and (3) the amount and temporal proximity (timespan) of data required to properly reconstruct seasonal palaeoclimate. We hope by this coverage to assist the design of maximally informative future investigations. We conclude with a case history that illustrates some of the points addressed and also demonstrates how sclerochronology can illuminate an issue associated with climate information from other sources: whether the data represent all of the year (thus providing an indication of annual mean conditions) or only a part (thus supplying an estimate for one 'season' alone). We concentrate on applications involving molluscs since this phylum has received the most attention from sclerochronologists. However, we refer to other phyla, and to non-sclerochronological approaches, where this aids development of our themes.

2. The habitat and habits of potential target taxa

2.1. Benthic taxa and hydrography

Climate is defined at the Earth's surface: with respect to temperature, by surface air values on land and typically by sea-surface values in the marine environment. Testing of model outputs for marine climate demands comparable proxy data, but some of that produced through sclerochronology potentially does not meet this standard because of its acquisition from subtidal benthic organisms. In shallow settings (<20 m), wave-action is nearly always sufficient for the water-column to be completely mixed throughout the year, and where tidal currents are strong, as in the southern North Sea at 53°N (Fig. 1A), this condition may pertain at locations with a water depth of 25 m or more. In such a hydrographic situation, therefore, a temperature record from a benthic organism could provide an accurate picture of surface seasonality. However, in deeper and/or less agitated settings the annual maximum temperature on the seafloor is typically lower than on the surface (and reached later in the year) because surface waters are preferentially heated by the sun, becoming less dense as a consequence and therefore resistant to downward mixing, leaving a cooler layer below (thermal stratification). In such a situation, as in the central North Sea at 57°N (Fig. 1B), a benthic organism could not provide an accurate picture of surface seasonality, or at least of summer surface temperature. The seafloor maximum temperature is only 2.6 °C below the surface maximum in the central North Sea, and it should be noted that the seafloor and surface minima are almost identical, as in the shallower and more agitated southern North Sea (Fig. 1A). However, while there is also little difference between seafloor and surface minima on the Virginia/northern North Carolina shelf of the eastern U.S.A. (*c.* 37°N), maxima differ by at least 3.4 °C at 20 m and between 6.3 and 9.2 °C at 30–40 m, despite variation of only 2.2 °C in maximum surface temperature between locations (Fig. 2). Much the same summer seafloor−surface temperature differences are observed in the northern Adriatic Sea (*c.* 45°N): 3.2–9.9 °C (mean 7.7 °C) over the period 2008–2016 at a location with a seafloor depth of 38 m, but again seafloor and surface winter temperatures are the same (Fig. 1C). From this, it is evident that at latitudes below 50°, profiles of temperature from benthic species are quite likely to provide serious underestimates of summer surface temperature, even if the organisms lived at a depth no greater than the mid-shelf range (20–40 m). Reasonably accurate records of winter surface temperature are, however, to be expected, subject to continuing growth and the actual existence of a significantly cooler season (in tropical regions, with little seasonal variation in surface temperature, stratification might persist; i.e., benthic species might provide underestimates of surface temperature over the whole year).

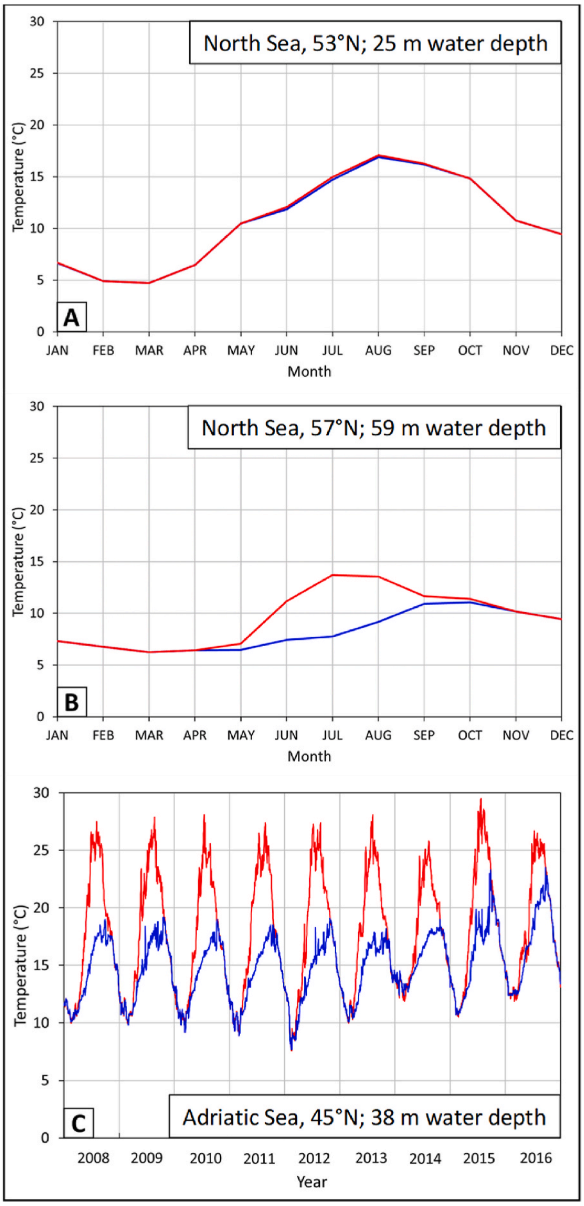


Fig. 1. Surface (red) and seafloor (blue; red where the same as surface) temperature profiles for locations in the southern North Sea (A; seafloor depth 25 m), central North Sea (B; seafoor depth 59 m) and northern Adriatic Sea (C; seafloor depth 38 m). Adapted from Johnson et al. (2021); the monthly average data in A and B were obtained from Austin et al. (2006).

Isotope-derived temperatures from subtidal benthic organisms, in this case certain bivalve mollusc species, were obtained by Wichern et al. (2023) and de Winter et al. (2024) from the Oorderen Member of the Lillo Formation, representative of the mid-Piacenzian Warm Period (mPWP; late Pliocene), at Antwerp, Belgium (51°N). These authors argued against summer thermal stratification for the horizons of the shells concerned (at least largely in the upper part of the Member) and therefore took their summer as well as winter isotopic temperatures as an accurate indication of surface values. By contrast, Johnson et al. (2022) made a modest upward adjustment (3 °C; commensurate with the latitude and inferred depth) of summer isotopic temperatures from other bivalves of the Oorderen Member at Antwerp, because of morphological, palaeoecological and taphonomic evidence of possible stratification at the horizons concerned (in the lower, probably deeper-water, part of the Member). The facts (1) that both the winter and summer surface temperatures inferred from these three studies are similar, despite different isotopic methodologies, and (2) that they are in close agreement with model estimates for the area in the mPWP (Fig. 3), suggest that with due consideration of hydrographic setting and appropriate adjustment for summer stratification (where necessary), it is possible to derive quite accurate estimates of seasonal surface temperatures from isotopic data supplied by benthic organisms. However, while it may be easy to determine that adjustment is necessary (e.g., from sedimentary evidence of low seafloor water agitation), it is more problematic to specify the exact amount appropriate, given the substantial variation in the difference between seafloor and surface temperature maxima over a small depth range in stratified settings, and the comparable variation over a small number of years at the same depth (see above). Even the promising development of ostracod eye-size as a tool for the precise determination of depth (error typically <10 m to *c.* 60 m; Tanaka et al., 2009; Tian et al., 2022) does not counter the problem caused by temporal variation in the intensity of summer stratification at locations where this occurs.

An obvious solution to the 'stratification' problem is to use taxa that are largely or entirely restricted to shallow marine environments, including the intertidal zone. Isotopic studies of modern intertidal

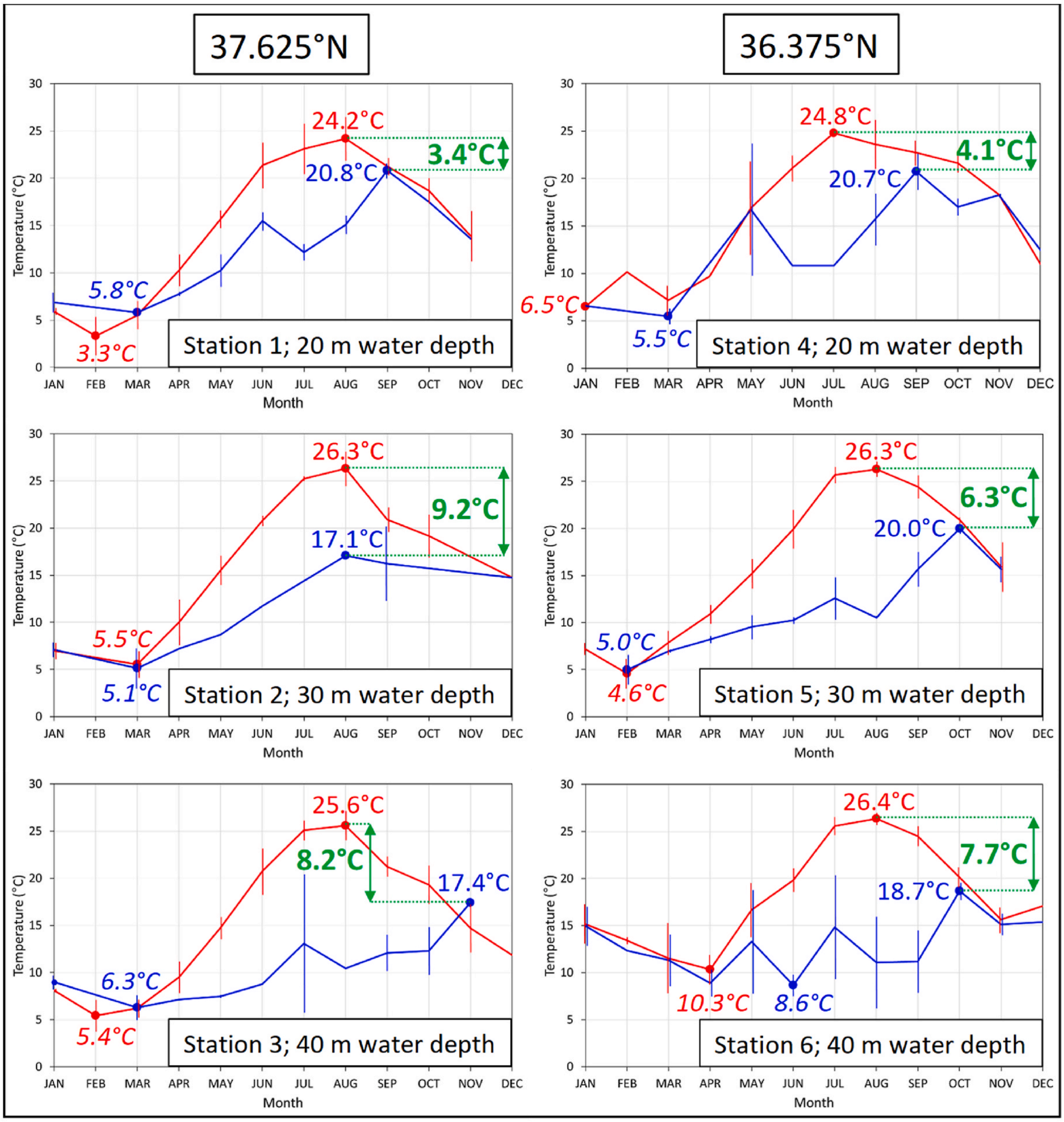


Fig. 2. Monthly temperatures (some missing values) for the surface (red line) and seafloor (blue line) at sites with differing seafloor depths (20 m, 30 m and 40 m) on the Virginia shelf (latitude 37.625°N; left column) and North Carolina shelf, north of Cape Hatteras (latitude 36.375°N; right column). Monthly temperatures are mean values (±1σ; 2–16 measurements for each month) or single values for the time interval 1975–1984. See Fig. 9 for positions of sites relative to onshore locations involved in the case history (Section 5). The numerals in normal and italic type refer to maximum and mimimum temperatures, respectively, at the surface (red) and seafloor (blue), the month concerned being identified by a filled circle in the corresponding colour. The numerals in bold green type refer to the difference between maximum surface and seafloor temperature. Raw data from Seidov et al. (2016); latitudes and longitudes according to the WGS84 coordinate system.

bivalve and gastropod molluscs have shown that they grow only when submerged and thus provide a record just of water, not water and air, temperature (Goodwin et al., 2003; Mannino et al., 2003; Kingston et al., 2008; Burchell et al., 2014; Milano et al., 2020; Cudennec and Paulet, 2022); however, some deviation from the temperatures recorded by shells from adjacent shallow subtidal settings is likely due to warming/cooling of the water by contact with surfaces exposed at low tide. Mollusc taxa that occupy shallow water are numerous, but many extend into settings where salinity is reduced—e.g., amongst the large number of cases, at least some species of the gastropods *Littorina* (Rosenberg and Rosenberg, 1972), *Nassarius* (Iannotta et al., 2009), *Nerita* (Jiang et al., 2024) and *Stramonita* (Veiga et al., 2016), and of the bivalves *Astarte* (Moss et al., 2021), *Crassostrea* (Surge et al., 2001), *Mercenaria* (Elliot et al., 2003) and *Saxidomus* (Hallmann et al., 2011). This imposes problems for δ^{18}O-based thermometry because the freshwater component that causes reduced salinity typically has a much lower δ^{18}O value than seawater and the amount of this component is usually variable—i.e., salinity, and therefore water δ^{18}O, is not only reduced but fluctuates. Fluctuations in water δ^{18}O often occur on quite short timescales and irregularly, as due to large-magnitude fluvial-input events (Goodwin et al., 2021). The difficulty of constraining water δ^{18}O can make for corresponding difficulty in interpreting seasonal temperatures from shell δ^{18}O profiles in reduced-salinity environments (e.g., Surge et al., 2003).

The Δ_{47} approach (described fully in Section 3) in principle provides a means of isotopic temperature determination in reduced-salinity situations. Certainly, Δ_{47} is dependent on temperature (including in mollusc carbonate; e.g., de Winter et al., 2022) and not dependent on

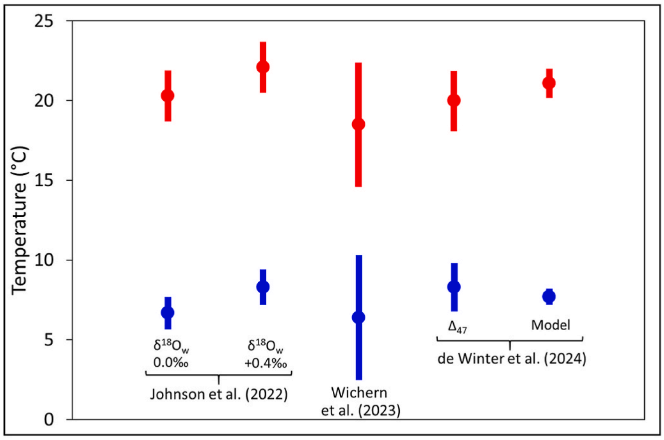


Fig. 3. Estimates (mean ± 1σ for Johnson et al., 2022; mean and 95‰ confidence interval (CL) for Wichern et al., 2023; de Winter et al., 2024) of winter (blue) and summer (red) surface temperature for the mid-Piacenzian Warm Period (Late Pliocene) at Antwerp, Belgium, from isotopic profiles of bivalves (Johnson et al., 2022; Wichern et al., 2023; de Winter et al., 2024) and modelling (de Winter et al., 2024). The isotope-derived estimates of Johnson et al. (2022) use shell $\delta^{18}O$ and model-based estimates of water $\delta^{18}O$ ($\delta^{18}O_w$; values indicated), and include a 3 °C 'stratification factor' for summer temperatures (see text). The isotope-derived estimates of Wichern et al. (2023) use shell $\delta^{18}O$ and a value for water $\delta^{18}O$ (+0.1 ± 0.9‰; 95% CL) back-calculated from shell Δ_{47}. The isotope-derived estimates of de Winter et al. (2024) use shell Δ_{47}. Note that Dearing Crampton-Flood et al. (2020, supplement) obtained higher winter temperatures (10.3 ± 1.7 °C; ± 1σ) and lower summer temperatures (16.3 ± 3.1 °C) for the same interval at a nearby location in the Netherlands from the evidence of two biomarker proxies for temperature, TEX_{86} and alkenone unsaturation ($U^{K'}_{37}$), respectively. While in combination these biomarkers give a picture of annual mean temperature similar to that from isotopic evidence, they provide a lower (probably inaccurate) estimate of seasonal range (for a fuller discussion, see Johnson et al., 2022).

water $\delta^{18}O$, but values have a relatively large 'analytical error' (strictly, 'measurement uncertainty'; International Association of Geoanalysts, 2024) such that some uncertainty attaches to calculated temperatures, and more uncertainty attaches to back-calculated water $\delta^{18}O$ values because of the small analytical error associated with shell $\delta^{18}O$ (e.g., Wichern et al., 2023). Notwithstanding this point, highly local coastal environments (including lagoons, open shorelines and places affected by groundwater discharge) can show clearly differentiated average reconstructed water $\delta^{18}O$ values and even seasonal fluctuations in reconstructed values (e.g., Zhang et al., 2021; Minnebo et al., 2024).

There are relatively few bivalves that live at shallow depths in the sea but do not extend into reduced-salinity environments—i.e., that are stenohaline. Giant clams (family Tridacnidae) provide examples as they usually occur at less than 10 m depth (Klumpp and Lucas, 1994) and always in fully marine settings (Moir, 1986). Unfortunately, they are restricted to the tropics (and some areas in the subtropics), but in this setting both modern and fossil forms have been extensively used to supply seasonal sea-surface temperature data from $\delta^{18}O$ evidence (e.g., Batenburg et al., 2011; Driscoll et al., 2014; Warter et al., 2015; Reuter et al., 2022; Wang, G. et al., 2022; Dong et al., 2024). A shallow-water, apparently stenohaline bivalve occurring outside the tropics is *Mercenaria stimpsoni*, found in the north-west Pacific from South Korea (Khim et al., 1998) to northern Japan (Tanabe et al., 2017) at depths of 5–30 m (Tanabe et al., 2017). A number of isotopic ($\delta^{18}O$) studies have been conducted on modern forms of this species (Khim et al., 1998; Kubota et al., 2017; Tanabe et al., 2017; Shirai et al., 2018a), and Pleistocene examples have now been investigated (Miki et al., 2024). Both giant clams and *M. stimpsoni* are long-lived—at least 60 years in one species of the former (Watanabe et al., 2004) and 92 years in the latter (Kubota et al., 2017; Tanabe et al., 2017)—which advantages them for reconstruction of climate (see discussion in Section 4). Other stenohaline bivalve species that are common in shallow waters are quite short-lived there and often not restricted to this depth—e.g., *Spisula solidissima*, which lives for only about 11 years in shallow settings (Jones et al., 1983) and extends to a depth of 45 m (below the mixed layer in summer; Arthur et al., 1983). The very long-lived (<507 years; Butler et al., 2013) bivalve *Arctica islandica* commonly occurs in mid-to deep-shelf settings (e.g., Mann and Wolf, 1983; Witbaard and Bergman, 2003) but is also found at shallow depths (e.g., Foster et al., 2009). It extends in addition into settings with reduced salinity (e.g., 19.2 in the Baltic Sea; Höche et al., 2022) so a 'marine' $\delta^{18}O$ value for ambient water cannot be automatically assumed in $\delta^{18}O$-thermometry using this species.

While gastropod species occurring in shallow, fully marine settings are many, they are almost entirely short-lived: even those that reach a large size (length 100 mm) usually live less than 10 years (e.g., Hollyman et al., 2018), and species that reach an exceptional size (length >500 mm) may live for a similarly short time (*Campanile* spp.; de Winter et al., 2020) or no longer than 20 years (*Triplofusus giganteus*; Herbert et al., 2022). *Haliotis* (abalone/ormer), which reaches ages up to 30 years (Andrews et al., 2013), is a rare example of a longer-lived form. It occurs widely at low and mid-latitudes (although not in eastern North America or western South America; WoRMS, undated), can supply an isotopic ($\delta^{18}O$) record of winter as well as summer temperature (i.e., no major reduction or cessation of growth occurs in winter; Jolivet et al., 2015), and is a common element in at least some archaeological shell accumulations (e.g., Bassett and Andrus, 2021; Glassow et al., 2021). However, despite its potential for isotopic studies of palaeoenvironment (Bassett and Andrus, 2021), only one archaeological shell appears to have been investigated isotopically to date (Jolivet et al., 2015). Earlier examples are rare and usually preserved as moulds, so despite a fossil record extending back to the Cretaceous (Geiger and Groves, 1999), *Haliotis* only offers opportunities for documenting marine palaeoclimate in the relatively recent past.

2.1.1. Note on possible isotopic resetting in molluscan material from archaeological sites

Because of their accessibility, both gastropods and bivalves from shallow waters have been exploited throughout human history as a source of food, their discarded shells occurring abundantly in middens dating back to the early Holocene (Gouvreau et al., 2023) and in beds within more natural stratified sequences dating back to the middle Pleistocene (Marean et al., 2007). These accumulations constitute a useful resource for isotope-based reconstruction of climate in the Quaternary and have been extensively used for this purpose (e.g., Jones et al., 2005; Ferguson et al., 2011; Surge and Barrett, 2012; Wang et al., 2012; Hallmann et al., 2011, 2013; Prendergast et al., 2018; García-Ezcárzaga et al., 2022), even if the taxa represented are usually not ideal in terms of their lifespans. One potential problem with this anthropogenic resource is resetting of isotopic signatures through cooking. For the aragonitic bivalve *Mercenaria campechiensis*, Müller et al. (2017) found that the temperatures of all forms of cooking caused reductions in both $\delta^{18}O$ and Δ_{47}, though the Δ_{47} reduction brought about by the relatively low temperature of boiling (*c.* 100 °C) was not statistically significant. Roasting at a somewhat higher temperature (*c.* 174 °C) did not leave obvious traces in the structure or integrity of shells, making for difficulties in distinguishing cooked from uncooked material (i.e., shells whose contents were eaten and/or extracted raw and which could be expected to preserve an isotopic signature of ambient temperature during life). The results for $\delta^{18}O$ from *M. campechiensis* essentially mirror those obtained from the aragonitic inner layer of the gastropod *Phorcus turbinatus* following cooking (Milano et al., 2016). The calcitic outer layer of the bivalve *Mytilus californianus* may not undergo any change in $\delta^{18}O$ through boiling but does at least sometimes through roasting, though this treatment is associated with obvious physical changes (Jazwa and Jantz, 2019). It is clear from these studies that archaeological shells showing any physical trace of heating are an inappropriate choice for palaeoclimatological research, and that isotopic data from apparently well-preserved shells should be treated with circumspection because of the possibility of cryptic alteration through cooking.

2.2. Pelagic taxa and mobility

As demonstrated above, use of benthic taxa is less than ideal in situations where summer stratification occurs because they will not record the summer surface temperature. In situations with year-round stratification they will of course not record winter surface temperature either. Use of pelagic taxa is, at first sight, a potential solution to this problem. However, while these rarely extend into reduced-salinity environments, they are by no means restricted to the surface mixed layer. Planktonic foraminifers, which have calcitic tests consisting of sequentially secreted chambers, typically occupy species-specific depth ranges in the open oceans, but individuals nevertheless tend to sink (because of their higher density than seawater) over the course of their short life (a few weeks; Spero, 1998). Use of whole tests for isotope thermometry thus yields a depth-integrated value for temperature (Pracht et al., 2019), probably with a bias towards the temperature at the deeper end of the depth range because this depth will be represented by the latest (largest) chambers. Notwithstanding the lack of precise depth association and likely bias towards relatively deep-water temperatures, use has been made of large sets of individual foraminiferal analyses (IFA; Thirumalai et al., 2013) to reconstruct surface seasonality (e.g., Ganssen et al., 2011). It is assumed in this that the short lifespans of the many individuals concerned together represent the whole year. This assumption is questionable (productivity is, for instance, higher in summer in *Globigerinoides ruber*; Mortyn et al., 2011) and in any case collections of individuals made from even small volumes of sediment may span millennia, introducing interannual and longer-term variations that make it difficult to determine seasonal variation (Thirumalai et al., 2013; see also Section 4). Chamber-by-chamber (i.e., ontogenetic) sampling of foraminifer tests for δ^{18}O is now a realistic option using so-called *in situ* analytical techniques (e.g., Kozdon et al., 2009, 2011; see Section 3 for an explanation) but it is doubtful whether this would improve the quality of surface seasonality reconstructions because of the brief life of individuals and depth migration over the course of it.

Pteropod gastropods constitute a potentially superior planktonic alternative because they can live for over a year (Boissonnot et al., 2021). While they undergo both diurnal and seasonal fluctuations in depth, calcification is principally at relatively shallow depths and in oxygen isotope equilibrium with ambient seawater (Juranek et al., 2003; Keul et al., 2017; Oakes et al., 2021). Pteropod shells are extremely thin and fragile but they can nevertheless be preserved in large numbers in pelagic sediments. At least within the Quaternary (Sreevidya et al., 2019), they are a potential (if imperfect) source of information on open-ocean surface seasonality that would be a very valuable complement to shelf data (Judd et al., 2020). Pteropods have not yet been investigated sclerochronologically (i.e., through the course of ontogeny) but, despite their small size (<2 mm), could be sampled thus for δ^{18}O by application of an *in situ* analytical technique. Like planktonic foraminifers, pteropods are typically much less abundant in shelf seas than in the open ocean, but they can sometimes occur in large numbers there (Hallenberger et al., 2022).

Organisms that are pseudoplanktonic (attached to floating objects such as logs) are in principle an ideal source of information on surface seasonality. However, Wignall and Simms (1990) showed that instances of this mode of life are uncommon in the geological record, and subsequent work has indicated that some species once thought to be pseudoplanktonic were in fact benthic (Etter, 1996; Schatz, 2005). Nevertheless, certain species of gooseneck barnacle are habitually pseudoplanktonic (Goehlich et al., 2024) and could supply isotopic records of surface temperature from their calcitic skeletal plates.

If the potential of planktonic organisms for reconstructing surface seasonality is reduced by changes in depth during life and short lifespans, that of nektonic organisms is reduced by both vertical and lateral changes of position. While isotopic (δ^{18}O) profiles from the statoliths of cuttlefish and especially squid (both dibranchiate cephalopod molluscs) reflect ambient temperature (Martino et al., 2022), cuttlefish migrate laterally tens to hundreds of kilometres and squid up to thousands of kilometres (Semmens et al., 2007), so temperature records from these organisms are not place-specific. Lateral migration has been invoked to explain the different δ^{18}O-temperature records from the guards of belemnites (Mesozoic dibranchiate cephalopods) compared to those from the shells of bivalves collected at the same location and horizon (Mettam et al., 2014). The consensus of opinion seems to be now that belemnite temperature records include a larger signal of vertical than lateral migration (Hoffmann et al., 2021; Wang et al., 2023), although in some instances they probably reflect a relatively fixed life position below the permanently mixed layer (Dutton et al., 2007). Whatever the case, it is difficult to obtain information from belemnites about surface seasonality at the collection location. The extant tetrabranchiate cephalopod *Nautilus* does not migrate far laterally (Semmens et al., 2007) but undertakes significant vertical migrations and always lives at a depth greater than 130 m (Dunstan et al., 2011; Tajika et al., 2022). Isotopic profiles from its external shell cannot therefore provide much insight into surface seasonality. From isotopic comparisons with other co-occurring taxa known to be benthic and pelagic (and on the assumption that the isotope data are uninfluenced by vital effects), it is likely that the ammonites of the Mesozoic include forms confined to deep and to shallow habitats, while some perhaps changed depth during life (Sessa et al., 2015). The other externally-shelled cephalopods of the past (ceratites, goniatites, etc.) may have had a similar diversity of depth habitats and so, while they are a potential source of high-resolution temperature records (cf. Sessa et al., 2015), the meaning of these requires careful consideration.

The same need for careful evaluation applies to isotopic temperature profiles from the otoliths of fish, in view of the varied habitats and habits (pelagic/benthic/migratory/sedentary) within this group. Profiles from large pelagic taxa such as tuna can be essentially a record of large-scale lateral migration (e.g., Kawazu et al., 2020) but those from smaller (epipelagic; 0–200 m) forms such as anchovies and sardines are potentially a record of seasonal surface temperature variation in a small area. Despite their sub-millimetric size (Nishida et al., 2020), the otoliths of small pelagic fish are large enough to be investigated using *in situ* analytical techniques (cf. Helser et al., 2018; Shirai et al., 2018b). The otoliths of epipelagic species are relatively rare (compared to those of mesopelagic species; 200–1000 m) in deep-sea sediments, possibly because of their small size and vulnerability to dissolution (Lin et al., 2017, 2023). While they occur in shelf sediments (Přikryl et al., 2016; Lin et al., 2017), there do not appear to have been any isotopic studies of them. Both of the existing isotopic studies of fossil otoliths from shelf sequences (Ivany et al., 2000; Vanhove et al., 2011) involved demersal taxa and the results are therefore subject to the same depth considerations as apply to data from other benthic taxa. Otoliths in archaeological accumulations are likely to be from shallow-water species and so (notwithstanding the possibility of lateral migration) are potentially a source of information on surface seasonality (e.g., Surge and Walker, 2005). The original δ^{18}O signature of otoliths seems to undergo minimal alteration through cooking (Wang et al., 2022).

3. The isotopic approaches available

Analytical advances have significantly reduced the sample volumes on which conventional isotope-ratio (e.g., δ^{18}O) analyses can be done. Standard *ex situ* measurement by gas-source mass spectrometry now requires <5 μg of carbonate sample (extracted by drilling or milling) for a precise δ^{18}O analysis (Vonhof et al., 2020). Secondary Ion Mass Spectrometry (SIMS) is a form of '*in situ*' measurement in which the surface of the specimen is sputtered by a focussed primary ion beam and ejected secondary ions are then collected and analysed in a mass spectrometer. Spatial resolution is at *c.* 10 μm scale (Helser et al., 2018). Although $\delta^{18}O$ values analysed by SIMS and *ex situ* mass spectrometry are shown to be offset for as yet unexplained reasons (Wycech et al., 2018), the seasonal range is conserved between both methods (Helser et al., 2018). Calibration of the SIMS-based oxygen isotope thermometer is improving (Medd et al., 2024).

From the best available evidence (the data of Moss et al., 2016, from 297 of many thousands of bivalve species), the typical accretion rate of bivalve shells in the direction of growth is 2–12 mm/yr (or *c.* 5–30 μm/day). Rates toward the upper end of this range are sufficient for precise resolution of seasonal variation (i.e., no significant time-averaging) from successive samples extracted for *ex situ* analysis by drilling (e.g., Johnson et al., 2024). At rates toward the lower end of this range similar resolution can be achieved from successive (smaller) samples extracted by milling (e.g., Schöne et al., 2005a), and at exceptionally slow growth rates (0.2 mm/yr) from *in situ* SIMS analysis (Hughes et al., 2023). Sub-daily resolution is sometimes achievable by drilling in bivalves of average growth rate (Hallmann et al., 2009) and should be readily obtainable in bivalves with exceptionally high growth rates (>100 mm/yr; e.g., Johnson et al., 2019; de Winter et al., 2020). Growth can of course be interrupted (i.e., it may temporarily slow to near zero, even if does not actually cease), but this is recognisable from internal and external features of the shell (e.g., Johnson et al., 2022, 2024).

As mentioned in Section 1, the $\delta^{18}O$ thermometer requires an estimate of the $\delta^{18}O$ value of the seawater in which the carbonate was precipitated. This value can be estimated for the past using isotope-enabled models of climate and oceanic variability (e.g., Lécuyer and Allemand, 1999; Werner et al., 2016) or, for the present and analogue situations in the past, by interpolation amongst modern seawater isotope measurements, where available (LeGrande and Schmidt, 2006). The reliability of the latter approach is highly dependent on the proximity of the nearest real water $\delta^{18}O$ measurements, which are sometimes hundreds of kilometres away (Zhang and Petersen, 2023; Scholz et al., 2024). Alternatively, the $\delta^{18}O$ value of seawater can be estimated from the $\delta^{18}O$ of vertebrate bone or tooth phosphate, either using empirically established relationships with seawater $\delta^{18}O$ (e.g., Walliser et al., 2015, 2016; Ciner et al., 2016) or, for material from homeotherms, by using the relationship between phosphate $\delta^{18}O$ and temperature, substituting a value for body temperature into the equation (Ciner et al., 2016). These approaches have the advantage of being potentially applicable to material from the same location and horizon as the sampled carbonate. However, by not being applicable to the actual organism that supplied the carbonate there is the risk that the estimate of water $\delta^{18}O$ obtained will be inappropriate (representative of a time when water $\delta^{18}O$ was different) for calculation of temperature from carbonate $\delta^{18}O$ values. This problem is overcome by back-calculating water $\delta^{18}O$ from a Δ_{47}–temperature derived from the same material (even the same specific sample) as supplied a value for carbonate $\delta^{18}O$ (e.g., de Winter et al., 2021a,b; Wichern et al., 2023; Zhang and Petersen, 2023; Minnebo et al., 2024). Water $\delta^{18}O$ values determined in this way do, however, have moderate uncertainty—e.g., ±0.9‰ (95% CL) in the study of Wichern et al. (2023). The Mg/Ca thermometer could in principle be employed in the same way but as noted in Section 1, is unreliable for molluscs.

There is also the question of which parts of shells (if not all) are secreted in oxygen isotope equilibrium with seawater, and which equation best describes this equilibrium. Huyghe et al. (2020) found that the $\delta^{18}O$ value of the juvenile part of oyster shells differed substantially from that predicted by environmental conditions, implying disequilibrium. Curley et al. (2023) found that the inner shell layer of some other bivalves had a $\delta^{18}O$ value somewhat different from that of the outer layer, and Trofimova et al. (2018) identified comparable differences between the inner and outer sectors of the outer shell layer in *Arctica islandica*. Both the latter studies imply a degree of disequilibrium. There are a variety of 'equilibrium' $\delta^{18}O$-temperature equations available, particularly for the calcite polymorph, each yielding a slightly different temperature for the same shell $\delta^{18}O$ value (see example calculations in Bemis et al., 1998; Johnson et al., 2021, 2022). The best choice can only really be determined in modern material by making comparisons with known environmental temperatures or by employing these and measurements of water $\delta^{18}O$ to obtain predicted shell $\delta^{18}O$ values using different equations and then comparing these values with the actual ones (e.g., Johnson et al., 2022).

Improvements in analytical workflows using carbonate preparation devices coupled to mass spectrometers through dual-inlet systems now enable clumped isotope analyses to be carried out on relatively small sample sizes (<100 μg), approaching those needed for regular $\delta^{18}O$ analysis, albeit with high precision uncertainties (Müller et al., 2017). Combined with community-wide standardisation (Bernasconi et al., 2021) and calibration efforts (Petersen et al., 2019; Meinicke et al., 2020; Anderson et al., 2021; de Winter et al., 2022; Daëron and Vermeesch, 2023), these developments have made the clumped isotope paleothermometer accessible for sclerochronological studies (e.g., de Winter et al., 2021b, 2024; Zhang and Petersen, 2023). The precision uncertainty on clumped isotope values from small aliquots can be overcome by binning clumped isotope results into seasonal averages (de Winter et al., 2021a), such that seasonal mean temperatures and $\delta^{18}O$ values of the water can be reconstructed (e.g., de Winter et al., 2021a,b, 2024; Zhang and Petersen, 2023; Minnebo et al., 2024). By appropriate sampling and binning, directly determined seasonal Δ_{47}-temperatures with an uncertainty of well under 2 °C (95% confidence level) can be achieved (de Winter et al., 2024).

Like the $\delta^{18}O$ thermometer, the Δ_{47} thermometer is sensitive to disequilibrium precipitation. Kinetic effects, caused for example by CO_2 degassing from or CO_2 absorption into the precipitation fluid, may cause inaccuracies in temperature reconstructions, as have been seen with data from non-molluscan taxa (Spooner et al., 2016; Bajnai et al., 2020). These kinetic effects, a subset of possible vital effects, may be recognised by use of the recently developed dual-clumped isotope method, in which clumped isotopologues of mass 48 (e.g., $^{12}C^{18}O^{18}O$ in CO_2) are measured in conjunction with mass 47 isotopologues (e.g., Fiebig et al., 2019, 2021; Bajnai et al., 2020; Swart et al., 2021). Notwithstanding the potential for kinetic effects, clumped isotope analyses on lab-cultured and live-collected specimens suggest that most molluscs precipitate their shells in clumped isotopic equilibrium (Henkes et al., 2013; Huyghe et al., 2022; de Winter et al., 2022). However, as for $\delta^{18}O$, aberrant Δ_{47} values have been found in the juvenile part of oyster shells (Huyghe et al., 2022) and the inner shell layer of some other bivalves (Curley et al., 2023). Δ_{47} values are more sensitive than $\delta^{18}O$ values to post-depositional alteration, adding further complexities to reconstruction of past temperature and seasonality using fossil shells. Closed-system solid-state reordering, a process that can alter the isotopic clumping in a carbonate without changing its isotopic composition, has been demonstrated, especially when samples have been heated above *c.* 100 °C (Stolper and Eiler, 2015), for example during cooking practices (see Section 2.1.1) or via geological processes (Brenner et al., 2018; Henkes et al., 2018; Jimenez et al., 2019). Internal water present in the carbonate can facilitate or accelerate this reaction (Brenner et al., 2018; Nooitgedacht et al., 2021). Use of an abrasive drill to extract samples can cause the thermal and mechanochemical inversion of aragonite to calcite, and change both the Δ_{47} and $\delta^{18}O$ value of the carbonate; it is therefore important to adopt sampling practices that minimise this possibility (Staudigel and Swart, 2016; Schmitt et al., 2024).

An important consideration for seasonality reconstructions using $\delta^{18}O$ or Δ_{47} data is differences in the rate of shell growth between the seasons (and between ontogenetic stages and taxa), and how that relates to sampling resolution and mass spectrometer precision (Zhang and Petersen, 2023). Clumped isotope analysis requires averaging together anywhere from 3 to 30 individual analyses (typically from a total of 3–15 mg of powdered material) to achieve the desired precision for seasonality studies (typically <3 °C at the 95% confidence level). In clumped isotope seasonality studies this has been achieved in different creative ways from fewer larger, more precise analyses to many smaller, less precise analyses, to combining 'summertime' analyses from multiple years of growth (Zhang and Petersen, 2023; de Winter et al., 2024). In the last case, exactly how individual analyses are assigned to a particular season is of vital importance for getting the ultimate seasonal temperatures correct. Several approaches have been suggested to compensate for seasonal change in growth rate and place data on a time axis for better seasonal averaging (e.g., Wilkinson and Ivany, 2002; Goodwin et al., 2003; Wang et al., 2015; Judd et al., 2018; de Winter 2022). However, in cases where the seasonal temperature variability is not readily approximated by a sinusoidal curve (e.g., seafloor data from Virginia and northern North Carolina; Fig. 2), these methods accrue high uncertainty and cannot fully replace chronological information gathered from growth increments. Limitations to sampling parts of the seasonal cycle can be circumvented by improving sampling resolutions with *in situ* methods like SIMS (e.g., Hughes et al., 2023) and SHRIMP (e.g., Aubert et al., 2012), or combining data from multiple taxa that grow during different seasons (e.g., Schöne et al., 2006; Walliser and Schöne, 2020). Growth rate variability can also affect the amount of time that is contained within the sample, depending on the sampling protocol and the shape of the area in a shell cross-section that is sampled, and therefore should be taken into account when deciding how to smooth or average sclerochronological data (Schöne et al., 2022). Issues of growth rate change can be avoided by targeting fast-growing taxa, especially the fastest growing and least interrupted early ontogenetic stages of these, where the possibility of obtaining a complete, high-resolution record within each season makes identification of them less fraught and estimation of maximum and minimum temperatures more accurate (Vriesman et al., 2024).

Generating reproducible intrashell chronologies to place data in one-month or three-month time bins is important to facilitate meaningful comparison between datasets from different times and regions, and between data and model outcomes, since the latter outcomes are reported in the time domain (see discussion in de Winter et al., 2021a,b). However, researchers should be cautious about comparing the seasonal growth of specimens that lived at different depths, as the timing of seasonal extremes can be delayed at greater depth. For example, in Virginia and northern North Carolina (Fig. 2), seafloor maximum temperature at 20 m depth is delayed by up to two months and reduced by 3–4 °C compared to the surface, while in the well-mixed southern North Sea it occurs at the same time (and same temperature) down to 25 m depth and beyond (Fig. 1A).

4. The appropriate amount and timespan of data

4.1. The merit of long, crossdated records

We noted in Section 2.1 the need to document surface conditions in order to specify climate. These conditions also need to be documented for a sufficient number of years to encompass short-term (interannual to decadal) fluctuations and to derive a long-term average. The standard time interval for specifying climate is 30 consecutive years (Arguez and Vose, 2011; World Meteorological Organization, 2017). Only two individual isotope profiles of this length, and at subannual resolution, have been obtained: a $\delta^{18}O$ record spanning the first 39 years of growth of a late Holocene *A. islandica* specimen (Schöne et al., 2005a) and another spanning the first 87 years of growth of a late Pleistocene example of this species (Schöne and Fiebig, 2009). In both cases samples were extracted by milling for standard (*ex situ*) isotope-ratio mass spectrometry, using steps as small as 20 μm in an attempt to maintain high temporal resolution within the context of ontogenetic decline in growth rate. In spite of this measure, the late Holocene shell shows a general reduction in the amplitude of seasonal $\delta^{18}O$ variation after 18 years (Fig. 4) and the late Pleistocene shell after less than 15, in each case no doubt at least partly due to greater time-averaging as a consequence of growth-rate reduction. Given the potentially higher spatial resolution, an *in situ* measurement technique (e.g., SIMS; Hughes et al., 2023) could probably deliver high temporal resolution over a much larger number of years from equivalent material. However, the same can also be obtained from sampling multiple individuals whose lifespans overlap, the necessary temporal alignment being achieved by cross-matching (and hence crossdating) of growth-increment profiles (Black et al., 2019). Under favourable circumstances (representation of all calendar years by the early ontogenetic years of specimens) this enables acquisition of a long, high-resolution record from samples extracted for standard *ex situ* measurement. Moreover, there is also the possibility of obtaining replicate datasets and hence of smoothing out (by averaging) inter-individual differences in the isotopic record of conditions (Mette et al., 2016; Vriesman et al., 2024).

Long, averaged records have been obtained from precisely dated bivalve chronologies founded on live-collected individuals and extended back beyond the birth-dates of these by incorporation of data from dead-collected, crossdated specimens. For instance, using *A. islandica*, a $\delta^{18}O$-derived temperature record at annual resolution has been provided for the period AD 1765–2015 off south-west Iceland (Mette et al., 2023) and for AD 953–2000 off north-east Iceland (Reynolds et al., 2016). Similarly, a record at subannual resolution has been obtained from *A. islandica* for AD 1866–2002 in the central North Sea (Schöne et al., 2005b) and from *Glycymeris glycymeris* for AD 1965–1995 off north-west France (Royer et al., 2013), although entirely from live-collected

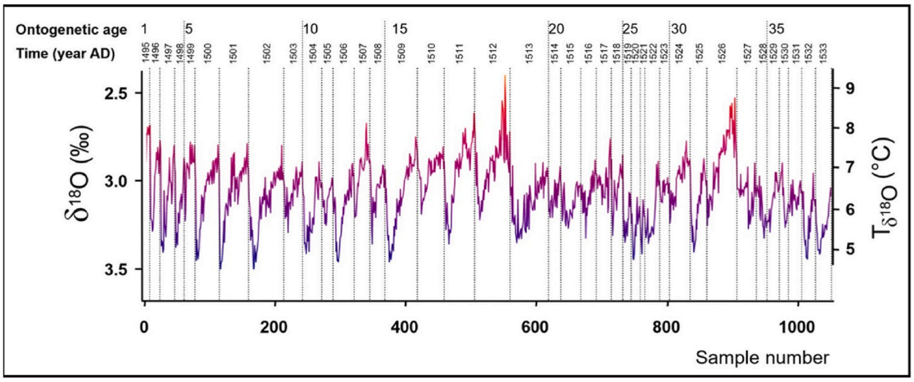


Fig. 4. $\delta^{18}O$-derived temperature record from the first 39 years of growth of a 374-year-old *Arctica islandica* specimen that was collected alive off the north-east coast of Iceland in July 1868. Age and calendar years determined through growth increment analysis. Note the generally lower amplitude of seasonal variation from age 19 onwards. Adapted from Schöne et al. (2005a).

individuals in both these cases. In each of the latter two studies high temporal resolution was achieved through sampling (by milling and drilling, respectively) the early ontogenic stages of specimens.

Comparable records have been obtained from imprecisely dated (‘floating’) bivalve chronologies spanning intervals entirely in the past. Estrella-Martínez et al. (2019) supplied a δ^{18}O-derived temperature record at annual resolution for 175 years of an *A. islandica* chronology from the northern North Sea dating to *c.* 8.2 ka, with the temperatures for 34 of these years being averaged from values provided by two shells. Trofimova et al. (2021) supplied δ^{18}O-derived temperature records at subannual resolution from two shells for 21 years of another northern North Sea *A. islandica* chronology (*sensu lato*) dating to *c.* 9.6 ka, with 11 of these years represented by information from both shells (Fig. 5). The temperature records of Trofimova et al. (2021), the oldest of any kind or resolution from crossdated shells, do not span a sufficient interval to meet the ‘30 consecutive years’ criterion for specifying climate. However, many more years were available for investigation in both shells and these might well have supplied data at subannual resolution through use of a technique (SIMS, or *ex situ* measurement of milled samples) capable of providing results for more closely spaced points than the one (*ex situ* measurement of drilled samples) used to provide the existing information. It is therefore entirely reasonable to suppose that a high-quality (replicated) seasonal temperature record of the requisite length could be obtained from shells of similar antiquity.

Trofimova et al. (2021) selected shells as potential early Holocene examples for crossdating on the basis of morphological (including preservational; Butler et al., 2020) differences from other (presumed younger) shells in material dredged from the seafloor. That this method of selecting approximately contemporaneous individuals was successful suggests that it might be applied to material of an age beyond the limit (*c.* 50 ka) of ^{14}C AMS dating, the method used by Trofimova et al. (2021) to confirm the early Holocene age and potentially overlapping lifespans of the individuals studied. In a situation involving more ancient shells, typically collected from specific beds in an exposed sedimentary sequence, there would be additional taphonomic information available (e.g., articulation and orientation) to assist identification of approximately contemporaneous specimens. However, given the interval potentially represented by a shell-rich horizon (up to tens of thousands of years; Kidwell, 2013; Scarponi et al., 2013; Dexter et al., 2014; Ritter et al., 2023) and the insufficient accuracy of absolute dating techniques to confirm approximate contemporaneity (i.e. potentially overlapping lifespans) in material older than *c.* 50 ka, there is no doubt that achievement of a crossdated chronology from shells of this greater antiquity would involve much trial and error.

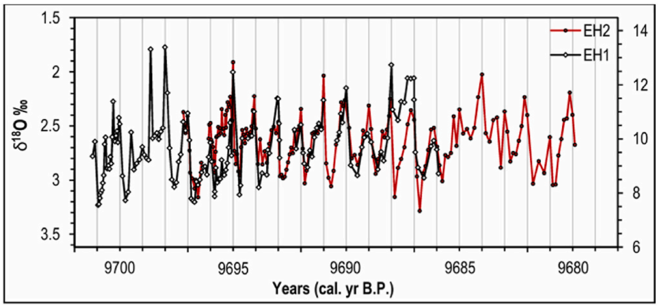


Fig. 5. δ^{18}O-derived temperature records from two cross-matched early Holocene *Arctica islandica* specimens of ontogenetic age 197 (EH1) and 233 (EH2) years from the northern North Sea (from Trofimova et al., 2021; reproduced under the terms of the Creative Commons CC-BY licence). The specific calendar years identified are based on radiocarbon (^{14}C AMS) dating and subject to error. Note the similarity of the temperature records for most of the 11 years over which they overlap. Although cross-matched, these shells do not provide a master chronology (i.e., a chronology *sensu stricto*) because of insufficient replication (see Black et al., 2019 and references therein).

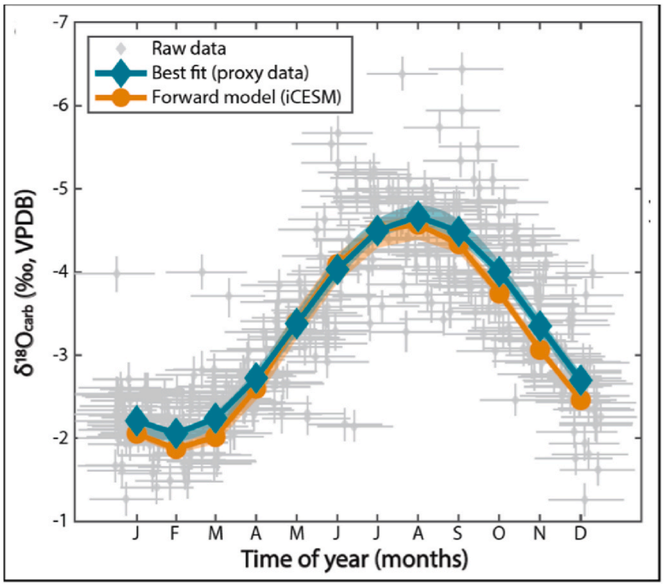


Fig. 6. Best-fit sinusoid for δ^{18}O data from an early Eocene bivalve (*Venericardia hatcheplata*) of the U.S. Gulf Coastal Plain compared with a forward-modelled δ^{18}O sinusoid for the time and area (reproduced from Ivany and Judd, 2022, with the permission of the Rightsholder: Annual Reviews, Inc.). Values are relative to the Vienna Pee Dee Belemnite (VPDB) standard, as normal for carbonates. The raw δ^{18}O data (grey diamonds) were temporally aligned using the GRATAISS model (Judd et al., 2018); the associated horizontal and vertical lines indicate the range of date and analytical uncertainty, respectively. The forward-modelled sinusoid was obtained using the isotope-enabled Earth System Model (iCESM) of Zhu et al. (2020), modified after Tierney et al. (2020). See text for further information on how Ivany and Judd (2022) constructed this diagram.

Notwithstanding the difficulties of crossdating ancient shells (or other accretionary biomineralised hardparts), the opportunities that would be opened up by doing so surely justify investment of the required time and effort. Trofimova et al. (2021) point out that (non-crossdated) *A. islandica* specimens have supplied isotopic (δ^{18}O) information on marine climate in the early Pleistocene (Crippa et al., 2016; von Leesen et al., 2017), and the same is true for the Pliocene (Buchardt and Símonarson, 2003; Vignols et al., 2019; Johnson et al., 2022; Cudennec et al., 2024). Furthermore, a specimen of *A. islandica* (together with individuals of other bivalve species) has supplied seasonal temperatures based on Δ_{47} for the mid-Piacenzian Warm Period (MPWP) of the Pliocene (de Winter et al., 2024). Application of the Δ_{47} approach to crossdated *A. islandica* (or other) shells from the MPWP would enable acquisition of long, seasonally resolved and accurate temperature records for this, the most recent interval in Earth history when global mean surface temperature was as high as anticipated for the end of the present century (Dowsett et al., 2013). Such records would enable detailed and rigorous testing of the models available for prediction of regional climate in a warmer world, building on data/model comparisons like that of de Winter et al. (2024).

A. islandica only extends back to the Oligocene (Marquet, 2005) but there are other bivalve taxa of almost the same longevity available for investigation of earlier warm interludes—e.g., species of *Glycymeris*, modern examples of which live for up to 192 years (Reynolds et al., 2013). Indeed, great longevity is not necessarily required for construction of a crossdated chronology: Schöne (2003) was able to construct one for AD 1982–1999 from shells of the bivalve *Chione* with a mean age of less than 10 years, although in this case no isotopic investigation of temperature was undertaken. As yet, no Δ_{47} data have been acquired from crossdated shells, but there is no doubt that they could be, and seasonal temperatures obtained from the data, given promising results from individual shells (Zhang and Petersen, 2023; de Winter et al., 2024).

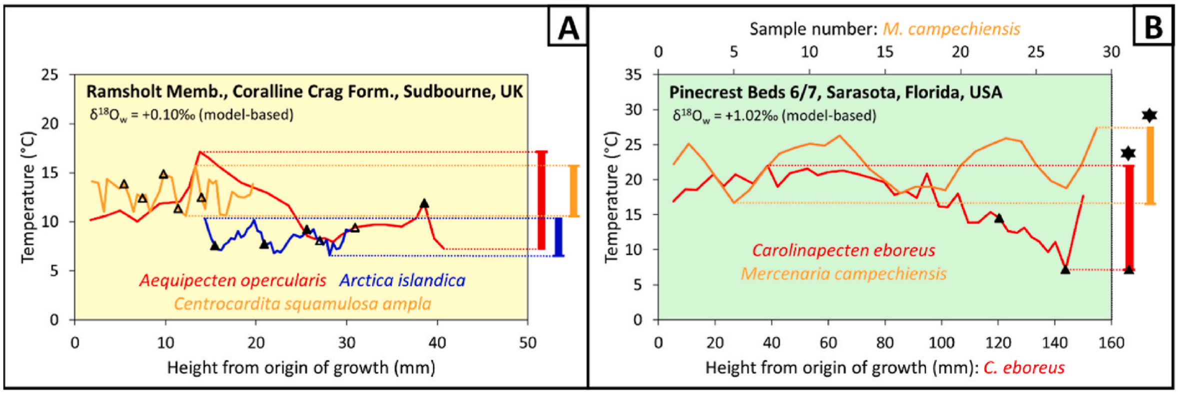


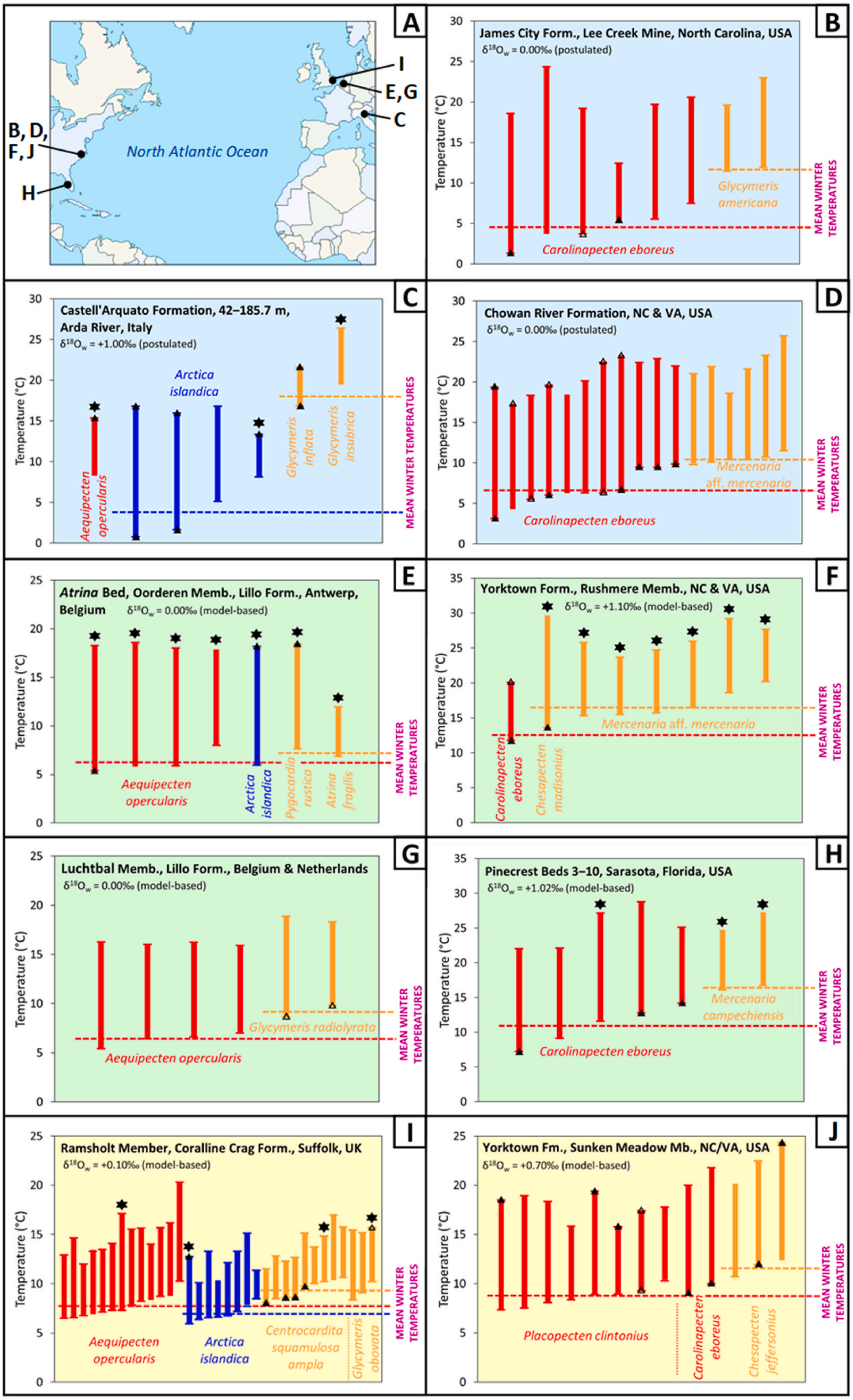
Fig. 7. Representative $\delta^{18}O$-derived temperature profiles from bivalve species of the Early Pliocene (yellow background) in the UK (A) and Late Pliocene (green background) in the USA (B), showing interspecies differences in the maximum and minimum temperatures recorded and the methodology involved in constructing Fig. 8. Temperatures calculated using the equations of O'Neil et al. (1969) for calcite sample sets and Grossman and Ku (1986) for aragonite sample sets, employing the indicated value for water $\delta^{18}O$ ($\delta^{18}O_w$), with an adjustment of −0.27‰ for the VSMOW/VPDB scale difference (Gonfiantini et al., 1995). Positions of moderate/major growth interruptions (temporary slowdowns if not actual cessations of growth) shown by filled triangles, and of minor growth interruptions by open triangles (interruptions recognised by 'growth lines' and classified by the prominence of these; see Johnson et al., 2017, 2021, 2022, 2024, for illustrations). Absence of a cap from a temperature-range bar signifies use of a profile-end value (potential underestimate for summer or overestimate for winter; Johnson et al., 2022). Stars in B indicate that the specimens are from effectively the same bed (Jones and Allmon, 1995). Neither growth interruptions nor differences in the temporal resolution of sampling can account for the disparities in seasonal temperature shown in each of A and B; for instance, growth interruptions in *C. squamulosa ampla* (A) are minor and do not coincide with the (high) winter temperature values, and *Mercenaria campechiensis* (B) shows a higher summer temperature than co-occurring *Carolinapecten eboreus* despite lower-resolution sampling. Shell $\delta^{18}O$ data from Jones and Allmon (1995) and Cudennec et al. (2024).

4.2. The potential inappropriateness of averaging data from short, non-crossdated records

Carré et al. (2012) described a method for quantifying the uncertainty associated with climate reconstructions from ontogenetic profiles of skeletal geochemistry, and Ivany and Judd (2022) described a method specifically for quantifying the uncertainty associated with analytical error in $\delta^{18}O$ and the date assigned to values (day within a year). The latter authors applied their approach to a large body of data from short (<10 years), non-crossdated profiles of a bivalve species (*Venericardia hatcheplata)* from an early Cenozoic (early Eocene) formation in the U.S. Gulf Coastal Plain, deriving a suite of 365-day sinusoids fitted to random selections of possible $\delta^{18}O$ values and dates, and selecting those with R^2 at or above the 95th percentile to define an uncertainty envelope. They then took the mean of the latter fits as the typical pattern of seasonal variation in shell $\delta^{18}O$ and by implication temperature, thus explicitly taking account of uncertainty to specify seasonality in the interval and area concerned. The mean sinusoid is very similar to a shell-$\delta^{18}O$ sinusoid forward-modelled from time- and area-specific seawater $\delta^{18}O$ and temperature values provided by an Earth System Model (Fig. 6). The close match suggests that the type of isotope data obtained from shells in this case (short profiles from a fairly large number of non-crossdated specimens, rather than long profiles with substantial temporal overlap from a few crossdated specimens) can, with appropriate handling, provide an accurate picture of climate.

While the approach of Ivany and Judd (2022) may be generally applicable to greenhouse intervals like the early Cenozoic, and would of course provide a more reliable picture of climate at those times than small datasets, it might not yield the most meaningful results for icehouse intervals like the late Cenozoic. This is because of their characteristic pattern of high-frequency (*c.* 100 kyr) fluctuation between two fundamentally different climate states (glacial and interglacial) and the possibility that collections from a sedimentary formation or even a single bed (see Section 4.1) might include shells sufficiently different in age to be representative of both. Averaging results from such material would give a picture of mean climate for that unit (useful for comparison with results from contiguous units and hence for documentation of long-term climate trends) but not of the range of climate states during its deposition. That shells representative of different climate states may be very closely associated is shown by seabed samples from the Gulf of Cádiz (south-western Iberian Peninsula) which contain, alongside the shells of mollusc species living in the area now, the shells of species whose present southern range limit is much farther north—e.g. the bivalves *A. islandica* and *Mya truncata* and the gastropod *Neptunea antiqua*, which do not now live south of the English Channel; and the bivalve *Chlamys islandica*, which does not now live south of southern Norway (Urra et al., 2023). Eight specimens of two of these 'Boreal Guest' (BG) species (*A. islandica* and *N. antiqua*) were ^{14}C-dated by Urra et al. (2023), yielding ages between 21.9 and 14.6 ka, corresponding to the last glacial (Marine Isotope Stage 2). Amongst the species collected there is, according to Urra et al. (2023), 'no taphonomic clue to differentiate which are BGs remaining from times of the last glaciation and which are recently dead specimens from the modern assemblage (or from any intermediate age).' Thus one would not have suspected mingling of shells representative of two climate states without knowledge of the thermal affinities of modern examples of the species concerned and/or of an age difference between specimens from ^{14}C-dating.

Cudennec et al. (2024) obtained $\delta^{18}O$ evidence of temperature from a late Cenozoic (Early Pliocene) formation in the UK containing *A. islandica* and a carditid bivalve (*Centrocardita squamulosa ampla*) whose closest modern relative (*C. aculeata*) is restricted to the Mediterranean Sea and a comparable latitudinal range in the eastern North Atlantic (including the Gulf of Cádiz). They determined substantially cooler temperatures from *A. islandica* than from *C. squamulosa ampla,* including from preservationally and taphonomically indistinguishable specimens from the same bed (Fig. 7A and 8I). The close association of these species mirrors the situation described by Urra et al. (2023), with the support for mingling of shells representative of two climate states coming from direct (isotopic) evidence of a temperature difference rather than the indirect evidence of radiometric dating. Notwithstanding their preservational and taphonomic similarity, it was reasonable to expect, from the geographic distribution of modern representatives/close relatives, that the two species concerned would supply different indications of temperature. One might not suspect this from a set of extinct species lacking close modern relatives, and go on to average data representative of two climate states, ultimately achieving an insight only into the mean state rather than each modal state. Use of (averaged, short-term) data from a single species (as in the study of



(caption on next page)

Fig. 8. δ^{18}O-derived temperature ranges from individuals of bivalve species in various late Cenozoic units around the northern North Atlantic (B–J; locations in A). Yellow background = Early Pliocene; green background = Late Pliocene; blue background = Early Pleistocene. Methodology and symbols explained in Fig. 7. Data arranged from left to right in order of increasing winter temperature within species, and divided into cool-water species (blue), warm-water species (gold) and some pectinid species that were evidently tolerant of cool waters but in many cases also of warm waters (red). The winter temperatures that these pectinids supply are lower than those provided by some other species (gold) from the same units, including individuals from the same bed (indicated by stars). Shell δ^{18}O data from Krantz (1990), Jones and Allmon (1995), Johnson et al. (2009, 2017, 2019, 2022, 2024), Valentine et al. (2011), Winkelstern et al. (2013), Crippa et al. (2016), Vignols et al. (2019) and Cudennec et al. (2024), with additional data (see Supplementary Information 1) obtained on behalf of ALAJ for a few further shells (four *Carolinapecten eboreus* in B and one in D; one *A. opercularis* in each of C and E). Very similar results to those from *Mercenaria* in the Chowan River (D) and Yorktown (F) formations were obtained by Braniecki et al. (2024) from this genus in correlative units (Waccamaw and Duplin formations, respectively) in North Carolina.

Ivany and Judd, 2022) is one way in which this risk could be avoided, but requires that the species is eurythermal and that investigators look out for the substantial range in δ^{18}O (or Δ_{47}) which would exist in a mix of individuals from glacial and interglacial intervals. Given the longer duration of glacials, one would expect in such mixed material a skew in the temperature distribution towards cooler values. Exactly this is observed in data from the UK Early Pliocene, where winter temperatures from the eurythermal pectinid bivalve *Aequipecten opercularis* (present range Norway to the Mediterranean; Vignols et al., 2019) are sometimes as warm as those from *C. squamulosa ampla* but mainly close to the cool values obtained from *A. islandica* (10 of the 13 *A. opercularis* specimens represented in Fig. 8I give winter temperatures lower than the highest winter temperature from *A. islandica*). The disparate isotopic temperatures (especially for winter) obtained from bivalve taxa in various other late Cenozoic units around the North Atlantic area (Fig. 7B; 8B-H, J) are an indication that two climate states may be represented at each of these sites, arguing strongly against multispecies-averaging and strongly for investigation of data from eurythermal species (e.g., pectinids; see Fig. 8) to confirm climate fluctuation and determine its extent. It might be the case that the time and effort involved in an investigation of range and skewness amongst data from short, non-crossdated profiles would be better rewarded by instead attempting to crossdate the shells of longer-lived species, followed by acquisition of replicated data for the continuous 30-year intervals needed to characterise climate. It would, of course, be necessary to use either a eurythermal long-lived species or both a 'warm' and 'cool' one to characterise each climate state. 'Warm' and 'cool' long-lived species certainly exist now (see Section 2) and isotopically demonstrated examples of such taxa are known from the past, even from the same bed (e.g., some of the 'warm' *Glycymeris* and 'cool' *A. islandica* specimens represented in Fig. 8C–I). Time-specific characterisation of climate, and resolution of climate change over quite short intervals, may therefore be achievable goals using sclerochronology.

5. Case history

The use of bivalve isotope data to interpret seasonal sea-surface temperatures, and the use of this information in turn to interpret temperatures from other proxies, can be illustrated with the following case history based on material from the Early and Late Pliocene Yorktown Formation of Virginia. We find winter and summer surface temperatures respectively lower than and similar to the corresponding seasonal temperatures inferred (for the Late Pliocene) from the planktonic foraminiferal assemblage, and summer surface temperatures similar also to the temperatures obtained (again for the Late Pliocene) from alkenone analysis. These results indicate that planktonic foraminiferal assemblages provide an overestimate of winter surface temperature but an accurate estimate of summer surface temperature, and that alkenones provide (accurate) estimates of summer, not annual mean surface temperature.

The case history involves δ^{18}O- and Δ_{47}-temperature data from the calcitic (in the sampled outer layer) pectinids *Carolinapecten eboreus* and *Placopecten clintonius*, both extinct species. The dotted curves in Fig. 9A are temperature profiles from specimens of these species, calculated from the high-resolution shell δ^{18}O data of Johnson et al. (2017, 2019) using the equation of O'Neil et al. (1969) and modelled values of water δ^{18}O from Williams et al. (2009): +1.1‰ for the Late Pliocene Morgarts Beach Member; +0.7‰ for the Early Pliocene Sunken Meadow Member (−0.27‰ scale correction applied, as in the temperature calculations for Figs. 7 and 8). Accompanying the curves are boxes indicating the height range of Δ_{47}-samples (four of about 15 mg each per specimen) and the variation in Δ_{47}-temperatures (mean ± 1 standard error) obtained from them. Each sample was analysed in three or four replicates, with temperatures calculated using Equation (1) of Petersen et al. (2019). Notwithstanding the within-sample variation in the Δ_{47}-temperatures obtained, it is clear that the pattern of values through the ontogeny of each specimen is similar to that of δ^{18}O-temperatures, implying a fairly uniform water δ^{18}O value over the interval represented. We determined a water δ^{18}O value for each specimen by averaging values back-calculated from each of the four mean Δ_{47}-temperatures and the corresponding mean shell δ^{18}O value, again using the equation of O'Neil et al. (1969). The values obtained (+0.58‰ for LPLI-MACP 2; −0.07‰ for LPLI-MACP 4; +0.11‰ for EPLI-MACP 2; +0.04‰ for VA2) were then used in place of the modelled water δ^{18}O value to derive a new temperature profile for each specimen (continuous curves in Fig. 9A).

There is of course uncertainty attached to the ultimate temperature profiles, particularly relating to the averaging of Δ_{47}-temperatures and shell δ^{18}O values in back-calculation of water δ^{18}O values, but also to the potential variability of water δ^{18}O values during the life of the specimens. The mean standard error for water δ^{18}O for each specimen (i.e., the mean of the standard errors for the four samples) is 0.62‰ for LPLI-MACP 2, 0.73‰ for LPLI-MACP 4, 0.76‰ for EPLI-MACP 2 and 0.58‰ for VA2. These moderate values translate into uncertainties of about 2.7 °C, 3.2 °C, 3.3 °C and 2.4 °C, respectively, in the recalculated temperature profiles (precise values cannot be given because the uncertainty varies with temperature due to the quadratic form of the δ^{18}O-temperature transfer function of O'Neil et al., 1969). Notwithstanding the fact that these uncertainties relate to the standard errors of the water δ^{18}O values calculated for the sectors of ontogeny sampled for Δ_{47}, they are probably fair estimates for each shell as a whole because the recalculated temperature profiles (derived using the average of the sectoral means for water δ^{18}O) generally pass through the boxes specifying the standard error of sectoral Δ_{47}-temperatures.

A summer temperature can be readily determined from each recalculated profile but because the profiles from *C. eboreus* are too short to include a winter inflection, only 'maximum' winter temperatures are supplied by this species. The value from specimen EPLI-MACP 2 is nevertheless only a little above the accurate winter temperature determinable from *P. clintonius* in the same unit (Early Pliocene Sunken Meadow Member), and there is a similarly small difference between the accurately determinable summer temperatures from *C. eboreus* and *P. clintonius* in this unit. These similarities between the species, together with the fact that the likely modern descendant of *P. clintonius*, *P. magellanicus* (a cool-water species), precipitates its shell in near oxygen-isotope equilibrium (Krantz et al., 1984; Tan et al., 1988; Chute et al., 2012), suggest that δ^{18}O-temperatures from *C. eboreus*, including specimens LPLI-MACP 2 and 4 of the Late Pliocene Morgarts Beach Member, are not influenced by any vital effect.

The Late Pliocene specimens, which date specifically from the mid-Piacenzian Warm Period (Dowsett et al., 2021), show summer temperatures about 2 °C higher than the Early Pliocene specimens, a finding consistent with evidence of climatic warming over the Pliocene in Virginia from faunal-assemblage evidence (e.g., Ward et al., 1991).

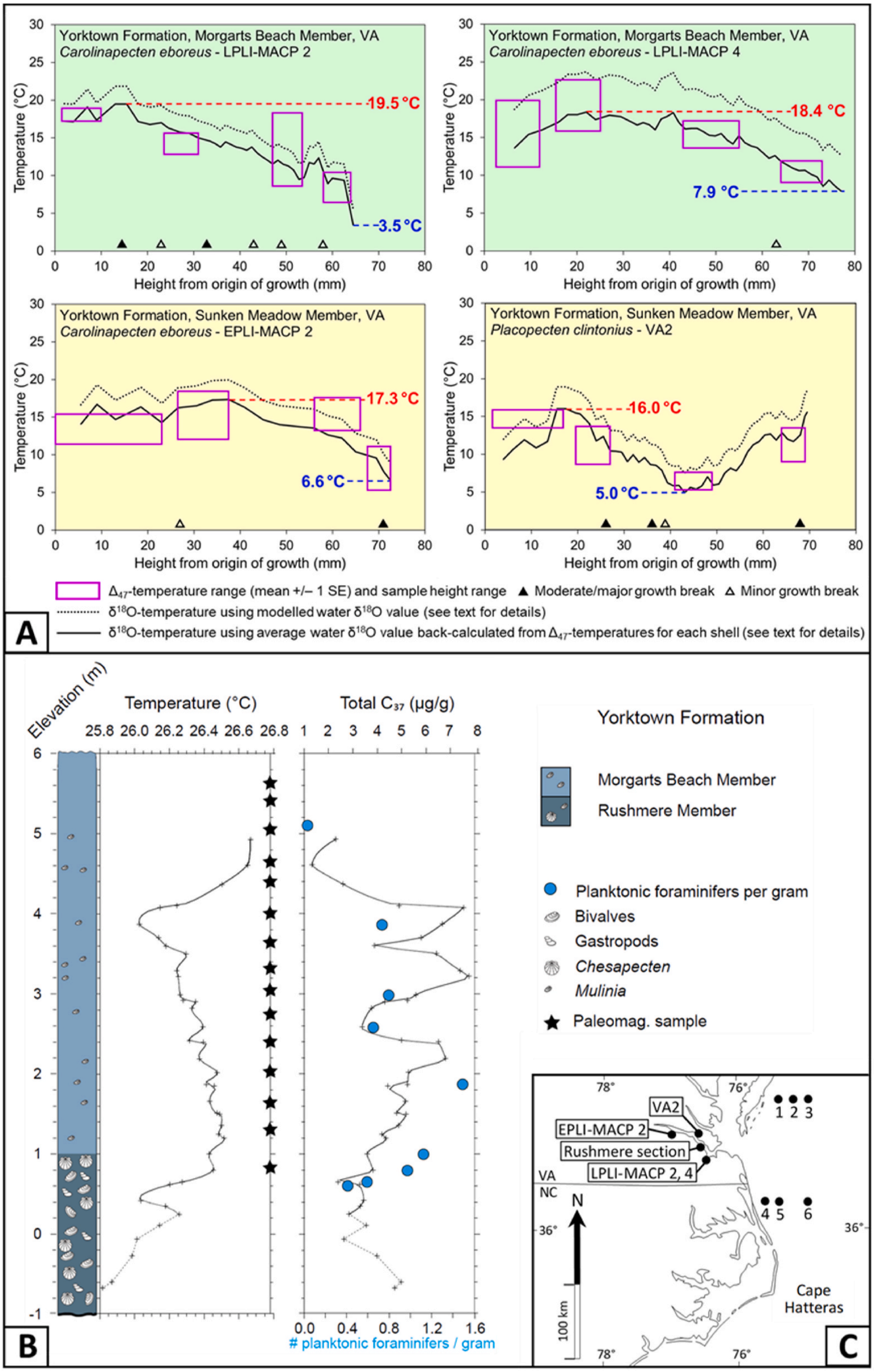


Fig. 9. A: Isotopic temperatures from pectinid bivalve specimens of the Early Pliocene (yellow background) and Late Pliocene (green background) in Virginia, USA (see text for further explanation; specimen codes and shell δ^{18}O data from Johnson et al., 2017, 2019; Δ_{47} data, together with Δ_{47}-temperatures, back-calculated water δ^{18}O values, associated uncertainties, etc., in Supplementary Information 1). B: Alkenone-unsaturation ($U_{37}^{K'}$) temperatures, together with total C_{37} (a measure of primary production) and the numerical abundance of planktonic foraminifers (a measure of temperature), through the Rushmere and Morgarts Beach members of the Yorktown Formation at the Rushmere section, Virginia (adapted from Dowsett et al., 2021). These members span the mid-Piacenzian Warm Period (Dowsett et al., 2021). C: location map for the Rushmere section, the studied bivalve specimens and the stations (1–6) for the modern temperature data depicted in Fig. 2.

However, all but the uppermost (Moore House) member of the Yorktown Formation is considered to have been deposited at depths of 20–40 m (Krantz, 1991; Dowsett et al., 2021) so, on the evidence of 2–3 °C variation in summer seafloor temperature over this depth range on the modern Virginia and northern North Carolina shelf (Fig. 2), one cannot rule out the possibility that the warmer isotopic summer temperatures for the Late Pliocene reflect a difference in water depth (shallower) rather than climate. Seasonal estimates for surface temperature are anyway needed to define climate. While winter surface temperatures would have been much the same as (*P. clintonius*) or perhaps somewhat below (*C. eboreus*) the lowest recorded δ^{18}O-temperatures, summer surface temperatures would almost certainly have been higher than the highest recorded δ^{18}O-temperatures, given the inferred depth and likelihood of summer stratification. We can use the modern summer seafloor−surface temperature differences in Fig. 2 to infer summer surface temperatures in the range 20.7–26.5 °C from EPLI-MACP 2, 19.7–25.2 °C from VA2, 22.9–28.7 °C from LPLI-MACP 2 and 21.8–27.6 °C from LPLI-MACP 4 (inclusion of the relevant uncertainties would of course increase these ranges). The ranges from the last two specimens span the range of temperatures derived by alkenone thermometry from the same specific unit at an adjacent location (Fig. 7B and C), supporting recent interpretations of other alkenone temperature data as summer rather than annual mean values (e.g., Bova et al., 2021). The summer surface ranges from LPLI-MACP 2 and LPLI-MACP 4 also span the summer temperature (25.9 °C) estimated from the planktonic foraminiferal assemblage of the same unit at another adjacent location (Dowsett and Wiggs, 1992). However, the 'maximum' winter temperatures from LPLI-MACP 2 and LPLI-MACP 4 (3.5 °C and 7.9 °C, respectively) are very much lower than the winter temperature (18.7 °C) indicated by the planktonic foraminiferal assemblage, showing the value of a sclerochronological approach incorporating isotopic analysis for an accurate understanding of seasonal temperature variation. It is worth noting that the commonly used Δ_{47}-temperature calibration of Anderson et al. (2021) gives temperatures about 2 °C lower than that of Petersen et al. (2019), so the conclusion that foram-assemblage analysis provides an overestimate of winter surface temperature is independent from the clumped-isotope temperature calibration. It is of course possible that the evidence of equilibrium fractionation in *C. eboreus* supplied above is misleading—i.e., that *P. clintonius*, which occurs with *C. eboreus* in the Early Pliocene Sunken Meadow Member and gives similarly low winter temperatures, differs from its probable descendant *P. magellanicus* in exhibiting a vital effect. However, until a firm indication of this is supplied by different (warmer) temperatures from precisely contemporaneous specimens of other species, there is no reason to doubt that *P. clintonius* precipitated its shell in isotopic equilibrium with ambient seawater, and *C. eboreus* likewise.

The sclerochronological approach could certainly have been applied more fully and effectively in this case (e.g., by investigation of more, ontogenetically older specimens from the same location as other sources of temperature information). However, the relatively limited data obtained give considerable insights into seasonal temperatures and the meaning and accuracy of temperatures from other proxies. More sclerochronological data would no doubt provide further, more refined insights.

6. Conclusions

Accurate estimates of seasonal sea-surface temperature from proxies are required for detailed and rigorous evaluation of outputs from numerical climate models. The accretionary biomineralised (principally calcium carbonate) hardparts of certain marine organisms offer a means of obtaining such data through sequential ontogenetic sampling and isotopic (δ^{18}O and Δ_{47}) analysis of the material. However, the subjects chosen for investigation should ideally be ones whose isotopic temperature profiles directly represent local surface conditions—e.g., shallow-water examples of benthic (essentially sessile) taxa. Pelagic organisms are unlikely to provide equivalent data in deeper-water settings because they commonly migrate vertically or laterally, or are in some cases too short-lived to record a full annual cycle of temperature variation. At least in the mid-shelf depth range (20–40 m) benthic organisms are a better choice, though an upward adjustment of summer isotopic temperatures may be necessary to compensate for the effects of thermal stratification. To at least mid-shelf depths, and subject to the existence of a distinct winter season (resulting in the loss of stratification) and to continuing growth of the investigated species, winter isotopic temperatures from benthic organisms are likely to accurately represent surface conditions, and to provide a far better picture of winter surface temperature than is afforded by other proxies. The very best data (both for winter and summer temperature) will usually be supplied by samples from early ontogeny, when growth is most rapid and least interrupted, hence providing scope for obtaining a record of high temporal resolution and completeness.

Benthic molluscs (bivalves and gastropods) are a suitable choice for investigation of marine climate through isotope thermometry because their shells generally contain a faithful record of ambient temperature, and where this is not the case offsets are commonly systematic and can be removed by a mathematical process. However, the originality of the signal must be investigated through studies of shell preservation, and for the δ^{18}O-thermometer an accurate estimate of water δ^{18}O is required. This can be derived through Δ_{47}-thermometry on the same material, although there may be moderate uncertainty attached to the water δ^{18}O value obtained, and hence to δ^{18}O-temperatures calculated with it. Alternatively, direct estimates of seasonal temperature can be made from Δ_{47} profiles of benthic molluscs, with lower uncertainty where appropriate sampling and data processing are undertaken. Minute pelagic molluscs (pteropod gastropods) may be able to provide at least some insight into surface seasonality in the ocean basins from ontogenetic δ^{18}O data, and should be investigated to this end using *in situ* analytical techniques, e.g., SIMS.

Climate parameters are defined as the mean state over a period of 30 consecutive years. In these terms, seasonal temperatures are not adequately specified by isotopically-derived values for a few years, from a few shells, although of course any information is better than none. Statistical analysis of large datasets from numerous shells, each providing information for a few years, is probably sufficient for proper characterisation of climate in greenhouse intervals. However, in icehouse intervals such as the late Cenozoic, marked by high frequency (high amplitude) climate fluctuation, this approach may not specify climate at any one time. Continuous 30-year records from long-lived bivalve species, preferably averaged from crossdated shells, are a superior source of insight into climate and climate change in these intervals, provided that either a eurythermal species or both a 'warm' and 'cold' species are used. Although difficult to obtain, such records provide a means of both detailed and rigorous evaluation of the outputs of numerical climate models.

Authors' contributions

ALAJ conceived the paper and led the writing, except the first draft of Section 3, which was written by NJW. Others provided information and comments according to their particular expertise: BRS in isotope sclerochronology in general; SVP and IZW in clumped isotope sclerochronology (including provision of data for Fig. 9); HJD in late Cenozoic (including Recent) climatology and oceanography; JFC in molluscan sclerochronology; EMH in molluscan ecology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to Whittney Spivey for compiling the data represented in Fig. 2, Kotryna Savickaite and Samantha Worne for undertaking the additional δ^{18}O analysis contributing to Fig. 8, Thom Hopkin for extracting the samples used to obtain the Δ_{47}-temperature data in Fig. 9, Michal Kowalewski for alerting us to useful papers on time-averaging in molluscan shell assemblages, and Tamara Trofimova and Linda Ivany for discussing the content of Figs. 5 and 6, respectively. Lucia Angiolini (Department of Earth Sciences, University of Milan), Annelise Folie (Royal Belgian Institute of Natural Sciences), Roger Portell (Florida Museum of Natural History and Adam Pritchard (Virginia Museum of Natural History) kindly loaned specimens in their care for isotopic analysis, enabling us to supplement the data from previous studies represented in Figs. 8 and 9. Internal review was conducted by Lynn Wingard and Deborah Stoliker of the U.S. Geological Survey; journal review was conducted by Donna Surge and an anonymous reviewer. We thank all these reviewers for their helpful comments, which led to considerable improvements in the paper. This work is a contribution to the project 'The limits of ecological uniformitarianism—a sclerochronological investigation', funded by the Leverhulme Trust (RPG-2021-090). ALAJ, BRS, J-FC and EMH are members of the project team and thank the Trust for its support. ALAJ also gratefully acknowledges an award from the National Environmental Isotope Facility (2535.0422) for isotope analytical services at the British Geological Survey, Keyworth, UK. SVP was supported by a Sloan Research Fellowship and NSF-CAREER award #2237429. NJW thanks the Netherlands Science Foundation (NWO) for financial support through a personal NWO VENI fellowship (VI.Veni.222.354) and an NWO-XS grant (OCENW.XS23.4.125), and the Flemish Research Council (FWO) for support through the FWO Scientific Prize Climate Research. HJD was funded from the USGS Ecosystems Land Change Science Program.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2024.109068.

Data availability

The additional data used to create Figs. 8 and 9 is provided in Supplementary Information 1 (the references cited in that are given in Supplementary Information 2).

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