

# RECONSTRUCTING PALEOSEASONALITY FROM ACCRETIONARY SKELETAL CARBONATES—CHALLENGES AND OPPORTUNITIES

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**ABSTRACT.**—Seasonal temperature variation at any location is most strongly regulated by the annual cycle of solar insolation, which is controlled by latitude and orbital parameters; other factors are continentality, albedo feedbacks, stratification and advection, and water depth. Seasonal minima, maxima, and range vary with change in mean annual temperature (MAT) across latitudes; seasonal variation in ocean-water temperature is highest in the mid-latitudes. Seasonal temperature range at depth is likely to be less than that at the sea surface. The chemistry of accretionary biogenic carbonate can preserve a record of seasonal temperature variation experienced by an organism over some portion of its ontogeny. Sampling early parts of ontogenies will yield a more complete temperature record because growth is faster (so temporal resolution is higher) and more likely to be continuous throughout the year. Biases due to preferential season of growth can be recognized by characteristic patterns of isotope data when plotted versus distance along the ontogenetic trajectory. Multiple years are needed to reliably characterize seasonal temperature range and inter-annual variability for a stratigraphic horizon in a given region; single-shell studies are less useful in this regard unless they contain very long records. Data from multiple time intervals or regions using the same taxon, sampled the same way, and from the same facies can establish meaningful trends in average temperature and seasonal range. Deep-time studies exploring seasonal temperature extremes and ranges can be coupled with proxies for mean annual temperature to offer a more complete understanding of changing climate conditions through time.

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## INTRODUCTION

SEASONALITY OF temperature variation has been somewhat of an enigma for paleoclimate research. While seasonal temperature extremes and the range they define are important from both a climatic and biologic perspective, rarely do we have that information available in the deep past. Knowledge of winter and summer temperatures are key to interpreting estimates of mean annual temperature (MAT) because those records can be biased by preferential production of proxy materials during one season over another. In addition, seasonal temperature extremes and ranges are included in the output of paleoclimate models and could prove very useful for evaluating competing models, but few data are as yet available for such comparisons. As well, the distributions of most organisms are limited by seasonal extremes much more than they are by MAT, and so the effects of climate change on the biota are easier to interpret

or predict when seasonal information is available. Nevertheless, despite its evident value as a complement to MAT, seasonality is mentioned in paleoclimate studies only occasionally, largely due to the difficulty associated with constraining it.

Seasonality is an elusive variable to quantify in deep time because of the necessity for sub-annual temporal resolution. Strategies for estimating aspects of the annual temperature cycle in terrestrial settings come from fossil plant assemblages or the presence of key taxa that are diagnostic of seasonal temperature range or extremes (e.g., Greenwood and Wing, 1995; Eldrett et al., 2009). A link between leaf physiognomic properties and seasonal temperature range also has been suggested (Wolfe, 1993; Spicer et al., 2004, but see Royer, this volume). Isotope-derived paleotemperatures from paleosol carbonate nodules may also offer insights into warm-season temperatures (see Passey, this volume). In the marine realm, microfossil assemblages have been linked

to temperature through transfer functions and modern analogs for a number of years (e.g., Imbrie and Kipp, 1971; CLIMAP, 1981; Pisias et al., 1997), but proxy-based estimates of seasonal range are possible as well, even using microfossils. Proxy data coming from short-lived plankton that grow preferentially in warm or cold months can provide indications of seasonal extremes or range (e.g., Haug et al., 2005; Leider et al., 2010). In addition, high-resolution, single-test studies of foraminifera can reveal variability expressed within or among individuals that may have grown their shells at different times over the year, and thereby can approximate seasonality, or at least indicate how it changes over time (Spero and Williams, 1989; Sadekov et al., 2008; Wit et al., 2010; Haarmann et al., 2011, see discussions in Pearson this volume). While these approaches certainly provide insight into seasonality, none directly record the complete annual cycle of warming and cooling. For this, sequentially ordered data with high (intra-annual) temporal resolution over one or more years are required. In the sedimentary record, deposits with this potential are rare, and occur only in specific and restricted settings. Varved terrigenous clastic and evaporate mineral units may provide annually resolved data, as can accumulations of seasonally produced biological material and speleothems. The best of these datasets can provide long and rather spectacular inter-annual records, but the intra-annual signal is often restricted to an on-off or high-low pattern with no obvious chronometer. While such records have been used with success to study inter-annual climate patterns like El Niño Southern Oscillation in deep time (Crowley et al., 1986a; Ripepe et al., 1991; Huber and Caballero, 2003; Galeotti et al., 2010; Lenz et al., 2010; Davies et al., 2011), often, they are not able to extend to records of temperature seasonality (but see Huang et al., 2001; Fairchild et al., 2006; Orland et al., 2009, 2012 for examples using speleothems).

Intra-annual resolution, while elusive in ancient sedimentary sequences, is not rare in the deep-time rock record from the perspective of a paleontologist. Many skeletonized organisms have hard parts that grow by accretion over one or more years. Seasonal environmental variations influence the growth of many species, therefore, growth banding in accretionary skeletons (or wood) often can reasonably, if cautiously, be interpreted as annual in nature (see extensive literature on sclerochronology, e.g., Pannella and

MacClintock, 1968; Hudson et al., 1976; papers in Rhoads and Lutz, 1980; Williams et al., 1982; Jones, 1983; Jones and Quitmyer, 1996; Schöne et al., 2002, ; and for a remarkable recent example, see Butler et al., 2010; Karney et al., 2011). Mineralized tissues record in their chemistry some measure of temperature at the time of precipitation. In sequentially sampled accretionary material, this can be used to reveal intra-annual temperature variation, and verify the time-significance of growth banding. This realization goes back even to the formative days of stable isotope paleothermometry, when Urey et al. (1951) subsampled a Cretaceous belemnite and found regular variation in  $\delta^{18}\text{O}$  with growth that they interpreted as annual in nature (see also discussion in Pearson this volume). As long as the relationship between chemistry and temperature is understood, and if the material is not subsequently modified by the organism or by diagenesis, fossilized remains can be used as paleoenvironmental archives with intra-annual temporal resolution that can provide surprisingly detailed information.

Accretionary biogenic carbonates, such as the shells of fossil mollusks, offer an opportunity to recover information about seasonality in Earth's deep past. High-resolution sampling and isotope analysis along the growth history of an organism can yield a detailed record of the temperatures experienced by an individual throughout some portion of its lifetime. Capturing a number of years within a particular stratigraphic horizon yields not only a robust measure of seasonal temperature range for that habitat, but also information about inter-annual variability. With adequate coverage, both of these variables can be examined in a temporal or geographic context to see how they relate to change in mean annual temperature. The approach is not without its challenges: sampling resolution can smear the seasonal signal, organisms do not necessarily accrete carbonate throughout the year, and the depth at which benthic aquatic organisms live correlates roughly with the seasonal range they experience. Nevertheless, with a bit of care, these kinds of data can offer new insights on the climate system and the anticipated consequences of global change.

This contribution will review methods to derive and interpret paleoseasonality in Earth's deep past using the oxygen isotopic compositions ( $\delta^{18}\text{O}$  values) of sequentially sampled accretionary carbonates. The focus of this paper is mainly on archives preserved in marine macrofossils, and on efforts to recover information about paleotem-

perature in particular. Similar approaches to those described here can also be applied to freshwater macrofossils (e.g., Dettman and Lohmann, 1993; Patterson et al., 1993; Smith and Patterson, 1994; Patterson, 1996; Dettman et al., 1999; Dettman et al., 2001; Wurster and Patterson, 2001; Kohn and Cerling, 2002; Morrill and Koch, 2002; Verdegaal et al., 2005; Versteegh et al., 2009; Nützel et al., 2010), but the pure temperature component embedded in such records often is difficult to separate from change in the isotopic composition of water associated with seasonal variation in other climate variables such as precipitation, evaporation, or moisture source. A substantial and growing body of work in terrestrial settings exists as well, again largely reflecting seasonality in some aspect of the hydrologic cycle. The phosphate or carbonate component of hydroxyapatite in fossil mammal teeth can record seasonal variation in oxygen isotope values (e.g., Koch et al., 1989; Bryant et al., 1996; Fricke and O'Neil, 1996; Kohn et al., 1998; Sharp and Cerling, 1998; Passey and Cerling, 2002; Fisher et al., 2003; Fox et al., 2007; Fan and Dettman, 2009; Higgins and MacFadden, 2009; Van Dam and Reichart, 2009; Passey, this volume; Souron et al., in press), as can the shells of land snails (Leng et al., 1998; Baldini et al., 2007), and the chemistry of organic matter in growth bands of well-preserved fossil wood has yielded remarkable insights into seasonal variation in precipitation and humidity in ancient forests (Jahren and Sternberg, 2008; Schubert et al., 2012). In addition, in both aquatic and terrestrial settings, seasonality in the physical environment often is accompanied by variation in biological productivity and other ecosystem properties, and these can be assessed with other types of proxies—most importantly, stable carbon isotopes. A review of that literature is outside the scope of this paper (but see McConnaughey, 1989a; McConnaughey et al., 1997; Heikoop et al., 2000; Gillikin et al., 2007; Koch, 2007; McConnaughey and Gillikin 2008; Passey, this volume).

#### **DOMINANT CONTROLS ON SEASONAL TEMPERATURE RANGE—PATTERNS ON THE MODERN EARTH**

Before discussing processes associated with reconstructing temperature seasonality from accretionary carbonates, it is worthwhile to first consider what we mean by the term itself, the factors that control seasonal temperature variation on

the modern Earth, and the patterns we might therefore expect to see in the fossil record.

The term 'seasonality' refers to cyclic variation in some measurable property that has a period of one year. This paper focuses on temperature seasonality, but one could also consider seasonality in precipitation, primary production, or for that matter, the detrended value of the stock market or the number of winter coats sold in Syracuse, NY. Temperature seasonality can be measured in any number of environments, including air (at various heights above the ground or water surface), soil, the sea surface, and at any depth within the ocean. Values for each of these will differ even if recorded over the same annual cycle, and so care must be taken when comparing different types of data. In addition, seasonality can be measured over a range of temporal resolutions and the data can be smoothed in a variety of ways; outcomes are predictably different at different levels of resolution. In theory, one could report seasonality as the difference between the highest daytime temperature and the lowest nighttime temperature over a year, and this range would be substantially higher than that determined by the difference between maximum and minimum monthly means. From a climatological perspective, seasonality typically is reported as the amplitude of the mean monthly temperature cycle. Lastly, the way people have measured even the same parameter varies with practice and historical circumstance. For example, raw recorded sea-surface temperatures have risen over the last century, in part because of the change from sampling water in buckets to sampling water in engine intakes; measured marine air temperatures have changed over time because of the shift to ships with higher decks and ships with metal construction that heats more during the day (e.g., Folland and Parker, 1995; Jones et al., 1999; Folland 2005). While these are examples using actual measurement of variables today rather than proxy measures from the rock record, the same sorts of concerns exist for geological studies. Awareness of, and correction for, differences in collecting and reporting style is important.

By far the most important variable influencing the seasonal range of temperature at a given place on the Earth's surface is solar insolation. The amount of radiation that Earth as a whole receives from the sun each year is a function of distance from the sun, and currently, this equals an annual average of about 1360 watts per square meter ( $W/m^2$ ) at the top of the atmosphere (Kopp

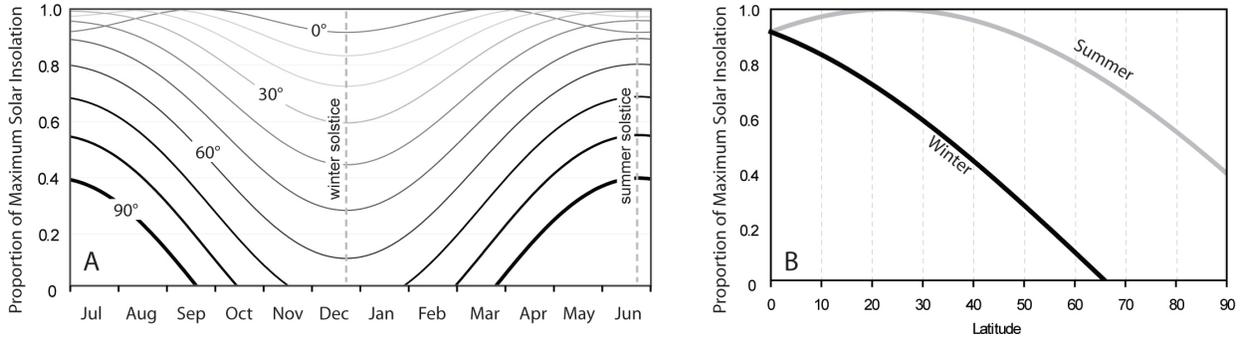


FIGURE 1.—Seasonal change in the proportion of solar radiation received per unit area on Earth. A) Variation in insolation throughout the year at different latitudes in the Northern Hemisphere; B) Insolation by latitude on the summer and winter solstices. The tropics exhibit two annual peaks in insolation as the sun moves back and forth overhead, and latitudes above the Arctic Circle ( $\sim 66.5^\circ\text{N}$ ) experience darkness for some portion of the year. These factors give rise to sinusoidal intra-annual variation in the amount of energy received from the sun at any given latitude (B). Temperatures on the Earth's surface reflect these variations in insolation with latitude and over the annual cycle, creating seasons. Air temperature at the surface generally tracks insolation, modified by the effects of albedo and heat capacity, but lags it by roughly a month. Sea-surface temperatures generally track the approximately sinusoidal variation in air temperature (except where sea ice is present), lag behind them, and are less variable due to higher heat capacity of the oceans (Prandle and Lane, 1995; Rayner, 2003).

and Lean, 2011). If the Earth were flat and oriented perpendicular to the plane of the ecliptic, then every place on the planet would receive the same solar irradiance,  $1360 \text{ W/m}^2$ , because the sun's rays would be striking normal to the surface of the planet. But, because Earth is spherical, in most places the surface is inclined relative to incident radiation so that the same amount of incoming solar energy is distributed across a broader area. Per unit area, the amount of energy received annually from the sun as one moves away from the equatorial region. Latitude therefore determines the amount of incident radiation received over an annual cycle (Figure 1A).

If the spin axis of Earth were oriented normal to the plane of the ecliptic, and if our orbit were perfectly circular, then solar influx at any given latitude would be constant throughout the year. There would be no seasonal variation, and energy flux per unit area would decrease away from the equator as a function of latitude. Earth's orbit, however, is not perfectly circular and its spin axis is tilted with respect to the plane of our orbit. Both of these factors give rise to sinusoidal intra-annual variation in the amount of energy received from the sun at any given latitude (Figure 1B). Temperatures on the Earth's surface reflect these variations in insolation with latitude and over the annual cycle (Figure 2). Hence, we have seasons. Air temperature at the surface generally tracks insolation, modified by the effects of albedo and

heat capacity (discussed below), but lags it by roughly a month. Sea-surface temperatures likewise generally track the approximately sinusoidal variation in air temperature except where sea ice is present (see below), lag behind them (e.g., see Figure 3B, C), and are less variable due to higher heat capacity of the oceans (Prandle and Lane, 1995, Rayner, 2003).

At a planetary scale over geologic time, seasonality is influenced by orbital parameters and their effects on insolation. The tilt of the earth's rotation axis (present-day =  $\sim 23.5^\circ$ ) determines how different the seasonal extremes will be. At times of low obliquity, winters and summers are less distinct. Likewise, the eccentricity of Earth's orbit around the sun will influence seasonal range, with low eccentricity corresponding to lower seasonality. In an eccentric orbit, precession of the axis controls how different the seasons are in the Northern versus Southern hemispheres. Today, the Southern Hemisphere points towards the sun (summer) at perihelion (when Earth is closest to the sun), and away from the sun (winter) at the planet's farthest point from the sun. Hence, the Southern Hemisphere experiences somewhat more extreme seasons with respect to irradiance than does the north. Likewise, in an eccentric orbit, Earth is moving around the sun faster at perihelion than at aphelion, and therefore, the perihelion seasons will be shorter than those when the planet is farther from the sun and moving more

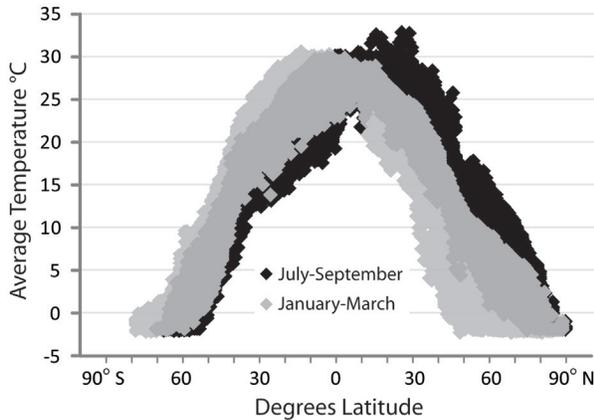


FIGURE 2.—Average sea-surface temperatures for July–September (black;  $n = 31,873$ ) and January–March (gray;  $n = 34,193$ ) plotted by latitude. Unfiltered data from Locarnini et al. (2010),  $1^\circ$  grid.

slowly. Milankovitch variation in Earth's orbital parameters give rise to periodic change in insolation and seasonality, which ultimately drive long-term climate shifts. Northern Hemisphere summer insolation, at least in part, has driven glacial-interglacial cycles over the last 2.5 million years (e.g., Hays et al., 1976), but there are consequences in deeper time as well. Coxall et al. (2005), for example, showed that the early Oligocene onset of Antarctic glaciation occurred during an interval of low eccentricity, low obliquity, and hence low seasonality. Cooler summers allowed for ice growth in a world where falling  $\text{CO}_2$  (DeConto and Pollard, 2003; Pagani et al., 2005; 2011) and changes in ocean circulation (Scher and Martin, 2006; Lyle et al., 2007; Cristini et al., 2012) already predisposed the continent to ice growth. In addition, De Conto et al. (2012) pointed out that times of both high eccentricity and high obliquity give rise to summers with greater solar insolation or longer duration (depending on the pole); during greenhouse climates, such as the Paleogene, these conditions are more likely to destabilize permafrost and release  $\text{CO}_2$ , leading to even warmer so-called hyperthermal episodes.

A second prominent control on the seasonal range of temperature variation expressed over the planet's surface is continentality (Crowley et al., 1986b). Water has a higher heat capacity than land, so marine settings experience smaller fluctuations in temperature with the seasons. Conti-

ental interiors can exhibit extreme seasonality, while seasonal change in sea-surface temperatures in ocean basins is comparatively muted. As an example, the average winter-summer temperature difference in Minnesota (winter =  $-14^\circ\text{C}$ , summer =  $15^\circ\text{C}$ , range =  $29^\circ\text{C}$ ; see <http://www.dnr.state.mn.us> for data) is significantly larger than that at a similar latitude in the Pacific Ocean (roughly  $7\text{--}13^\circ\text{C}$ , range =  $6^\circ\text{C}$ ; data from Locarnini et al., 2010). Shelf settings, from which many of the examples discussed below are drawn, will reflect the competing influences of marine and continental conditions.

Albedo also plays a role in modifying the influence of incoming solar radiation and temperatures expressed at Earth's surface. Snow and ice are highly reflective, and so cold regions with this cover tend to experience positive feedbacks that make them cooler than otherwise expected for their location. The effect of snow/ice albedo on air temperature differs in continental versus marine settings. On land, the transition from seasonal to permanent snow cover has a strong influence on summer temperatures, cooling them and reducing the overall seasonal range. In maritime settings, however, the formation of sea ice has a stronger effect on winter air temperatures (Denton et al., 2005; Rinke et al., 2006). The ocean has a low albedo, and so areas with open water in winter absorb more incoming radiation and stay warmer. Once temperatures cool enough to form sea ice, however, ice grows until it is thick enough to insulate the ocean from further heat loss to the atmosphere. While the air can become significantly colder, giving rise to extreme winter temperatures and high seasonality, ocean temperatures do not fall below about  $-2^\circ\text{C}$  unless the water is unusually salty. The unusually high seasonality seen in a variety of air temperature proxies during cooler intervals of the Holocene in the northern latitudes has been attributed to the presence of seasonal sea ice blocking the moderating influence of the ocean in winter (Denton et al., 2005). Lastly, clouds can have a significant effect on albedo and thereby influence the amount of incoming radiation that makes it through to Earth's surface. The higher albedo of clouds is in part balanced by the insulating effect of water droplets and particulates in the atmosphere, so there is much uncertainty about their impact, seasonal or otherwise (see, e.g., discussion in Tollefson, 2012).

Seasonality of maritime temperatures is also modulated by stratification and circulation. Upwelling can significantly modify the seasonal

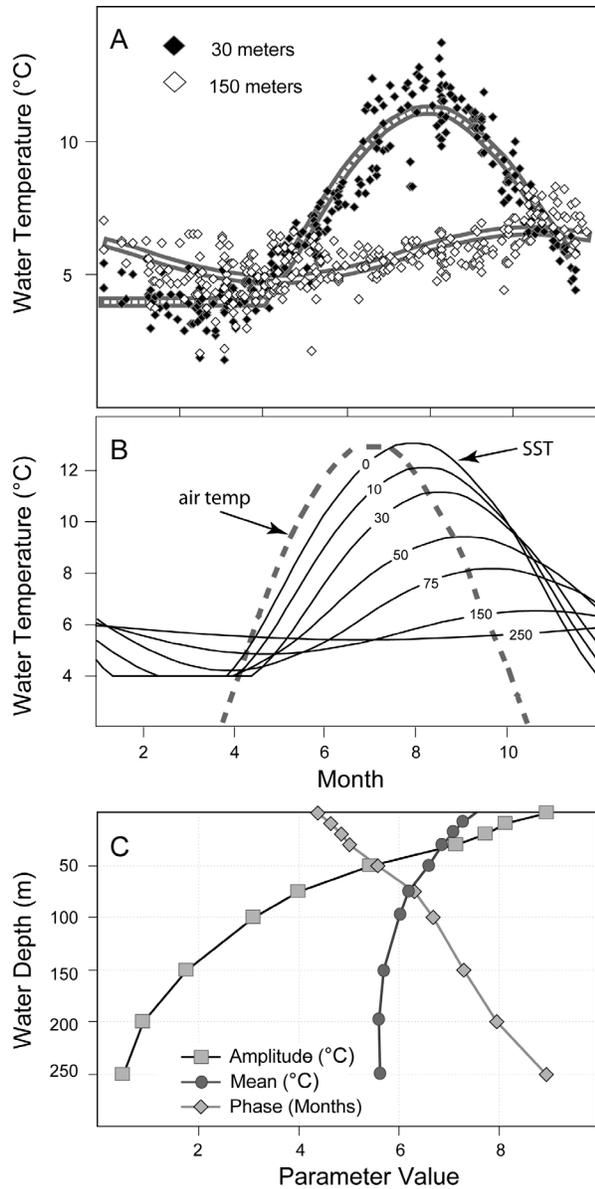


FIGURE 3.—Temperature with depth from the Gulf of Alaska (Royer, 1989, 1993; Xiong and Royer, 1993), as summarized in Wilkinson and Ivany (2002). A) Water temperatures over the year for 30 m and 150 m depths; B) best-fit curves through seasonal temperature data from the sea surface (SST) to 250 m, with air temperature for comparison; C) change in the mean, amplitude, and phase of the seasonal cycle with depth. Note that seasonal amplitude decreases with depth, primarily in association with a decrease in summer temperatures, and consequently mean temperature also decreases with depth. With greater depth in the water column, the time of maximum temperature occurs progressively later in the year (phase shift in panel C).

range in temperatures expressed in shallow/surface water (and air), bringing cooler water up from depth in winter when the water column is well mixed, with the effect of increasing the observed seasonal range. Conversely, seasonal thermal stratification can reduce the range of temperatures on the bottom in comparison to well-mixed water columns (Prandle and Lane, 1995). In this case, bottom waters experience less warming in summer, bringing about a reduction in seasonal range (e.g., Weidman et al., 1994; Austin et al., 2006). Advection plays an important role too. Liu et al. (2005) found that western boundary currents have the effect of increasing seasonal range when they flow toward the equator (cold currents), and the opposite effect when warm water flows poleward. The Gulf Stream, for example, brings a tongue of comparatively warm and less-seasonal water far to the north of where those conditions are typical (Liu et al., 2005).

Perhaps most critical for the goal of extracting seasonality data from benthic macrofossils preserved in marine shelf settings is the influence of water depth on seasonal range. As depth increases in the water column, the magnitude of seasonal temperature variation decreases, even independent of the effects of stratification (Figure 3A, B; Prandle and Lane, 1995). The decrease in seasonal amplitude with depth is not likely to result from symmetric decreases in summer maxima and increases in winter minima, but rather is more often the result of cooling summers with depth. Winter temperatures tend to be more consistent with depth because the water column is more likely to be well mixed and therefore isothermal on the shelf at that time. Summer temperatures at the surface, however, are likely to exceed those at depth because warm surface waters are isolated from deeper cool water due to solar heating of the surface and resulting thermal stratification (Figure 3B). This results in a shift in mean annual temperature with depth from that seen at the surface (Figure 3C), with more stratified water columns showing progressively lower mean temperatures with depth (Prandle and Lane, 1995; Austin et al., 2006).

Interaction of the above variables means that the observed pattern of seasonal range in sea surface temperatures with latitude (Figure 4) is not directly equivalent to that expected solely from the distribution of solar irradiance. Indeed, there are minima near the equator, where insolation is high all the time, and near the poles, where water stays cold all the time. From the equator to the

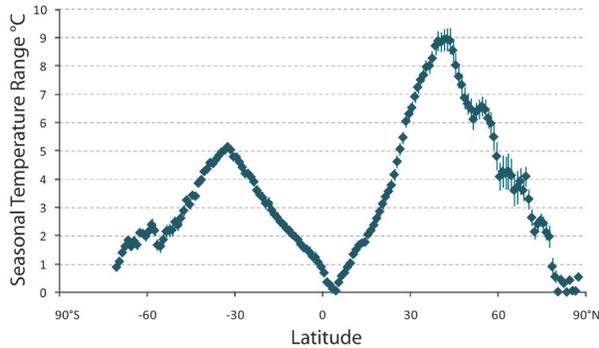


FIGURE 4.—Seasonal sea surface temperature range by latitude from Locarnini et al. (2010). Data are as in Figure 2. Seasonality is somewhat reduced because winter and summer temperatures are averaged over the three months of the season. Error bars are  $\pm 1$  standard deviation as calculated for the difference between two means.

poles, seasonality increases and then decreases as winter and summer insolation diverge moving away from the tropics, and as winter temperatures become increasingly constrained to near freezing temperatures and summers cool approaching the poles. Interestingly, the patterns in each hemisphere are not symmetrical—peaks in seasonal range occur at different latitudes in each hemisphere, and the overall seasonality of the Northern Hemisphere is greater than the southern (Figure 4; see also Jones et al., 1999), despite insolation showing the opposite pattern. The influence of greater continentality in the Northern Hemisphere and a glaciated Antarctica in the south overwhelm the insolation signal to produce this modified pattern. Climate models have now reached a point where this asymmetry is faithfully reproduced for present-day conditions, and a similar phenomenon is manifest in models for the early Cenozoic Earth (e.g., Huber and Caballero, 2011). There is also variation in this pattern within ocean basins, as shown in Figure 5, where advection influences the position of maximum seasonal range with latitude (Shearman and Lentz, 2010).

Lastly, while perhaps an obvious point, it is important to keep in mind that temperature data are variable both within and among years. Daily or monthly mean temperatures collected throughout a year do not fall perfectly on a sinusoid, but rather exhibit noise around it. Data on air temperatures from Ann Arbor, MI, serve to illustrate this point (Figure 6A, see also Figure 3A), and marine data show a similar pattern. Generally, the variation defines a trend that can be approximated

by a sinusoid, and the variation around that best-fit sinusoid is Gaussian (Figure 6B). Note that variation increases with increasing temporal resolution, and hence highly resolved data will yield more extreme individual values than coarsely resolved data (compare daily to monthly means in Figure 6A). Likewise, there is variation in mean temperature and seasonal range from one year to the next, and that variation is also Gaussian (Figure 6C, D). Given this, it is clear that multiple years are required to characterize mean annual temperature and seasonal range accurately for a given place. The higher the degree of interannual variation, the more years that are needed to provide confidence in the estimate.

### MICROSAMPLING ACCRETIONARY RECORDS FOR PALEOSEASONALITY

#### Choice of materials for sampling

Skeletonized organisms selected for seasonal or mean annual paleotemperature reconstruction should meet several criteria. First, and perhaps most important, unless you are interested in doing your own calibration work or are concerned only with the delimitation of seasons or years but not their actual temperatures, the taxon selected should be one for which the relationship between temperature and skeletal  $\delta^{18}\text{O}$  is known.

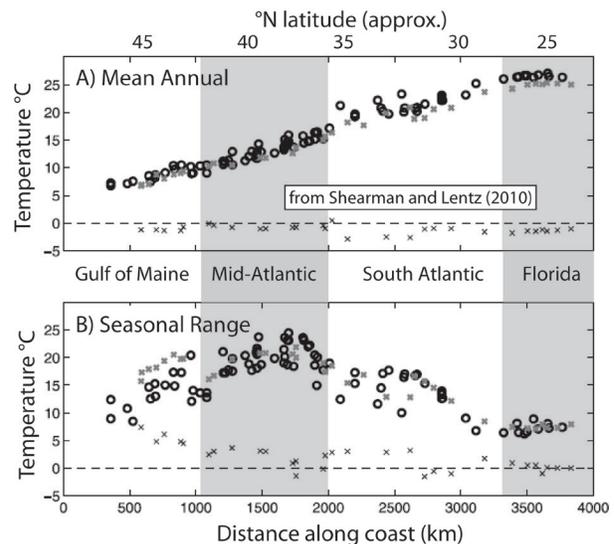


FIGURE 5.—Mean temperature (A) and seasonal range of temperature (B) for coastal SSTs (black circles), atmospheric temperatures (gray crosses), and the difference between them (black crosses) on the Atlantic coast of the US, from Canadian border at left to the Dry Tortugas at right. Figure modified from Shearman and Lentz (2010).

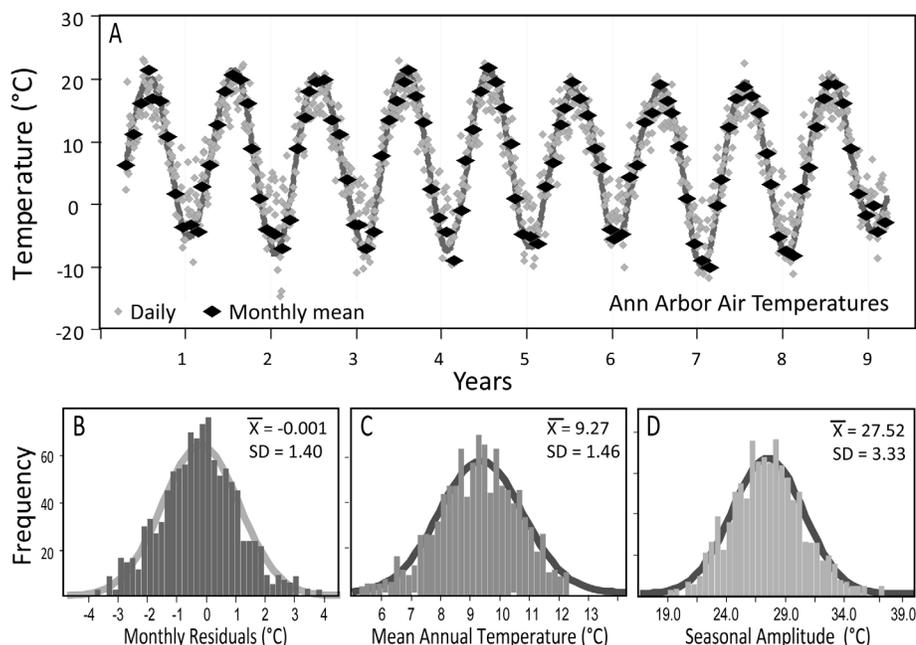


FIGURE 6.—Variation in air temperatures from Ann Arbor, Michigan, derived from the National Climate Data Center's Summary of the Day database (<http://www.ncdc.noaa.gov/ol/ncdc.html>). A) Daily (gray diamonds) and monthly (black diamonds) means with best-fit sinusoid over a portion of the record from January 1897–December 1907. B) Frequency distribution of differences between measured monthly mean Ann Arbor air temperatures and those calculated assuming sinusoidal seasonal change for a 91-year record of Ann Arbor air temperature (of which panel A is a subset); note a mean near zero. C, D) Best-fit sinusoid showing interannual variation in mean annual temperature and seasonal range, respectively, through a 91-year record of Ann Arbor air temperature. See Wilkinson and Ivany (2002) for further explanation.

A number of higher taxa are known to generally precipitate biominerals in isotopic equilibrium, and these are the ones from which most data come from: mollusks, articulate brachiopods, many foraminifera, ahermatypic corals, sclerosponges, bryozoans, polychaetes, and fishes (otoliths). Characteristically out of equilibrium because of vital effects are the hermatypic corals, echinoderms, many benthic and larger foraminifera, and calcareous algae (Anderson and Arthur, 1983; McConnaughey, 1989a; Wefer and Berger, 1991; Böhm et al., 2000; Baumiller, 2001; Mas et al., 2010; see also Grossman, this volume, Passey, this volume). Hermatypic corals can yield beautifully long and detailed records (e.g., Swart et al., 1996; Hughen et al., 1999; Watanabe et al., 2011) and their isotope values are consistently related to temperature, but each taxon has its own calibration equation (e.g., Weber and Woodhead, 1972; Swart, 1983; McConnaughey, 1989b; Roulier and Quinn, 1995; Leder et al., 1996). In the deep-time record, unless the taxon chosen is extant (or has close extant relatives) and has been calibrated,

absolute temperatures obtained will be somewhat suspect. Seasonal range, however, is less subject to calibration uncertainties because both maximum and minimum temperatures will be similarly offset from equilibrium.

While mollusks are nearly always found to be in isotopic equilibrium with respect to oxygen, a number of living taxa have been studied specifically to validate their use as paleotemperature recorders in the recent and deep past, in both marine (e.g., Arthur et al., 1983; Jones et al., 1983; Grossman and Ku, 1986; Goodwin et al., 2001; Surge et al., 2001; Schöne et al., 2006; Surge and Walker, 2006; Fenger et al., 2007) and freshwater settings (e.g., Dettman et al., 1999; Verdegaal et al., 2005; Goewert et al., 2007; Versteegh et al., 2009). The same is true of brachiopods to a somewhat lesser extent (Carpenter and Lohmann, 1995; Buening and Spero, 1996; Curry and Fallick, 2002; Yamamoto et al., 2010a), and some have cautioned about vital effects (Yamamoto et al., 2010b). Otoliths of fishes have received a good deal of attention due in large part to their

utility in fisheries research (Devereux; 1967; Kalish 1991a, b; Iacumin et al., 1992; Patterson et al., 1993; Radtke et al., 1996; Thorrold et al., 1997; Weidman and Millner, 2000; Høie et al., 2004; Storm-Suke et al., 2007; Dorval et al., 2011). While most of these authors above find that precipitation is close to equilibrium, it is not clear why that should be given that precipitation takes place inside the head of a fish rather than in contact with seawater; there are some indications of vital effects as well (Kalish, 1991a; Thorrold et al., 1997; Storm-Suke et al., 2007). For higher taxa that produce carbonate in oxygen isotopic equilibrium with seawater, paleotemperature equations based on empirical work are available for high- and low-magnesium calcite and aragonite (see detailed discussions in Pearson this volume, and Grossman this volume), in some cases specifically calibrated under warm or cool conditions.

Second, the oxygen isotope value of carbonate is dependent upon both the temperature of precipitation and the isotopic composition of the water from which it precipitates. If determination of paleotemperature is the ultimate goal, then it is wise to choose materials from settings in which the isotopic composition of water is anticipated to be constant and reasonably well constrained. Open, fully marine conditions are best in this regard. The oxygen isotopic composition of fresh water usually is significantly more negative, and its values depend upon latitude, elevation, distance from its source, and evaporation (e.g., Craig and Gordon, 1965; Siegenthaler, 1979; Rozanski et al., 1993; Coplen and Kendall, 2000; Bowen and Wilkinson, 2002; Dutton et al., 2005, see also discussion in Passey this volume). Composition often varies seasonally, and in some cases, that variation is more than what might be expected from seasonal temperature change. Similarly, brackish water settings mix varying amounts of fresh and salt water, often seasonally, and hence are difficult to constrain due to uncertainties about the composition of the freshwater end-member and salinity (Ingram et al., 1996; Surge et al., 2001). While the surface ocean exhibits heterogeneity in isotopic composition associated with evaporation and precipitation, these patterns are fairly well understood (Schmidt et al., 1999; Bigg and Rohling, 2000). The whole-ocean value is consistent and reasonably well constrained for the ice-free early Cenozoic and, with somewhat less certainty, the same is true for the Neogene as well (e.g., Shackleton and Kennett, 1975; Zachos et al.,

1994, see extensive discussion and references in Pearson this volume). Therefore, if a choice is available, fully marine taxa are more likely to offer interpretable information with respect to paleotemperature.

Third, chosen taxa should produce an accretionary skeleton with annual growth increments thick enough to enable reasonable sampling resolution. This will depend upon the type of analytical work planned and the tools available for sampling (see below), but typically chosen groups are the mollusks, brachiopods, fish (otoliths), and corals. For those with access to laser, synchrotron, microprobe, or ion-probe technologies, much finer sampling resolution is possible for isotopic or elemental work, so smaller or slower growing taxa become more tractable (see, e.g., Weidel et al., 2007; Kozdon et al., 2011; Limburg et al., 2011). Fine-scale growth increments should be visible, persistent along their length, and uninterrupted. Taxa with discontinuous/episodic growth (e.g., some gastropods) or those capable of significant remobilization of carbonate following initial deposition (e.g., some unionid bivalves) should be avoided if the goal is a continuous climate record. Growth banding in brachiopods can be difficult to recognize and interpret (Buening and Carlson, 1992). A variety of techniques are available to enhance the visibility of growth increments (e.g., see papers and appendices in Rhoads and Lutz, 1980; Schöne et al., 2005a; Karney et al., 2011); digital manipulation of images also can be quite effective.

Fourth, the organism sampled ideally should have an ecology such that it remains in one place for the duration of its life. Sessile benthos are ideal, and mobile benthos that do not move far are also good choices. Organisms that swim pose problems because of the potential for migration, both geographically and up and down in the water column, which can have a significant impact on the resulting isotope (or elemental) trajectories (e.g., Weidman and Millner, 2000; Rowell et al., 2005; Weidel et al., 2007; Limburg et al., 2011). The same is true for migrating terrestrial animals (e.g., Fricke et al., 2011).

Lastly, material chosen should be carefully screened for diagenetic alteration. If the original isotopic composition has been altered post-depositionally, then  $\delta^{18}\text{O}$  values will no longer reflect earth-surface conditions at the time of growth. Sharp (2007) reviewed the literature and summarized the qualities that suggest samples are less likely to be altered: 1) skeletal mineralogy,

such as aragonite or high-Mg calcite, is diagenetically unstable, and that mineralogy is retained; 2) original skeletal mineralogy is low-Mg calcite, a diagenetically stable phase; 3) seasonal variation in isotope values occur along the growth trajectory; 4) skeletal  $\delta^{18}\text{O}$  values from marine organisms are more positive than secondary carbonate associated with meteoric diagenesis, which tends to be negative; 5) the material is non-luminescent and/or has low Mn and Fe content, which tend to be introduced during diagenesis. Retention of primary shell microtextures also is suggestive of unaltered material, but replacement phases can closely mimic original crystal fabrics in some cases (Turekian and Armstrong, 1961; Towe and Hemleben, 1976; Budd and Hiatt, 1993); SEM evaluation may be necessary to discriminate among samples (Cochran et al., 2010). Interestingly, Olson et al. (2012) found that crystal orientations of modern bivalve nacre as revealed by a suite of new microscopy techniques correlate with the  $\delta^{18}\text{O}$  values of shell determined using secondary ion mass spectrometry (SIMS), and therefore with the temperature of precipitation. This work may offer the potential for a structural paleothermometer that can reveal seasonality even without geochemical analysis. Pearson (this volume) and Grossman (this volume) discuss various approaches to assess the potential for alteration of biogenic carbonates.

### **Sampling: how, where, and how much?**

Sampling of accretionary carbonate to produce powders for mass spectrometry can be done by hand or with use of a computer-controlled microsampling system. Choice of approach depends on the spatio-temporal resolution of the carbonate, the desired temporal resolution of the study, and the three-dimensional shape of the growth axis. In any case, samples are collected by drilling/milling lines of carbonate parallel to growth increments (so that each sample comes from carbonate precipitated at the same time) and in an ontogenetic sequence. Hand sampling may be more practical when complex, three-dimensional shapes are involved, such as high-spined gastropods, or when shells grow fast enough and attain a size large enough (usually early in ontogeny) that sufficient temporal resolution is ensured. When sampling fossil material on an outer surface as opposed to a cross section, the surface should be very clean, free of any adhering cement or matrix, and free from microborings that might harbor cement or micrite. Light abrasion of the surface to expose

fresh shell material is advised as long as growth increments are not obscured. Hand-held dental drills and drill bits (also used for milling) are available from Brasseler (brasselerusa.com) and are more precise than a Dremel™ (or similar) rotary tool, although the latter are fine for low-resolution work.

Milling is required for very high spatial resolution (on the order of tens of microns), and is most easily done on polished cross sections through an ontogenetic sequence (Figure 7). Sections are best prepared along the line of maximum growth (for the most expanded record possible) and such that the surface of the section is normal to growth banding. This way, the vertically oriented drill bit stays within the same growth increment as it penetrates below the surface of the section. Samples are mounted below a fixed drill on a computer-controlled moving stage. A digital video camera focused through a microscope provides the interface between the computer and the mill, enabling the user to digitally define sampling paths on the image of their specimen and specify depth of drilling. Some microsampling systems enable sampling on a three-dimensional surface, so it is possible to mount (e.g.) a complete bivalve shell, the excised top of a low-spined snail, or a tooth without sectioning. Several milling systems are available, and the most widely used is the MicroMill made by ESI's New Wave Research (formerly Merchantek). It is also possible to construct a system from individual components following guidelines originally provided in Dettman and Lohmann (1995). Additional details about milling accretionary carbonates can be found in Dettman and Lohmann (1995) and Wurster et al. (1999); Spötl and Matthey (2006) offer a comparison of methods in the context of sampling speleothems.

Spatial sampling resolution is on the order of tens of microns (or less), and is limited by the width of the chosen drill bit tip, the ability of the user to digitize growth increments accurately, and the sample size required for analysis. Depending on the mass spectrometer and whether it is coupled to an automated carbonate preparation device, requisite sample size for analysis might be as little as 10–20  $\mu\text{g}$ , but could be significantly more. There is a general tradeoff between length and depth of the milled sampling path in order to generate sufficient powder. Long, shallow sampling paths can be very narrow (assuming a conical bit) and have the potential for higher temporal resolution, but have a greater risk of straying from

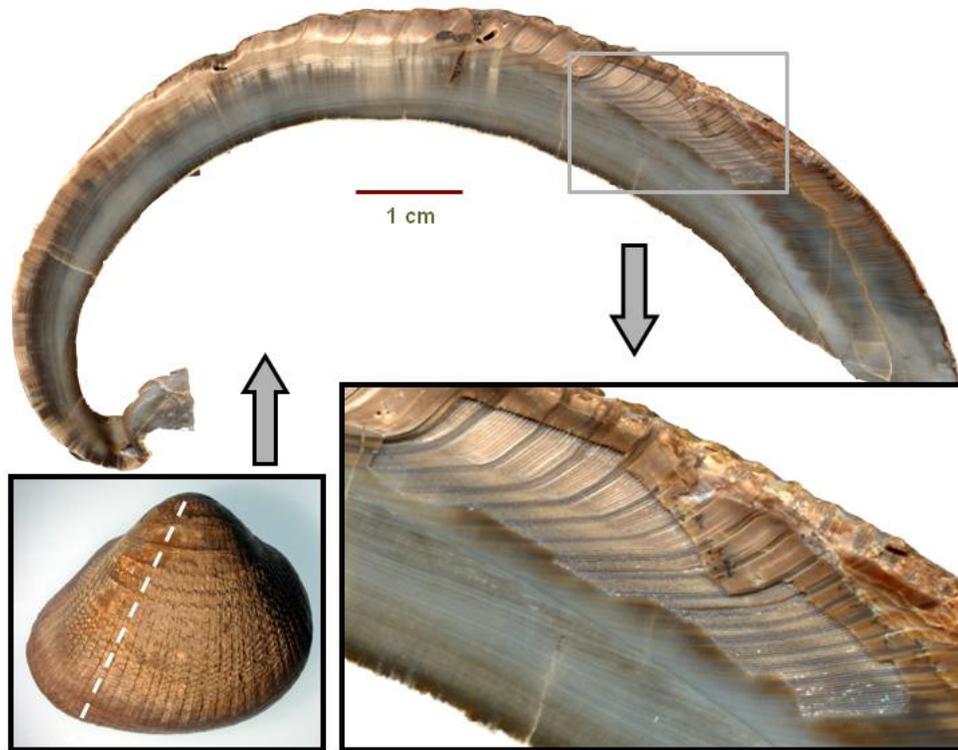


FIGURE 7.—Shell of *Cucullaea raea*, an Eocene bivalve from Antarctica, the cross-section through the shell revealing growth bands, and the interval milled out for isotope analysis; 137 samples were collected spanning 16 years of this clam's life and about 2 cm of accretionary shell. Note areas of shell damage were avoided during sampling. See Buick and Ivany (2004).

the targeted increment. Shorter sampling paths need to be drilled deeper, and may intersect adjacent growth increments if they are not oriented normal to the sampling surface. A series of fairly straight growth increments of consistent width are the easiest and most reliable to sample, and the morphology of the specimen in question will determine whether longer or shorter sampling paths are more practical.

Computer-controlled systems have the capability to remove all carbonate from an interval of shell growth by milling away successive growth increments as the sample paths advance laterally from one to the next. Alternatively, paths can be disjunct, leaving an intervening ridge of unsampled material between adjacent paths. Desired temporal resolution together with growth rate of the accretionary record being sampled will dictate which approach is the most reasonable. The width of the carbonate increment being removed (in the latter case, the width of the drill bit) in combination with the rate of accretion along the sampling trajectory will determine the degree of time-averaging represented by each sample. Wider

sampling paths will integrate more time and reveal less of the variation that may be present in the carbonate record. Near-ubiquitous variation in accretion rate, however, makes the degree of time-averaging per sample change along the micro-sampled trajectory. Corrections have been proposed for these 'averaging effects' (Beelaerts et al., 2009, 2010).

When beginning a new study, often the most difficult decision is about sampling resolution. As mentioned above, if distinct growth bands are present, a reasonable initial hypothesis is that the bands are annual, thus providing a guide for decisions about sample frequency (Figure 8). This is not always the case though, particularly for tropical taxa (Bemis and Geary, 1996; Sessa et al., 2012). An initial approach might be to sample one individual at high spatial resolution, and use those data to inform about subsequent sampling. Weekly or better temporal resolution of individual samples is possible in many circumstances, but the researcher may opt for lower temporal resolution to balance the constraints of time, cost, and number of years to be sampled. Sampling at the

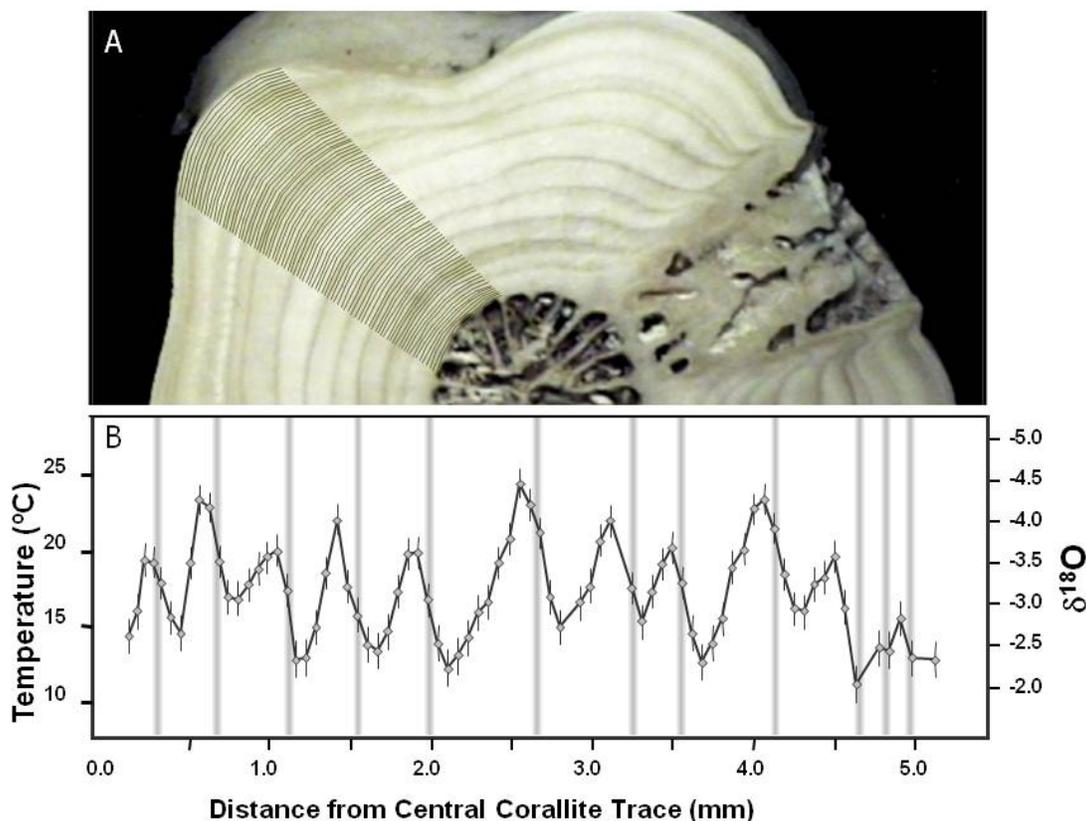


FIGURE 8.—A) Annual growth banding expressed in an early Oligocene coral from Mississippi, USA, and the 81 digitized sampling paths used to mill the specimen using a MicroMill. Resolution is ~8–9 samples per year. B) Resulting isotope data, with temperatures calculated assuming  $\delta^{18}\text{O}_w = -0.5\text{‰}$ . Gray bars correspond to positions of growth bands. See Ivany et al. (2004a) for more details.

highest resolution possible will produce an impressive-looking isotope record, but it may be overkill for the question at hand. If the desire is to produce an annual record of temperature resolved to compare with climatologies based on monthly means, then 12 time-integrated samples per year is sufficient. The basics of a simple annual cycle are captured even at six samples per year; less than that will attenuate the signal and observed amplitude will drop. Note, however, that if individual samples are themselves very temporally constrained rather than time-integrated, then variability in the climate record may make the seasonal signal more difficult to discern (Wilkinson and Ivany 2002). The higher the temporal resolution of sampling, the more variation will become apparent.

#### INTERPRETING ACCRETIONARY ISOTOPE DATA

#### The influence of growth

Once isotope data from sequentially sampled accretionary carbonates are in hand, temperatures can be calculated using the appropriate equation (see Pearson this volume; Grossman this volume) and making necessary assumptions about water composition based upon available information. Before moving directly to inferences about climate, however, one must first consider the influence of biology on the resulting record. Organisms are not perfect recorders of the conditions in which they live. If they were, isotope records would effectively be regular sinusoids and one could simply calculate the arithmetic mean of the analyses to arrive at MAT, and use the extreme values as the seasonal extremes. However, growth determines the amount of carbonate available for sampling from any particular time of the year. Growth is not necessarily continuous throughout the year, and growth rate nearly always varies with conditions in the environment. Growth slowdowns or cessations are what give rise to growth

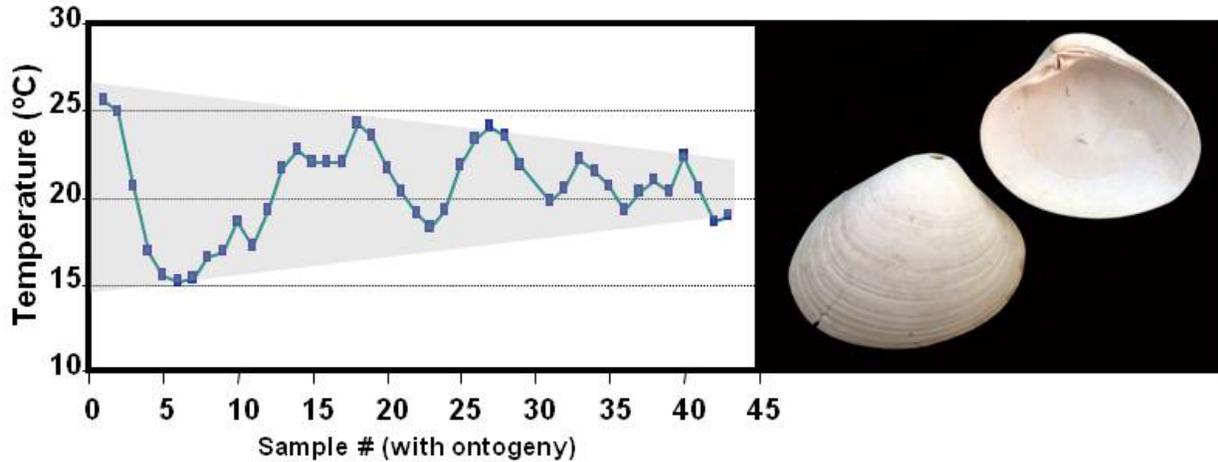


FIGURE 9.—Temperature profile derived from sequential oxygen isotope analyses of the Oligocene bivalve *Callista sobrina* showing the influence of decreasing growth rate on seasonal amplitude when samples are evenly spaced. Samples become progressively more time-averaged with age, temporal resolution decreases, and apparent amplitude drops (shaded region).

banding, and growth banding is nearly ubiquitous among accretionary taxa (Kennish, 1980; Lutz and Rhoads, 1980). These variations in growth will influence the shape of the isotope trajectory, and that shape can provide important clues to the potential biases embedded in the record (e.g., Jones and Quitmyer, 1996; Wilkinson and Ivany, 2002; Goodwin et al., 2003).

In general, solitary organisms tend to grow faster and over more of the year earlier in their ontogenies. With age, growth slows, and more so during parts of the year during which the animal is physiologically stressed. Often, this is in association with one or the other (or both) seasonal extremes, or during times of sexual reproduction.

The result is that these time intervals are represented by less carbonate than times of faster growth, or may not be represented at all. Ontogenetic slowdown decreases temporal resolution if samples maintain the same spacing, and therefore can decrease the amplitude of seasonal variation recovered from later in ontogeny (Figs. 8, 9; Beelaerts et al., 2010). Preferentially slower growth during one season over another will affect the ability to recover seasonal maxima and/or minima, and thereby influence estimates of mean annual temperature as well. In this situation, the resulting isotope trajectory will look scalloped or cusped, with one season represented by far more samples than the other (Figure 10). Seasonal

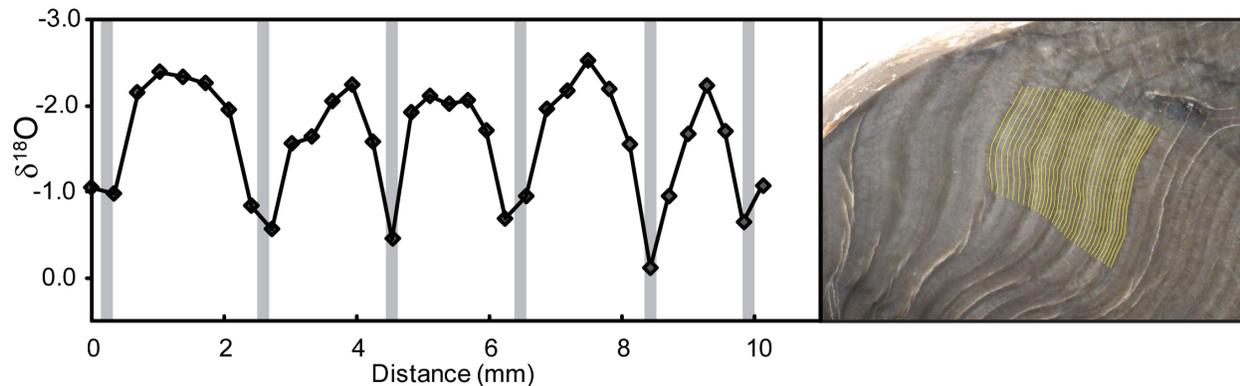


FIGURE 10.—Oxygen isotope data from the early Permian bivalve *Eurydesma* from Maria Island, Tasmania, showing the cusped pattern characteristic of seasonal (winter) growth slow- or shut-down (Beard et al., 2012). Gray bars indicate positions of growth bands in shell. At right is a cross-section through a portion of the umbo showing growth bands and sampling paths.

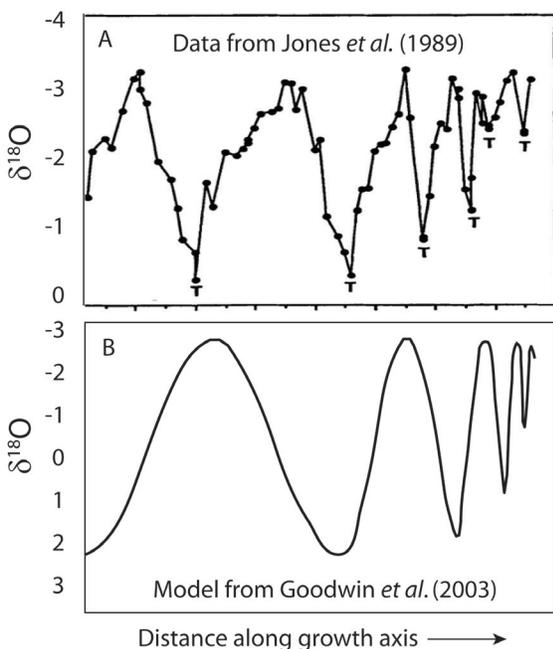


FIGURE 11.—A) Seasonally resolved isotope data from the bivalve *Mercenaria* from Narragansett Bay, RI, from Jones et al. (1989). B) An independent synthetic model for isotope value with age by Goodwin et al., (2003). Modeled shell growth assumes slowing growth rate and progressively less winter growth with age, and describes the general patterns in the observed data well. In (A), “T” indicates the positions of translucent (dark) growth bands, consistent with the growth slow-downs or cessations during winter months modeled in (B).

slowdowns tend to become more pronounced with age, and, if growth stops altogether, the interval during which no shell is accreted can lengthen with age (Figure 11). Some authors have suggested ‘shut-down’ temperatures either in winter (Dettman and Lohmann, 1993; Weidman et al., 1994) or summer (Schöne et al., 2009) beyond which growth does not take place; but, it is more likely that thresholds vary as an organism ages. Even during seasons when shells are accreting, Schöne et al. (2009) found that many taxa do not faithfully record measured extreme temperatures, indicating that shell growth is discontinuous on a daily, tidal, or hourly scale. Goodwin et al. (2003) modeled various scenarios of slowing and seasonally truncated growth, and presented a series of useful schematics to illustrate the expected patterns of isotope variation in serially sampled shells (e.g., Figure 11B). These observations make clear that, if the goal is a record of paleo-

climate conditions, it is generally prudent to sample earlier parts of the ontogenies of accretionary biogenic carbonates. Growth is faster, so the record is more expanded and allows for higher temporal resolution, and growth is more likely to be continuous throughout the year. In addition, Schöne et al. (2009) point out that different co-occurring taxa may have different thermal tolerances and therefore windows during which growth takes place. Sampling multiple taxa will increase the likelihood of capturing more of the seasonal cycle if different taxa have discordant growing seasons. When sample spacing varies along the sampled trajectory, plotting data by distance rather than sample number makes it easier to recognize growth patterns that may bias interpretations of the data.

### Extracting paleotemperature information

If the isotopic composition of water is thought to be fairly constant, and if fossil material has not been altered, then temperature variation should be the primary influence on  $\delta^{18}\text{O}$  in a microsampled trajectory. The expectation then is for a roughly sinusoidal pattern, modified as above by the growth of the organism recording the signal. Deviations about that sinusoid due to noise in the climate record are anticipated to be Gaussian (Martinson et al., 1982; Wilkinson and Ivany, 2002). Strong and/or persistent deviations from a sinusoidal pattern are likely indications of changing water composition such as that associated with salinity variation, partial to complete diagenetic resetting of values, or sampling resolution too coarse to be able to consistently resolve the seasonal cycle. Another possibility, depending on the ecology of the organism being sampled, is that it has moved and/or migrated over its lifetime so that isotope values reflect changing habitat with time. It is unlikely that vital effects would have an impact on the  $\delta^{18}\text{O}$  values of biogenic carbonate precipitated by organisms otherwise typically in equilibrium unless the precipitation rate were exceedingly fast (McConnaughey, 1989a, b); such effects are more prominent in carbon isotope and elemental data (e.g., Purton et al., 1999; Gillikin, 2005; Sosdian et al., 2006; McConnaughey and Gillikin, 2008; Izumida et al., 2011, Lowenstein and Hönisch, this volume). If sinusoidal variation is apparent, then paleoclimate work can proceed.

Typical variables of interest in paleoclimate studies include mean annual temperature, seasonal extremes, and seasonal range. Keeping in

mind the influence of growth on isotope records, one can explore options for how best to approximate these variables from microsampled data. The temptation simply may be to average all data for an approximation of mean annual temperature, but the tendency toward preferential growth in one season over another makes this an unadvised strategy. While the approach yields a mean annual isotopic composition for the taxon, this value suffers from the same potential for bias discussed above for bulk samples. A better tactic is to determine the best approximations for seasonal extremes and take the midpoint between them. For this, one might choose the maximum and minimum values expressed in the entire dataset but, given the inter-annual and stochastic variation present in most climate records, this is likely to overestimate the typical seasonal range. Another option is to use the mean of all local maxima (or minima) that confidently can be assigned to seasonal peaks. This approach incorporates the natural inter-annual variation in the system and affords a measure of confidence around each estimate. Seasonal range might be computed as the mean difference between all adjacent, or all possible, pairs of seasonal extremes—at least those likely to be unbiased by growth. Again, careful consideration of sampling resolution should be incorporated, as high-resolution records will overestimate seasonal extremes if only the extreme values are chosen, and low-resolution records will minimize the seasonal extreme due to time averaging, even independent of any growth bias.

An alternative approach is to fit models through the data and use model parameters to give insight about the underlying climate variables. A range of approaches exists, with varying degrees of complexity and embedded assumptions (see review by de Brauwere et al., 2009). The challenge for all is to convert distance measured along the growth axis into time, when accretion rate is unknown and almost surely not constant, either inter- or intra-annually (Figure 12). A simple approach to converting distance into time is to identify two or more anchor points in a data series that can confidently be assigned a time/age within an annual cycle (e.g., peak summer temperatures from annual cycles separated by one or several years of data), then scale all remaining data points to their respective ages within annual cycles. Derived from the technique to produce linear age models for sediment accumulation, it assumes a constant growth rate between adjacent anchor points. Individual data are therefore scaled in time

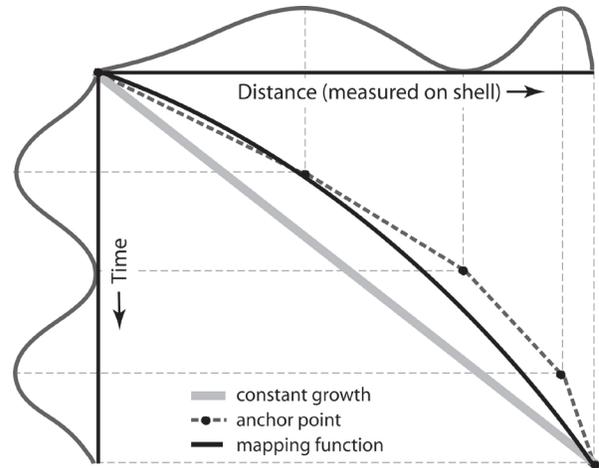


FIGURE 12.—Several models for relating distance along an accretionary axis to time, assuming a constant growth rate, stepwise changes in growth rate using anchor points, or a simple mapping function (Martinson, 1982).

directly by their distances between anchor points. When anchor points are chosen well and spaced as closely in time as possible, the outcomes are very reasonable (e.g., see application by Gillikin et al., 2005). The method is sensitive to outliers if they are chosen as anchor points, and it becomes less reliable as seasonal cycles become more difficult to recognize and distinguish.

A step beyond this approach is to assume that the underlying signal is periodic and generally sinusoidal, and then use the relevant parameters that define the best-fit curves as the annual climate variables. These sorts of methods are better at accommodating Gaussian noise in the data, downplay the significance of single outlier points, and require neither an equal distribution of data points in time nor the presence of data points at the extremes of seasonal cycles. A modification of the anchor-point method by Martinson (1982) gets around the assumption of constant growth between anchor points by iteratively determining a mapping function that relates points on a distance axis to those on a time axis such that the correlation is maximized. When the assumption is for a sinusoidal mapping function, one can use this approach on seasonal accretionary data.

De Ridder et al. (2004) likewise began with the simple anchor point method, but developed a procedure to determine the ‘time base distortion’ from that initial presumption of linear growth. Assuming the primary signal is periodic (the annual temperature cycle), a spectral analysis should

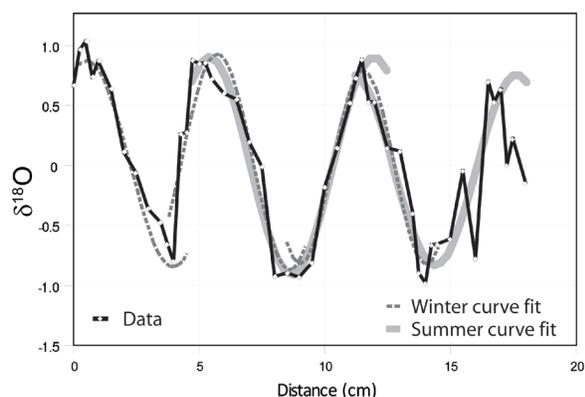


FIGURE 13.—Microsampled data collected along the spiral growth axis of the early Oligocene gastropod *Conus alveatus*, from Kobashi et al. (2004), and best-fit sine curves for several seasons of growth using the Wilkinson and Ivany (2002) approach. Summer and winter seasons are each fit separately to minimize curve-fitting over intervals of different growth rates, even though this record is reasonably symmetric. Best-fit curves are shown extending in both directions farther than the data points that were used to constrain them to illustrate the full shape of the curve. Note that potential outliers, such as that at ~16.5 cm (perhaps a freshwater spike or diagenetically altered carbonate), do not substantively affect the curves.

reveal a single frequency peak at one year if growth rate were indeed constant. Deviations from that expectation can be used to reveal the actual differences in growth rate that are embedded in the record. Because this approach begins with defining anchor points and assuming constant accretion between them, it is subject to the uncertainty in recognizing anchor points for individual years and to the noise inherent in a climate record (De Ridder et al., 2004).

Wilkinson and Ivany (2002) described a method for iteratively fitting sine curves to successive portions of a seasonally resolved dataset. Best-fit curves over many different subsets of the data generate a number of estimates for position ( $\approx$ mean annual temperature) and amplitude ( $\approx$ seasonal range) for a given dataset, so confidence limits can then be computed about those mean values. A significant advantage is that the mean position of the resulting sine curve and its amplitude can be derived from portions of the data that do not themselves define a complete annual cycle. For example, a best-fit curve to a single summer will produce parameters for the full annual cycle that best describes that summer, even if winter

values are not used to constrain the resulting sine curve (Figure 13). In addition, anchor points are not used, removing the uncertainty associated with their recognition and magnitude. A limitation, however, is that growth rate is assumed to be constant over the individual windows of data being fit. De Ridder et al. (2007) offered a modification to the original method that allows for variable growth rate by scaling observations to their temporal positions within an annual cycle, but this method assumes no variation over the record in position and amplitude, and hence inter-annual variation in these parameters cannot be addressed. The former approach may be more useful for paleoclimate work, while the latter is preferred for ontogenetic studies of growth with age. In either case, the number of data points included in each subsequent fit of the data is somewhat arbitrary, and trial and error may be needed to produce a satisfying model.

De Brauwere et al. (2008) combined the Martinson approach with the time base distortion method to offer a parametric technique for which the model relating distance to time is not fixed, but itself is optimized. A rigorous evaluation of all these approaches is given by De Brauwere et al. (2009), and their outcomes on both modeled data and a real bivalve dataset published by Gillikin et al. (2005) are compared. Keep in mind that the necessary choices made during implementation of each method (e.g., choice of anchor points, mapping function, number of data points in the interval of data to be fit) are subjective to some degree, and may not be the same as those of other researchers. Performance and outcomes of the various methods will differ depending on those choices.

### The influence of habitat on measured versus target climate variable

Acknowledging that there are potential deviations due to variation in water composition or growth rate, calcifying organisms preserve a record of temperature variation of the water in which they grew in the isotope values of their skeletons. An important consideration for paleoclimate work is how temperature in the habitat in which the organism grew might compare to the target climate variable, e.g., sea-surface temperature. Most accretionary macrofauna are benthic, and, as mentioned above, water depth tends to inversely correlate with mean temperature and seasonal range of temperature variation. This is likely not a concern in shallow, well-mixed shelf

settings, where conditions at the bottom closely mirror those at the surface (Austin et al., 2006). But, in deeper or stratified water columns, the range of seasonal temperature variation on the bottom can be substantially less than that at the surface (Prandle and Lane, 1995; Austin et al., 2006; Locarnini et al., 2010). Mollusks living below the thermocline, for example, may not capture the full seasonal temperature range expressed at the surface, even if they grow continuously throughout the year (Arthur et al., 1983; Austin et al., 2006). In such cases, winter temperatures are often similar across all depths, but summer temperatures are progressively more underestimated with depth (see Figure 3). This clearly poses a conundrum, for depth is a parameter only qualitatively and indirectly constrained in the sedimentary record (Peters and Loss, 2012; but see Olson et al., 2012, for an interesting hypothesis). A comparison of benthic temperatures with those at the surface inferred from co-occurring planktonic organisms might help determine whether the benthic record is likely to be biased and if so, by how much. If mean values are similar (and the planktonic record is thought to approximate MAT), then one could conclude that the water column is well mixed. If seasonal range at the surface could also be approximated, it might be possible to solve for water depth by making an assumption about the vertical eddy-dispersion coefficient (e.g., see discussion in Prandle and Lane, 1995).

#### **DEEP-TIME ACCRETIONARY RECORDS: WHAT CAN WE LEARN?**

The confluence of a growing interest in sclerochronology, the use of stable isotope values of fossils as climate proxies, and technological improvements that allow for automated preparation and isotopic analysis of very small samples has led to the increasing appearance of seasonally resolved isotope profiles from modern and fossil materials in the literature since the 1980s. Due to the time- (and money-) intensive nature of micro-sampling work, most papers still report data from only one or a few individuals. Single-shell studies of fossils can be tremendously useful, but their real impact is in the context of life history, ecology, and evolution, where even just one account of lifespan and growth can be enough to resolve long-standing debates and/or point out surprising and unexpected phenomena (e.g., Jones and Gould, 1999; Buick and Ivany, 2004). However, given the potential biases and complications dis-

cussed above, the heterogeneity within environments, and the temporal variability on many scales that characterizes the climate system, it is difficult to know what kind of paleoclimatologic significance to ascribe to such data. ‘Shallow-time’ studies are more straightforward because taxa often are still extant, have known ecologies, and in most cases, have been calibrated to known environmental conditions. Data from the Pleistocene and Holocene can be directly compared to current conditions and yield important insights. Jones et al. (2005), for example, used micro-sampled data from modern and subfossil specimens of the bivalve *Donax variabilis* to propose that conditions during the mid-Holocene Hypsithermal interval were more seasonal than today at the same location in NE Florida. In deep-time studies, however, meaningful comparisons with the modern can be tenuous. While authors have constructed eloquent and elaborate climate hypotheses from a single shell (present company not excepted, e.g., Ivany et al., 2004b), the significance of these sorts of data in isolation is difficult to assess. Without a larger dataset of similar construction into which to place isolated profiles to provide context, interpretations about climate can be ambiguous. I return to this issue in more detail in the last section below.

#### **Checking for seasonal bias in bulk data**

One context in which seasonally resolved data can contribute to deep-time climate studies is through providing an important complement to bulk-sample data that often comprise the majority of large-scale or long-term studies. While it may not be practical to obtain seasonally resolved data for hundreds of individuals, it is not too difficult to obtain bulk average compositions for that same number of specimens or more. High-resolution sampling of just a few individuals from a much larger dataset can give insights into the significance of those data with respect to climate. For example, Ivany et al. (2008) used bulk shell data from two genera of bivalves to construct a paleoclimate record through the Eocene section on Seymour Island, Antarctica, and found that the two taxa yielded different isotope values despite living together in the same settings. While an unexplained vital effect might have otherwise been invoked, microsampling of only 4 specimens (in comparison to 187 shells sampled for bulk values) revealed that one genus grew preferentially during the winter, explaining why its bulk isotope values were consistently more positive than the other

taxon. This allowed data from both taxa to be incorporated into a single, more accurate composite record. Likewise, if accretionary skeletal material is available from a section through which microfossil or organic molecular data have been obtained, microsampling can reveal whether there might be a seasonal bias in those organic or molecular data. Many of the taxa from which those data are derived live for only one or a few months, and precipitate the bulk of their carbonate (or organic matter) over substantially less time than that. If there were a tendency for particular taxa to proliferate during only one part of the year, their bulk data would be biased toward conditions in that season. While this limitation is often acknowledged, most authors presume that population growth occurs over enough of the year that a mixed sample of a number of individuals will integrate to approximately mean conditions. However, this may not be the case, particularly for some planktonic taxa (e.g., Hemleben et al., 1989; Gooday, 2002; Dekens et al., 2007; Fraile et al., 2009; Leider et al., 2010; Lowenstein and Hönisch, this volume; Pearson, this volume). In such cases, average temperatures determined from bulk compositions may be quite different than the often-desired mean annual temperature (the so-called ‘seasonal effect’ of Scourse et al., 2004; Austin et al., 2006, for benthic organisms). Seasonally resolved  $\delta^{18}\text{O}$  measurements offer a way to assess this concern, as long as both types of taxa are present and inhabited the same water mass (e.g., see comparisons of macro- and microfossils in Moriya et al., 2003; Dutton et al., 2007; Keating-Bitonti et al., 2011).

#### **Evaluating diagenesis in ancient isotope data**

Another contribution from even single-shell records of seasonal variation derives from research on very ancient carbonates. The bulk of the published work resolving seasonal variation using high-resolution  $\delta^{18}\text{O}$  analysis of fossils comes from the Cenozoic and Cretaceous. Oxygen isotope paleothermometry is more secure in this part of the rock record, as described by Pearson (this volume) and Grossman (this volume). Farther back in time, the pattern of decreasing  $\delta^{18}\text{O}$  values with increasing age becomes apparent (Veizer et al., 1986, 1997, 1999), and the debate about its significance comes into play (reviewed in Jaffrés et al., 2007; discussed also in Grossman, this volume). Microsampled profiles showing strong seasonal cycles from the early Mesozoic and Paleozoic can contribute to this discussion because

the preservation of seasonal variation in accretionary carbonates of great age suggests that their original oxygen isotopic composition is more likely to have been retained. If  $\delta^{18}\text{O}$  values can be shown to be primary, and therefore indicative of earth-surface conditions at the time of deposition, one potential explanation for decreasing isotope values back through the Phanerozoic—that ancient materials are progressively more altered with age—becomes less likely (Ivany and Runnegar, 2010). Seasonal cycles in skeletal  $\delta^{18}\text{O}$  have now been described from Pennsylvanian (Mii and Grossman, 1994; Seuss et al., 2012), Permian (Ivany and Runnegar, 2010; Beard et al., 2012; Mii et al., 2012), Triassic (Nützel et al., 2010), and Jurassic (Jones and Gould, 1999; Lécuyer and Bucher, 2006) sections, but to date, there are still few such studies. Most Paleozoic isotope work on fossils has been done as spot samples from thin sections or on isolated shell fragments (see Grossman, this volume). There is great potential in seasonal studies of Paleozoic macrofauna if, as some have argued (e.g., Brand, 2004), unaltered shell material is more common than previously thought.

#### **Documenting inter-annual variation**

Also possible with one or a few very detailed records is an examination of patterns of inter-annual variation. While there are other options in the sedimentary record that afford good annually resolved data, accretionary biogenic carbonates provide unambiguous records of year-to-year variation, both in their physical growth increments as well as in their chemistry. The tradeoff for using biogenic records in this regard is that often one has to sacrifice the length of the time series obtained because it is limited to the lifespan of the organism, the duration of time over which accretion of the skeleton is taking place, or the interval of growth that provides spatio-temporal resolution practical for sampling. This limitation can be overcome, however, when sampling very long-lived individuals (e.g., Romanek and Grossman, 1989; Buick and Ivany, 2004; Schöne et al., 2005b) or records from long-lasting colonies such as corals or sclerosponges (Swart et al., 1996; Quinn et al., 1998; Guilderson et al., 2001; Swart, 2002; Stephans, 2004; Watanabe et al., 2011). Microsampled records from long-lived accretionary skeletons allow for examination of inter-annual variation in deep time, such as that due to phenomena such as the El Niño Southern Oscillation (Quinn et al., 1998; Hughen et al.;

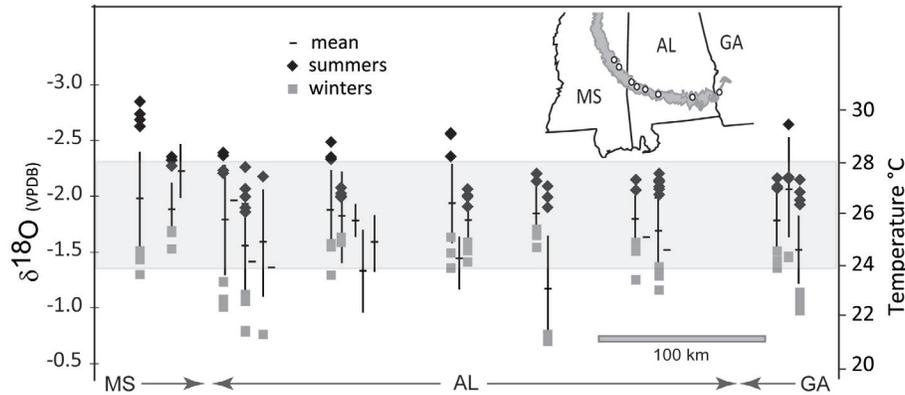


FIGURE 14.—Stable oxygen isotope data from the bivalve *Venericardia bashiplata* from the earliest Eocene Bashi Marl, U.S. Gulf Coastal Plain. Bashi outcrop belt and sample localities given in inset. Shell means and standard deviations indicated by vertical lines and horizontal hatches. Shells with multiple bulk samples (not milled) do not show seasonal temperatures; single bulk samples do not report SDs. Micromilled values are the 10% most positive and most negative winter and summer values within shells. Shells are grouped by locality. Temperatures are calculated assuming  $\delta^{18}\text{O}_{\text{water}}$  of  $-0.36\text{‰}$ . Mean seasonal range ( $4^{\circ}\text{C}$  around an MAT of  $26^{\circ}\text{C}$ ) for all shells is depicted in shaded region. Data show strong consistency within and between localities across  $\sim 400$  km of paleoshelf in both mean and seasonal extremes. See Sessa et al. (2012) for details.

1999; Ivany et al., 2011; Watanabe et al., 2011; Welsh et al., 2011). In cases such as these, even just one strong record can establish the fingerprint of inter-annual periodicity characteristic of a particular phenomenon.

### Seasonality in space and time

Perhaps the most compelling question that can be asked with paleoseasonality data is how seasonal range and extremes vary across latitude and through time deep in Earth's past, when surface conditions were unlike those today. While tempting to generalize trends from only a few shell profiles, such questions require multiple years from multiple individuals and multiple localities to establish a real pattern. Prerequisite to studies of this nature, where samples from two or more regions or time intervals will be compared, is to ensure that the data from each of those regions or time horizons are internally consistent so that they can be compared meaningfully. As discussed above, there is both inter- and intra-annual variability in climate time series, and this variability, in addition to potential variation introduced by growth and local environment and sampling strategy, can lead to differences in records from co-occurring specimens. Added to this is the potential for decadal or millennial variation that might be subsumed within one time-averaged stratigraphic horizon, such that two individuals collected next to each other might have lived hun-

dreds or even thousands of years apart from one another. To address spatio-temporal patterns, co-occurring records from one place need to be no more variable than sets of samples from different places. If there is more variation between shells within a time plane than is seen between time planes, for example, one will not be able to establish the validity of any postulated temporal trend. Ivany et al. (2008) employed a nested sampling strategy when evaluating change in bulk composition through time, and a similar approach is advocated for seasonal data. Variation among multiple shells from the same site, and multiple sites from the same temporal horizon, was assessed using analysis of variance, and time horizons were compared only after establishing that shells from different collecting localities along the same horizon were recording the same information. Significant differences among correlative sites in what is presumably the same facies would prove problematic and prevent further work on temporal trends. Sessa et al. (2012) explored the consistency of seasonally resolved data among shells collected from multiple localities in a single time plane along hundreds of kilometers of paleocoastline in the U.S. Gulf Coastal Plain, and found that mean temperature and seasonal extremes are generally consistent from place to place, despite some variation among shells (Figure 14). Data such as these demonstrate that microsampled records from shelf macrofossils can preserve a regional

climate signal, and can contribute meaningfully to assessments of climate through time.

Exploring the influence of change in mean temperature on seasonal range and extremes is not only important from the more esoteric perspective of understanding how ancient climate has changed, but also is directly relevant to predictions for how conditions are expected to change in the future in association with global warming. The primary control on seasonal range is orbital configuration, and because of this, seasonality is theoretically independent of mean annual temperature. For example, an increase in atmospheric greenhouse gases might increase mean annual temperature and seasonal extremes across the planet, but the range in values at any one place should remain essentially the same, aside from albedo-related feedbacks. What limited evidence we have from the geologic record, however, makes it clear that the situation is (perhaps not surprisingly) a good deal more complex than this.

Examples from the Eocene greenhouse illustrate the conundrum: marine shell profiles from Europe and tropical west Africa suggest seasonal ranges comparable to the present, despite warmer overall temperatures (Andreasson and Schmitz, 1996; Purton and Brasier, 1997b; Andreasson and Schmitz, 1998, 2000; Vanhove et al., 2011; but also see Purton and Brasier, 1997a). Comparable data from the U.S. Gulf Coast and Panama, however, suggest that warm Eocene conditions were less seasonal than today (Andreasson and Schmitz, 2000; Ivany et al., 2000; Kobashi et al., 2001; Tripathi and Zachos, 2002; Ivany et al., 2003; Kobashi and Grossman, 2003; Ivany et al., 2004b; Keating-Bitonti et al., 2011; Sessa et al., 2012). The difference between the two regions likely relates to paleoenvironmental effects (e.g., fresh water, evaporation) or circulation/upwelling patterns, but either way, it is difficult to know if comparisons with the modern are reasonable, because current conditions are so different from those during the Eocene.

A better way to resolve these sorts of uncertainties is to systematically investigate seasonal range through time using the same metrics in a particular region, holding as many variables constant as possible (e.g., taxon, facies, sampling strategy), and determine how seasonality relates to change in MAT. The few studies that have done this find that as mean annual temperature goes up, seasonal range goes down. Ivany et al. (2000; in prep) and Kobashi et al. (2001) reported seasonal data from fish otoliths and mollusks, respectively,

through the Paleogene section in the U.S. Gulf Coast that show similar patterns of cooling and increasing seasonality through time, despite a constant paleolatitude. They relate this, at least in part, to change in the structure of the water column associated with cooling of deep water (Ivany et al., 2003; Kobashi and Grossman, 2003; Kobashi et al., 2004). In another example, Steuber and colleagues (Steuber, 1996; Steuber et al., 2005) produced some rather spectacular isotope records from rudist bivalves around the Mediterranean during cool and warm intervals of the Cretaceous; they found a similar pattern of more seasonal conditions associated with cooler mean temperatures. Hence, it appears from these studies that, at low-to-mid latitudes, warmer intervals correspond to times of reduced seasonality (all else being equal), and cooling is associated with more seasonal conditions—in particular, with cooler winter temperatures. This pattern is even more exaggerated in continental interiors (e.g., Greenwood and Wing, 1995; see extensive discussion and references in Huber, this volume).

The high latitudes offer an exception to this pattern. Miklus (2008) used mollusk isotope profiles to build on initial results of Dutton et al. (2002), and showed that during the warm Eocene, temperatures in coastal waters off Antarctica were far more seasonal than they are today, and that seasonal range collapses with cooling mean temperatures, particularly (in this case) when associated with cooling summer temperatures. Warm and quite seasonal temperatures in the high latitudes during greenhouse times are supported by data from Dutton et al. (2007) in the Antarctic Cretaceous using belemnites, Bice et al. (1996) and Tripathi et al. (2001) in Arctic waters during the warm late Paleocene, and Oleinik et al. (2008) in the north Pacific during the Middle Miocene Climatic Optimum. Proxies recording air temperature from the high latitudes instead find significant increases in seasonality with cooling temperatures (Eldrett et al., 2009), perhaps as expected due to differences in heat capacity, albedo effects on land, and constraints on minimum marine temperatures.

While these few studies seem to be consistent in their trends through time as mean temperatures change, they are only a drop in the proverbial bucket. Several studies of Holocene climate based on mollusk isotope records further demonstrate that relationships between mean annual temperature and seasonal range are complex, at least as inferred by these sorts of data, and we are far

from establishing generalities. Wanamaker et al. (2011) found that warmer conditions are associated with less seasonal water temperatures in the Gulf of Maine, but Schöne and Fiebig (2009) found the opposite in the North Sea—in one case colder conditions were found to be less seasonal than today, while another cold interval had seasonal ranges comparable to today. Recall as well the Jones et al. (2005) study mentioned earlier that suggested more seasonal conditions during the warm Holocene Optimum. It would appear that nothing is straightforward!

Clearly the situation is more complicated than one might anticipate given a simple model of only solar insolation driving seasonal range, modified by the influence of continents. In any one place, when latitude and continental configuration do not change, and when sampling resolution, taxon, and facies are held constant, change in mean annual temperature appears to be accompanied by change in seasonal range of temperature variation. The magnitude and direction of that shift depend to some degree upon latitude, but change is not always consistent from place to place, nor is it always as predicted. Change in water-column stratification and circulation, often themselves associated with change in temperature, evidently play a large role in determining the magnitude and direction of change in seasonality. Given that these phenomena are linked, one might wonder whether it is possible to see a change in mean annual temperature and not expect an associated change in seasonal range.

Understanding how seasonality is affected by climate change in the past will require robust and meaningful comparisons among sets of samples from different times or places. The most useful studies on very ancient materials are those that sample a number of individuals, produce records from a number of annual cycles, and array those data in space and/or in time to make any large-scale trends apparent. Characterizing the variability within and among shells is important before making claims about spatial/temporal trends, so sampling coverage should be sufficient that overall trends can be established despite the inherent noise in the system (e.g., Stephans, 2004; Ivany et al., 2008; Sessa et al., 2012). If the same taxon from the same facies is used consistently to generate the data, then statistically significant trends are likely to be meaningful, even despite uncertainties about when the taxon grew or how the particular environment being sampled compares to, for example, sea-surface temperature. Assum-

ing a taxon's ecology is fairly consistent across its geographic and temporal range allows these major sources of error to be ruled out, increasing confidence in documented trends. If a pattern observed in one taxon can be verified with work on a co-occurring species, that pattern becomes even more robust. Given that temperature is less likely to be dependent upon water depth during the winter season, plotting winter temperatures through time might provide a more accurate picture of regional climate change than mean values. Trends in seasonal range in association with changing winter temperatures are more likely to be real and not driven by change in paleodepth. When approached in this manner, hypotheses about climate change in general, and seasonality in particular, can be tested even if recovered temperatures cannot be directly equated to those at the sea surface. A change in seasonality of a given magnitude and direction from time A to time B, documented from a number of different individuals of the same taxon in each time horizon, sampled in the same way, and from the same facies, should be robust, and therefore calls for an explanation.

## CONCLUSIONS

There is no question that seasonally resolved isotope data provide a treasure trove of information for paleontologists with respect to questions of growth rate, longevity, ecology, and evolution. However, the fossil record of accretionary skeletons has much to offer paleoclimatology, too, if we can remove the biological and environmental footprints on the data to see the larger patterns. How likely are datasets from one or a few individuals to contribute a greater understanding of paleoclimate? Not very. However, we now have the tools and techniques at our disposal to address the complexity evident in the rock record and begin to make sense of it. Studies can be designed with the limitations of the record in mind, and sampling coverage and intensity can be adjusted to both accommodate the variation in the system and allow recognition of patterns at the desired scale of interest. Spatial and temporal comparisons of similar types of data will enable the documentation of trends for which magnitude and direction of change are robust. With seasonally resolved data comes a richer understanding of climate change. Not only can we demonstrate warming or cooling at some time in the past, but we can resolve how that happened—changing summer temperatures, winter temperatures, or

both—and thereby provide clues as to the mechanisms behind that climate change (e.g., Crowley et al., 1986b). Trends can be compared with predictions from climate models to identify and ultimately minimize data-model mismatches, and, if biases are well constrained, then absolute values will be useful as well. Potential sources of bias in proxy data increasingly are being recognized and discussed in the context of climate models (e.g., Poulsen et al., 1999; Trenberth and Otto-Bliesner, 2003; Huber, 2008, this volume; Huber and Caballero, 2011), and efforts are being made to circumvent or account for bias with multiproxy studies and careful attention to preservation (Pearson et al., 2001; Zachos et al., 2006; Pearson et al., 2007; Hollis et al., 2009; Douglas et al., 2011; Keating-Bitonti et al., 2011; to name just a few examples from the Eocene).

Better constraints on seasonal range and extremes through time will not only offer a deeper understanding of the climate system and how it evolves in response to forcing factors (Crowley et al., 1986b), but also afford insights into how organisms and ecosystems have been, and will be, affected by climate change (Valentine, 1983; Coma et al., 2000; Troost et al., 2009). Accretionary skeletal records may be the only archive to offer the potential for consistent and quantitative estimates of seasonal temperature maxima and minima and how they change in deep time. Paleontologists, geochemists, climate modelers, and physical oceanographers working together can devise sampling protocols that allow for tighter constraints on seasonal extremes given variability in the system, develop more refined hypotheses using seasonally resolved data, and construct effective data-model comparisons. This is already starting to happen. The next decade should prove to be an interesting and fruitful one!

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